HANDBOOK OF FISH BIOLOGY AND FISHERIES
Volume 1

Also available from Blackwell Publishing:

Handbook of Fish Biology and Fisheries
Edited by Paul J.B. Hart and John D. Reynolds
Volume 2   Fisheries

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VOLUME 1

FISH BIOLOGY

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Preface

The goal of the two volumes of the *Handbook of Fish Biology and Fisheries* is to help integrate the study of fish biology with the study of fisheries. One might not expect these two subjects to need further integration. However, strong declines in many fish stocks around the globe, combined with growing concerns about the impact of fisheries on marine and freshwater biodiversity, are raising new questions about aspects of fish biology that have traditionally dwelt outside mainstream fisheries research. Thus, fisheries biologists and managers are increasingly asking about aspects of ecology, behaviour, evolution and biodiversity that had traditionally been studied by different people who attend different conferences and publish in different journals. By bringing these people and their subjects together in the two volumes of this *Handbook*, we hope to foster a better two-way flow of information between the studies of fish biology and fisheries.

A tradition runs through the prefaces of the other volumes in this series whereby the editors distance themselves from a literal translation of the word 'Handbook'. In keeping with this tradition, we wish to make clear that this is not a cookbook of recipes for how to study and manage fish populations. Instead, we have tried to produce a pair of reference books that summarize what is known about fish biology and ecology, much of which is relevant to assessment and management of fish populations and ecosystems. Of course, much of the material in the first volume may never find applications in fisheries, and that is fine with us. We encouraged our authors to provide a wide coverage of fish biology simply because the topics are interesting in their own right, and because the borders between pure and applied research are fuzzy. We therefore decided not to restrict information according to its direct relevance to fisheries as this subject is understood today. We hope the result will be of value to undergraduates and graduates looking for information on a wide variety of topics in fisheries science. The books are also aimed at researchers who need up-to-date reviews of topics that impinge on their research field but may not be central to it. The information should also be useful to managers and decision makers who need to appreciate the scientific background to the resources they are trying to manage and conserve.

In the first volume, subtitled *Fish Biology*, our introductory chapter explores the underpinnings of fisheries biology and management by basic research on fish biology. Part 1 then examines systematics and biogeography of fishes, including methods for determining phylogenetic relationships and understanding spatial patterns of diversity. Part 2 examines production and population structures of fishes, beginning with chapters on physiology and growth, followed by recruitment, life histories, migration, population structure and reproductive ecology. Part 3 considers fishes as predators and as prey, making use of conceptual advances in behavioural ecology to link predator–prey interactions to the environment. In Part 4 we scale up from individual interactions to communities and ecosystems. The chapters include comparisons of freshwater and marine

communities, as well as interactions between fishes and parasites.

In the second volume, subtitled *Fisheries*, we begin with a chapter that considers the human dimension of fisheries management. Part 1 then gives background information for fisheries, including fishing technology, marketing, history of fisheries, and methods of collecting and presenting data. Part 2 provides fundamental methods of stock assessment, including surplus production models, virtual population analyses, methods for forecasting, length-based assessments, individual-based models and economics. We have also tried to consolidate this information by reviewing the various options available for modelling fisheries, including the pros and cons of each. Part 3 explores wider issues in fisheries biology and management, including the use of marine protected areas, conservation threats to fishes, ecosystem impacts and recreational fishing.

We are very grateful to our 54 authors from 10 countries for their hard work and patience while we attempted to herd them all in the same general direction. We also thank Susan Sternberg who first suggested that we take on this project, and Delia Sandford at Blackwell Science who has overseen it. The final stages of production have been greatly helped by two people. Valery Rose of Longworth Editorial Services worked patiently and efficiently to shepherd the book through the copy editing and production stages, and Monica Trigg, did an excellent job with the gargantuan task of constructing the two indices. Paul Hart would like to thank the University of Bergen, Department of Fisheries and Marine Biology, for providing him with space and support during the final editing of the manuscript. John Reynolds would like to thank his many colleagues at the University of East Anglia and at the Centre for Environment, Fisheries, and Aquaculture Science (Lowestoft) who have helped build bridges between pure and applied research.

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Paul J.B. Hart and John D. Reynolds
Leicester and Norwich

Abbreviations

AFLP	amplified fragment length polymorphism		MSVPA	multispecies virtual population analysis
CPUE	catch per unit effort		NTP	nucleotide triphosphates
CV	coefficient of variation		OFT	optimal foraging theory
EPIC	exon-primed intron-crossing PCR		PCR	polymerase chain reaction
ESD	environmental sex determination		RAPD	randomly amplified polymorphic DNA
FAO	Food and Agriculture Organization		RFLP	restriction fragment length polymorphism
GFR	glomerular filtration rate		RQ	respiratory quotient
GSI	gonadosomatic index		SCFA	short-chain fatty acids
IBI	indices of biotic integrity		SSVPA	single-species virtual population analysis
ICES	International Council for the Exploration of the Seas		TMAO	trimethylamine oxide
ICLARM	International Center for Living Aquatic Resources Management		VBGF	von Bertalanffy growth function
IFD	ideal free distribution		WCMC	World Conservation Monitoring Centre
JAM	judicious averaging method		WRI	World Resources Institute
MPA	marine protected area		YOY	young of the year
MSA	mixed stock analysis			

1 Banishing Ignorance: Underpinning Fisheries with Basic Biology

PAUL J.B. HART AND JOHN D. REYNOLDS

1.1 INTRODUCTION

Tourists mingle with local people among the stalls set out by Zachariasbryggen, Bergen, Norway. Young men and women in bright orange oilskin overalls, fluent in several languages, sell fresh crabs (*Cancer pagurus*), lobsters (*Homarus gammarus*), mackerel (*Scomber scombrus*), cod (*Gadus morhua*) and farmed salmon (*Salmo salar*) to Japanese, German, British, American and Dutch tourists. People from Bergen buy their supper as they pass by during their lunch break. Unseen by the mill of tourists and locals are the fishers who started from port at four in the morning to set their nets, go trawling or lift their crab pots. If you travel about a kilometre along the western shore of Vågen, the bay surrounded by the centre of Bergen, you come to Nordnes, the location of the Institute for Marine Research, the public aquarium and the offices of the Norwegian Fisheries Ministry. The tall building is full of biologists working on fish stock assessments and on research into the marine environment. At the Fisheries Ministry the coastguard and fisheries officers plan and execute monitoring programmes and quota allocations. On the other side of Vågen can be found the Bergen Fisheries Museum as well as the warehouses and factories of fish processing and distribution firms. On the southern edge of the city centre, scientists in the Department of Fisheries and Marine Biology of the University of Bergen are researching the ecology of marine organisms, work that underpins the conservation of biodiversity. This area of Bergen, covering perhaps $2\,km^2$, contains all the elements of the community that the two volumes of this book are designed to serve. In other parts of the world the various institutions of fisheries are not as close to each other as they are in Bergen but the elements will be some local version of what exists around Vågen. The heart of the system is the fisher and the market at which the produce is landed and sold.

1.2 GLOBAL FISHERIES

According to the United Nations Food and Agricultural Organization (FAO), there was a steady increase of fish catches until the middle of the 1990s when the catch began to level off (Fig. 1.1). Recent work by Watson and Pauly (2001) has shown that in reality the total marine catch of fish has been declining by some 10% a year since 1988. The apparent continued increase until the mid-1990s was due to inflated catch statistics reported by China, the world's biggest fishing nation. This was thought to be due to local managers being under pressure to show increased production to meet the goals of a centralized communist economy. FAO estimates that 47–50% of the world's fish stocks are fully exploited, 15–18% overexploited and 9–10% depleted (FAO 2000). A drop in fisheries production in 1998 was primarily due to the El Niño event that took place in 1997–8. This influenced most directly the Southeast Pacific region, one of the regions that contributes
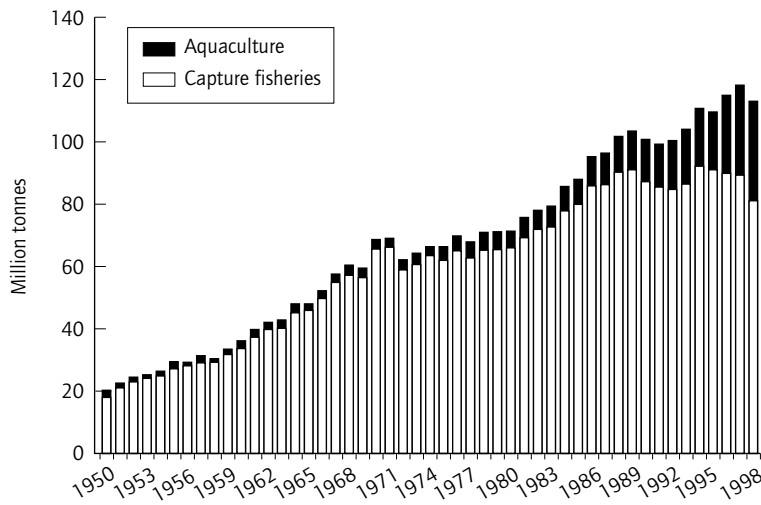
Fig. 1.1 Global landings of marine and inland capture fisheries and aquaculture. Data from 1970 corrected for misreporting of marine landings (Watson and Pauly, 2001; R. Watson, personal communication). (Source: from FAO 2000.)

most to the catch of marine fish, mainly anchovy (*Engraulis ringens*) and Chilean jack mackerel (*Trachurus murphyi*) (Fig. 1.2).

As shown in Table 1.1, the catch of fish taken by capture fisheries in inland waters continued to grow between 1994 and 1999. In 1999 about 27 million fishers landed 92 million tonnes of fish and shellfish. A further 9 million people were busy producing 32 million tonnes of farmed fish. International trade in fisheries commodities was worth some US$53.4 billion in 1999. The marine fishing fleet consisted of around 23 014 vessels over 100 tonnes. In reality there are probably at least as many vessels again under this quite large lower weight limit. The fish caught by all these vessels and people were processed and sold in a variety of ways. In 1998, the latest year for which data are available, 79.6% of fish landed was used for direct human consumption while the remainder went into non-food production. Of the proportion being used directly as human food, 45.3% was sold fresh, 28.8% was frozen, 13.9% was canned and 12% was cured. Fifty years ago the proportion that was frozen would have been much smaller and the part cured or canned much higher.

Fish form an important part in the diet of many people. Average consumption per head has grown considerably over the past 40 years, increasing from 9 kg per person per year in the early 1960s to
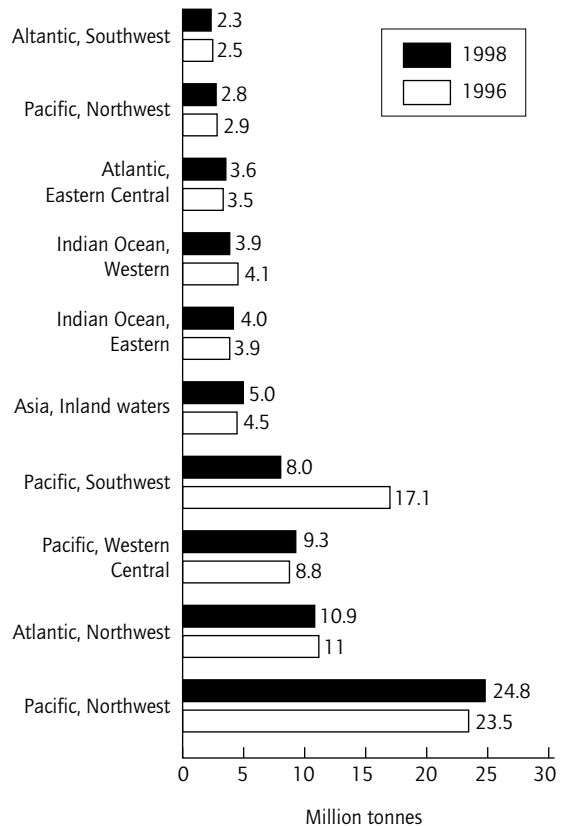
Fig. 1.2 Capture fisheries production by major fishing regions in 1996 and 1998. (Source: from FAO 2000.)

Table 1.1 Recent trends in world fisheries production and utilization. The data in this table are given without correction for the inflated catches documented by Watson and Pauly (2001). (Source: from FAO 2000.)

	1994	1995	1996	1997	1998	1999
Production (million tonnes)						
Inland						
Capture	6.7	7.2	7.4	7.5	8.0	8.2
Aquaculture	12.1	14.1	16.0	17.6	18.7	19.8
Total inland	18.8	21.4	23.4	25.1	26.7	28.0
Marine						
Capture	84.7	84.3	86.0	86.1	78.3	84.1
Aquaculture	8.7	10.5	10.9	11.2	12.1	13.1
Total marine	93.4	94.8	96.9	97.3	90.4	97.2
Total capture	91.4	91.6	93.5	93.6	86.3	92.3
Total aquaculture	20.8	24.6	26.8	28.8	30.9	32.9
Total world fisheries	112.3	116.1	120.3	122.4	117.2	125.2
Utilization						
Human consumption (million tonnes)	79.8	86.5	90.7	93.9	93.3	92.6
Reduction to fishmeal and oil (million tonnes)	32.5	29.6	29.6	28.5	23.9	30.4
Human population ($\times 10^9$)	5.6	5.7	5.7	5.8	5.9	6.0
Per-capita food fish supply (kg)	14.3	15.3	15.8	16.1	15.8	15.4

16 kg per person per year in 1997 (FAO 2000; Table 1.1). In developed countries consumption per head over the same period has risen from 19.7 to 27.7 kg per year. Countries at the other end of the wealth scale have much less fish available, although they too have experienced a rise in supply from 4.9 to 7.8 kg per person per year. In poor countries fish can form 20% of a person's protein intake. African countries have access to much less fish than do countries in Southeast Asia (excluding China).

1.3 THE QUEST FOR KNOWLEDGE

When T.H. Huxley made his infamous remarks in 1883 about fish being too fecund for their numbers ever to be influenced by fishing, he was showing supreme confidence in his knowledge of fish and their biology. This confidence meant that others had to work hard to collect information before he could be proven wrong (see Smith, Chapter 4, Volume 2). We now realize that uncertainty about fish biology and fishing systems is inherent and has to

be taken into account at all times. Uncertainty comes in different forms and has been categorized by Charles (1998) into three types: (i) random fluctuations, (ii) uncertainty in parameters and states of nature and (iii) structural uncertainty. The latter can be put more bluntly as ignorance; we just do not know how the system works. Ecology is a difficult subject, especially when the species under study is not easy to see and its population dynamics display unpredictable fluctuations, a phenomenon widespread in the natural world. Uncertainty in parameters and in the state of nature can now be embraced by various estimation procedures, ranging from simulation methods to Bayesian statistics to fuzzy logic (Wade 2001). When all else fails, we may have to tackle structural uncertainty by learning more about the system.

The first volume of this book reviews the extent of our knowledge about many aspects of fish biology, while the second volume integrates this knowledge with descriptions of a wide range of topics in fisheries biology and management, from how fish are caught to methods for assessing their populations and predicting impacts of exploitation

on the targeted species and their ecosystems. In effect, the first volume tries to show what we know and to demarcate the limits of structural uncertainty about basic biology. Along the way the authors also show the degree to which our knowledge is plagued by the other two sources of uncertainty. Some of the chapters inevitably overlap and the different viewpoints on the same part of nature are reminiscent of a passage from John Steinbeck's (1952) foreword to *Between Pacific Tides* by his friend Ed Ricketts. He wrote: 'There are good things to see in the tidepools and there are exciting and interesting thoughts to be generated from the seeing. Every new eye applied to the peep hole which looks at the world may fish in some new beauty and some new pattern, and the world of the human mind must be enriched by such fishing.' We think that these different viewpoints are important as they illustrate how there is often not enough known of an ecosystem or species to allow a definitive account to be given.

Structural uncertainty is meat and drink to the scientist. Problems are rarely solved entirely, because we are always uncovering new layers of complexity. The view is often expressed that we really need to do more research on this or that problem so that we can better understand what is going on and therefore be in a better position to manage it. To a point this is true, but as Ludwig et al. (1993) wrote:

> Recently some of the world's leading ecologists have claimed that the key to a sustainable biosphere is research on a long list of standard research topics in ecology. Such a claim that basic research will (in an unspecified way) lead to sustainable use of resources in the face of a growing human population may lead to a false complacency: instead of addressing the problems of population growth and excessive use of resources, we may avoid such difficult issues by spending money on basic ecological research.

There is a danger that those interested in fisheries management and conservation will not know when to stop in the quest for more knowledge.

These two volumes show that we do know a great deal about fish biology and ecology, yet the world's fish stocks are still being reduced mercilessly. The problem is that knowing about the resource is not enough. As Walters (1986) has said, fisheries management is more about managing people than ecosystems, a point that we return to in our introduction to the second volume.

With two volumes composed of 34 chapters written by 54 people, we hope we have provided a holistic view of fisheries science. In this chapter we want to draw attention to our reasons for including the chapters we have in the first volume. In addition we also try to show how the study of commercial fish populations has led to new insights in many basic areas of biology and ecology. The early years of fisheries science created a discipline that was considered very separate from the rest of biology (Graham 1956). The need to tackle practical problems often made it hard for fisheries scientists to contribute to the literature on basic ecology. Despite this, scientists such as Hjort, Hardy, Beverton and Holt (see Smith, Chapter 4, Volume 2) left a lasting legacy in ecology as well as in the specialist field of fisheries.

1.4   PART 1: BIODIVERSITY

This volume starts with two accounts that tell us what fish there are, how we determine which taxa are related to one another, and where they can be found (Gill and Mooi, Chapter 2; Mooi and Gill, Chapter 3). These are fascinating studies in their own right, and the information also underpins several aspects of fisheries science. For example, recent work that attempts to predict which species are likely to be vulnerable to exploitation has used phylogenetic information to guide comparisons of responses to fishing. Common responses could be due to close taxonomic relatedness and this component needs to be accounted for explicitly (see Reynolds et al., Chapter 15, Volume 2). Without this systematic knowledge, it would not be possible to make the comparisons necessary to derive rules of thumb telling us which species are likely to be vulnerable to exploitation and

which will be robust. Similarly, Hutchings (Chapter 7, this volume) makes comparisons of life-history variation in well-defined taxonomic groups. Furthermore, Rickman et al. (2000) showed that variation in recruitment depends in part on fecundity, but this relationship only becomes apparent when comparisons are made between populations of the same species. Good systematics is also necessary for the analysis of substocks within species as described by Ward (Chapter 9, this volume). Finally, data collection, as described by Evans and Grainger (Chapter 5, Volume 2), and stock assessment (Sparre and Hart, Chapter 13, Volume 2) are only possible if species can be identified. Many tropical fisheries suffer from poor knowledge of the systematics of the exploited fish. For example, the trawl fishery on Lake Malawi catches 177 different taxa, most of which are unnamed (Turner 1995). We can say without a doubt that all the methods described in Volume 2 require good systematics at the species or stock level.

Knowledge of biogeography not only allows us to know where important species are found but also shows up hotspots of diversity where conservation measures may be particularly needed. Biogeographical knowledge also defines the type of fish fauna expected from different habitats. Polunin and Pinnegar (Chapter 14, this volume), Persson (Chapter 15, this volume) and Jones et al. (Chapter 16, this volume) deal with the dynamics of communities in different biogeographical zones.

Knowledge of contemporary distributions will be increasingly useful as fisheries biologists are required to pay more attention to the influence of climate change. This process will influence the distribution of fish, and knowledge of present biogeographical limits makes it possible to identify sensitive species. An example is the North Sea stock of cod (*Gadus morhua*), which is at the southern limit of the species' distribution (O'Brien et al. 2000). Recruitment is poor in warm years. Should the North Sea continue to get warmer it will become harder for the cod to maintain its current distribution and the limited area closures employed in the spring of 2001 to protect the fish from exploitation during spawning may not be enough.

1.5   PART 2: PRODUCTION AND POPULATION STRUCTURE

Sustainable fishing is maintained by the growth and reproductive output of individual fish. Growth is governed by physiological ability to cope with environmental challenges. Some of the physiological mechanisms that fish have for living in water are described by Brix (Chapter 4, this volume). Fish stocks are often divided into local subunits, with their own adaptations to local conditions. A good example of this is provided by the different haemoglobin genotypes possessed by cod that live close to the Norwegian coast. Brix describes how these genotypes are linked to temperature-sensitive oxygen-binding properties of the haemoglobin molecule, which adapt fish to the conditions in which they live. The haemoglobin genotypes also have an influence on competitive behaviour (Salvanes and Hart 2000). The temperature sensitivity of the haemoglobin genotypes links back to the comments made earlier about cod being at their southern limit in the North Sea. Fish are fine-tuned to the particular conditions they face and knowledge of physiology will make it possible to predict which fish will suffer or benefit from a warming of the seas. Similarly, the physiological and behavioural attributes of fishes will determine how they can respond to pollution in estuaries and the nearshore environment (Jones and Reynolds 1997).

In the next chapter, Jobling (Chapter 5, this volume) discusses the processing of energy and its consequences for growth. Jobling also describes the way in which a fish develops and the models that can be used to predict growth. The model of growth that is used most often is the von Bertalanffy equation, which pops up in many analyses of stock production. One interesting development is by Schnute and Richards (Chapter 6, Volume 2), who show how a generalized version of

this model can also be used to describe population growth.

From individual productivity we move on to population productivity. Myers (Chapter 6, this volume) describes the pattern of recruitment in a range of species and discusses what is known about the causes of variation. This is a key question in fisheries science (Cushing 1996). Myers' chapter underpins Chapters 6–13 in Volume 2, which deal with aspects of stock assessment and modelling. A key issue for the conservation of stocks and for rebuilding those that have been overexploited is whether stocks at low abundance have the ability to produce enough offspring to regenerate the stock (compensatory reserve). An analysis of 246 fish populations has shown that the maximum annual reproductive rate, determined at the origin of the stock–recruit curve, is between 1 and 7. This assumes that the stock–recruit curve goes through the origin and implies that there are no disruptions to the reproductive process as the spawning stock becomes very small (the Allee effect). Frank and Brickman (2000) showed that this Allee effect can exist at the subpopulation level and this may be obscured if data are aggregated from several subgroups.

The study of life histories (Hutchings, Chapter 7, this volume) follows naturally from studies of recruitment. For example, an important link between fishing and recruitment is the size and age at which fish become sexually mature. These depend on growth rates and other components of life histories that schedule reproduction in relation to the lifespan. A major determinant of this schedule is the stage at which the animal experiences the most severe mortality. Law (1979) showed theoretically how increasing the mortality at some particular age would lead to the evolution of increased reproductive output in the years before that mortality occurred. This may lead to a reduced age at maturity. A recent review by Reynolds et al. (2001) has shown that large late-maturing fish are the most vulnerable to exploitation. Thus, it is not surprising that other studies discussed by Hutchings have shown that the principal life-history changes due to fishing are reduced size and age at maturity. These may be plastic responses of the growth

process or evolutionary responses mediated by gene frequency changes.

One aspect of life histories reviewed by Hutchings (Chapter 7, this volume) concerns relationships between characteristics such as body size, body growth rate, natural mortality rate and length of first reproduction. These relationships were first studied by Beverton and Holt (1959) and have since been formalized and extended to other taxa by Charnov (1993). These life-history invariants have proved useful for predicting the vulnerability of populations to fishing (Pope et al. 2000). Likewise, Roff (1981, 1984) did pioneering work on the lifetime allocation of energy to growth and reproduction and concluded in the earlier paper for the Pleuronectidae that reproductive lifespan within the group was not a response to variations in reproductive success but to variations in the age at maturity. Researchers such as Charnov (1993) and Charlesworth (1994) have since developed these early studies of aspects of life histories into modern life-history theory, which is applicable to a wide range of sexually reproducing species.

Life histories and recruitment feed into migration, reviewed by Metcalfe et al. (Chapter 8, this volume). Indeed, this chapter shows that migration is a fundamental facet of the life histories of many commercially important fish species. In diadromous species, the life history has become split between two habitats, one of which is better for feeding and the other for reproduction. Salmon species provide classic cases of this lifestyle. Migration also makes them particularly vulnerable to fishing, because they must pass through a narrow bottleneck on their way to spawn, and to environmental degradation through silting of spawning grounds and general deterioration in water quality (see Reynolds et al., Chapter 15, Volume 2).

Information on migration is essential for the management of many stocks. The movements of the fish will determine where the fishing boats will be. The way in which fishing effort is applied to the stock will be determined by this spatial correlation and should be incorporated into models (see Sparre and Hart, Chapter 13, Volume 2). An understanding of animal movements is also fundamental to the success or failure of marine pro-

tected areas (see Polunin, Chapter 14, Volume 2). For example, the closure of 40% of the North Sea to cod fishing in the spring of 2001 is a sign that very large areas have to be enclosed if a marine protected area is designed to conserve a species that migrates over large distances. Indeed, many biologists are sceptical about whether even this area of closure was sufficient to have had appreciable conservation impacts on the stock.

From migration we move on to a review of population genetic structure of fish stocks (Ward, Chapter 9, this volume). Stocks used to be identified by morphological characters such as the number of vertebrae or the number of fin rays in dorsal or other fins, in conjunction with tagging studies. Ward reviews the modern molecular methods that are now used, often in conjunction with advanced technology to track fish migrations (see Metcalfe et al., Chapter 8, this volume). The increasing evidence of the importance of substock structure in fish populations provides a growing market for this information. Molecular methods are also helping to determine relationships among taxa that can then be compared to understand population characteristics while taking into account phylogenetic relationships (Reynolds et al. 2001). Ward also describes uses for new molecular techniques, such as identifying fishes or fish parts in markets, and identifying endangered species offered for sale in disguised form. A recent guide to Australian seafood contains a cellulose acetate-based fingerprint for each of 380 species.

The final chapter in Part 2 rounds out the reviews of various aspects of production and population structure with a review of reproduction (Forsgren et al., Chapter 10, this volume). Traditionally, models in fisheries science have assumed that behavioural aspects of reproduction are not important. Cushing (1968) in his book on fisheries biology devotes just one sentence to the spawning behaviour of the Norwegian cod in Vest Fjord, in the Lofoten Islands: 'The male fish arrive in the Vest Fjord first, and spawning takes place in the midwater layer where the fish are caught by drift nets, long lines and purse seines . . .'. Subsequent work has led Nordeide and Folstad (2000) to argue that cod may have a lekking system, which

implies considerable behavioural complexity. Details such as this can be important in understanding spatial vulnerability of individuals, as well as reproductive success. For example, Chapter 10 (this volume) shows how fertilization mode, aggregation behaviour, sex changes and sperm limitation all determine vulnerability to Allee effects (depensation). In the many reef species that undergo sex change, impacts of fishing on the populations depend on the cues that determine sex change. Fisheries typically remove the largest individuals, and in many wrasses and groupers these are males that had been females when they were younger. If sex change is flexible according to the females' perceptions of presence or absence of males, the loss of males to the fishery may be replaceable. But if sex change occurs at a fixed size, males may not be replaced fast enough, and sperm depletion is possible.

1.6 PART 3: FISH AS PREDATORS AND PREY

Three chapters on feeding ecology illustrate the truth of Steinbeck's observation about how different people see the world in different ways depending upon which 'peep hole' they use. Mittlebach's view in Chapter 11 (this volume) of predator–prey relationships is very much influenced by the theoretical structure that he employs to understand trophic ecology and habitat use. He is interested in explaining the ways that interactions between fish species in freshwater lakes can be predicted from a knowledge of the costs and benefits of different prey types. The view of Juanes et al. in Chapter 12 (this volume) focuses more clearly on the perspective of fish as predators, with most attention paid to the way in which feeding habits shape the life histories, body form and ecology of predators. Krause et al. in Chapter 13 (this volume) take the prey's point of view, emphasizing how their ecology and behaviour are moulded by predation pressure.

All three foraging chapters take advantage of huge advances in our understanding of foraging

theory through the application of optimization methods (Stephens and Krebs 1986; Giraldeau and Caraco 2000). They feed directly into the trophic models of fisheries, reviewed in the second volume by Pauly and Christensen (Chapter 10, Volume 2), as well as multispecies virtual population analysis reviewed by Shepherd and Pope (Chapter 7, Volume 2). For example, details of predatory behaviour determine the shape of the 'functional response' of diet choice in relation to availability of alternative prey types (see Juanes et al., Chapter 12, this volume). The shape of this relationship is important in multispecies models of fisheries.

The basic research into prey choice and habitat choice reviewed by our triumvirate of chapters also feeds into our understanding of the role of piscivores in trophic webs (Chapters 14–16, this volume). For example, in freshwater systems, predation on planktivorous fish species can lead to trophic cascades. This information has been used to improve water quality in many freshwater ecosystems through biomanipulation. Although it is unlikely that marine systems could be managed in the same way because of differences in scale, fishers have changed the structure of marine food webs by reducing the abundance of large organisms in much the same way as piscivores reduce the abundance of planktivores (see Pauly and Christensen, Chapter 10 and Kaiser and Jennings, Chapter 16, Volume 2). Another market for the information on foraging behaviour (Chapters 11 and 12, this volume) is in stocking programmes designed to boost freshwater sport fisheries (see Cowx, Chapter 17, Volume 2). We need to be able to predict the likely benefits for anglers and the environmental damage that may be caused by stocking programmes (see Reynolds et al., Chapter 15, Volume 2). The chapter by Krause et al. (Chapter 13, this volume) looks specifically at the antipredator adaptations of fish that can lead to a species being very vulnerable to fishing. For example, schooling behaviour, which is so effective against the attacks of individual fish predators, is a disadvantage in the face of fishing. Schooling makes it relatively easy for purse seiners (Misund et al., Chapter 2, Volume 2) to find fish using long-range sonar and to catch species such as mackerel

(*Scomber scombrus*) and herring (*Clupea harengus*). Schooling behaviour also makes catch per unit effort (CPUE) useless for estimating the abundance of the stock as high CPUE is observed until the stock is virtually extinct. The catch rate of large aggregations of cod off Newfoundland remained constant at 1.5% of all cod catches right up until 1992 when the stock collapsed (Hutchings 1996).

1.7   PART 4: FISH IN ECOSYSTEMS

The final four chapters of this volume take the details of behavioural interactions involving fish as predators and prey (Part 3) and scale them up to understand community ecology. Polunin and Pinnegar (Chapter 14) focus on marine food webs, Persson (Chapter 15) examines freshwater communities and Jones et al. (Chapter 16) make explicit comparisons between these habitats. An important theme that emerges is that as fish grow their niche changes so much that the young and adults inhabit different worlds. Thus, in Swedish lakes the interactions between European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) are a mixture of competition and predation that depend on the age and size of the interacting fish. A similar relationship holds for cod and gobies (*Gobiusculus flavescens*) in Norwegian fjords. When cod are small they compete for food with gobies but gobies are eaten by larger cod (A.G.V. Salvanes, personal communication). The same is true of the largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*) in North American lakes. This information is critical for the implementation of multispecies models (see Shepherd and Pope, Chapters 7 and 8, Volume 2) and ecosystem models (see Pauly and Christensen, Chapter 10, Volume 2).

The final chapter of the first volume presents a detailed examination of fish parasites (Barber and Poulin, Chapter 17). The mixture of pure and applied research reviewed here includes evidence that parasites can change behaviour and drive population events. For example, threespine stick-

lebacks infected with *Schistocephalus solidus* are more likely to take risks when feeding near predators than are uninfected individuals (Milinski 1984). Likewise Milinski (1982) found that competitive interactions between sticklebacks were altered by parasite load. That parasites seem able to drive population cycles was shown by Kennedy et al. (1994) for *Ligula intestinalis* infecting roach in a lake in Devon, UK. For marine populations, there is little evidence for this type of population effect, although Holst et al. (1997) have shown that there is a possible link between abundance of Norwegian spring-spawning herring (*Clupea harengus*) and infections of the fungal parasite *Ichthyophorus* sp.

Parasites in fish can endanger human health. Herring often contain the nematode worm *Anisakis simplex*. The preparation of pickled herring, particularly popular in Scandinavia and the Netherlands, does not always kill the parasite in the fish flesh and the worm can be passed on to the human consumer, sometimes finding its way to the brain. Such infections can seriously undermine marketing efforts to persuade people to eat more fish (see Young and Muir, Chapter 3, Volume 2).

One of the biggest problems on salmon farms in Norway and Scotland has been the sea louse (*Lepeophtheirus salmonis*). Estimated costs to the industry vary widely but are likely to exceed £20 million a year in both Scotland and Norway. Low fish growth, stock losses and a reduced price at harvest cause these costs. In addition the farmer has to pay for monitoring and treatment, which can have severe environmental impacts. At present, efforts are being made to use wrasse (Labridae) to act as cleaners so reducing the need to use chemical treatments. The study of parasites is one area in fisheries science where there is little argument over the need for basic biological information.

1.8 IGNORANCE BANISHED?

As this chapter has outlined, the principal purpose of Volume 1 of the *Handbook* is to provide the biological basis for the tools of management and conservation described in Volume 2. Along the way, we have allowed ourselves (and our authors) the luxury of following paths that have led through a considerable amount of additional background information that may never find its way directly into fisheries management, but which enriches our overall understanding of fish biology. We will never reach the limits of our ignorance about the way the fish world works but in the context of management we do not need to know everything.

How much do we need to know? Ludwig et al. (1993) present the case that it is silly to always argue that we cannot act to manage stocks sustainably until we have more information. However, we cannot divorce the management of fishers from the biology of their prey. As fish stocks have collapsed, the search for solutions has led to new questions. As Hutchings (2000) has noted, many of these concern ecology and evolution, subjects that are reviewed in this first volume. Hutchings draws examples of questions from the collapse and slow recovery of Atlantic cod along the eastern Canadian coast, to which we can add a few of our own. Could the slow rate of recovery be due to changes in mating behaviour and Allee effects (depensation) at small population sizes? What new predator–prey relationships might be in place now that the fish occur at less than 5% of their population biomass of 30 years ago? Have ecosystem shifts occurred that hinder recruitment? What is the role of habitat disturbance? Are temperature changes important? Have there been evolutionary impacts on the populations? How many populations are there, and what kind of source–sink dynamics might be involved in population recovery?

Few of these questions were being asked in any fishery 10 or 15 years ago. They are common now, and we do need the answers for effective management of many fish populations and ecosystems. How large should a marine reserve be and how close should it be to other reserves (see Polunin, Chapter 14 and Reynolds et al., Chapter 15, Volume 2)? How will our management of one species affect populations and yields of others (see Pauly

and Christensen, Chapter 10 and Kaiser and Jennings, Chapter 16, Volume 2)? How can we estimate natural mortality rates of target species, in order to make accurate forecasts from models (see Shepherd and Pope, Chapter 7, Volume 2)? How do life histories, behaviour and economic value affect vulnerability to extinction (see Reynolds et al., Chapter 15, Volume 2)?

Many of the contributors to these two volumes have never worked alongside one another before. We hope that these two volumes will help to bridge the gap between pure and applied research, leading to a productive dialogue between those who study fish biology for different reasons but whose interests may have more in common than they realize.

1.9   CONCLUSIONS

We have tried in this chapter to illustrate how the material in the 17 chapters of Volume 1 of this *Handbook* can be used for an intelligent application of the methods covered in Volume 2. Fisheries scientists are often accused of being so preoccupied with the details of stock assessment that they forget about individual interactions by fish within stocks as well as connectivity between stocks and the rest of the ecosystem. We hope that the information in this volume will be of interest for its own sake, and for helping to put ecology and evolution back into fishery science and management.

ACKNOWLEDGEMENTS

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Part 1
Biodiversity

2 Phylogeny and Systematics of Fishes

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2.1 INTRODUCTION

The term 'fish', in the conventional sense, refers to craniate animals (i.e. hagfishes and vertebrates) that are aquatic, with permanent gills borne on pharyngeal pouches or arches, median fins supported by cartilaginous or bony rays, and usually paired fins but never limbs bearing digits. Fishes represent a diverse group that includes over 25 000 extant species, or roughly half of the Craniata (J.S. Nelson 1994; Helfman et al. 1997; Lundberg et al. 2000). However, as so defined, they do not constitute a 'natural' or monophyletic group (see below) because they do not share a common ancestor exclusive of the Tetrapoda (reptiles, birds, mammals and amphibians).

Systematics, or phylogenetic systematics, is the field of biology involved with the investigation of phylogenetic relationships and classification of organisms. Cladistic methods have come to dominate systematic investigation over the past few decades, and for this reason, as well as our own subscription to this method, we write this chapter from a cladistic perspective.

The aims of this chapter are (i) to outline methods of inferring phylogenetic relationships among organisms and of classification focusing on cladistics; and (ii) to provide an overview of higher fish taxa that includes brief details of taxonomic diversity, habits and general distribution, and to direct the reader to literature that details relationships within and among such taxa.

2.2 PHYLOGENETIC METHODS AND CLASSIFICATION

Over the last 40 years, three main methods have vied for support as techniques that can be used to classify and infer relationships among organisms: (i) numerical taxonomy or phenetics; (ii) evolutionary taxonomy; and (iii) cladistics or phylogenetic systematics. Space constraints do not allow a detailed discussion or comparison of these methods; we offer only a brief contrast, mainly to aid the reader in interpreting our discussion of fish orders and their interrelationships. Numerous publications discuss and contrast the three methods in much greater detail (e.g. Hennig 1966; G.J. Nelson 1972; Nelson & Platnick 1981); much of the debate regarding the aims of systematics was played out in the journal *Systematic Zoology* (now *Systematic Biology*) during the 1970s. Moreover, debate about methods in cladistics continue, particularly in the journal *Cladistics* (journal of the Willi Hennig Society). The interested reader should consult these references.

The three methods differ fundamentally in how characters are analysed and how taxa are classified (Fig. 2.1). Characters are the observable parts or attributes of organisms, and are effectively the units of systematic analysis. Obviously, in order that characters may be used to differentiate taxa, they must vary; that is, they must express two or more character states. Numerical taxonomy is based on a concept of overall similarity, whereupon rela-

tionships are inferred without regard to whether character states are derived (apomorphic) or primitive (plesiomorphic). For example, given the simple matrix in Fig. 2.1, a pheneticist would infer a close relationship between taxa B and C, because these taxa possess the same character states for two characters (Y and Z), whereas only one character (X) suggests an alternative close relationship between taxa A and B. A resulting phenetic classification would place taxa B and C in a more general taxon that excludes taxon A. Complex statistical methods are typically used in phenetic studies and the development of phenetics coincided with the development of computer technology; in particular, cluster analyses are often used, usually in association with large arrays of characters under the assumption that this leads to greater objectivity. Nevertheless, relationships generated by phenetic methods are concerned with general similarity rather than genealogy, and have mostly fallen out of favour with systematists. They do persist in certain fields, however, particularly in biochemical systematics, illustrated by analyses based on genetic distance.

Cladistic methods, which were first formulated by Hennig (1950; later revised and published in English, Hennig 1966), differ from phenetic methods in giving importance only to derived (apomorphic) character states. The presence of a given apomorphic state in two or more taxa (synapomorphy) is evidence of common ancestry.

This conclusion is based on a concept of parsimony: in the absence of evidence to the contrary, such as a conflict with other characters (see below), it is more parsimonious to conclude that a derived character state has evolved once in a common ancestor with inheritance by descendant taxa than to conclude multiple independent origins of the apomorphy. The shared presence of primitive (plesiomorphic) characters (symplesiomorphy) neither refutes nor supports common ancestry. Moreover, the presence of apomorphic characters in a single taxon (autapomorphy) does not contribute to an understanding of that taxon's relationships to other taxa. Thus, in the matrix given in Fig. 2.1, only one derived character (X) is shared by two taxa (A and B), leading to a conclusion that these are sister taxa. The apomorphic states for characters Y and Z are found only in taxon A, and do not contribute to an understanding of its relationships to the other taxa. However, notions of synapomorphy, autapomorphy and symplesiomorphy are dependent on perspective, on the level of generality of the analysis at hand. For example, if we consider that taxon A is a family consisting of multiple species, the apomorphic states (1 in Fig. 2.1) for characters Y and Z, which we have already indicated are autapomorphies of A in an analysis of the relationships of A, B and C, are also synapomorphies uniting the various species in the family A together; but they are also symplesiomorphies, and so uninformative, in an analysis of relationships among the species in A.

Phylogenies are inferred from hierarchically distributed synapomorphies. However, in reality, there is almost always conflict among characters; apparent synapomorphies may suggest different phylogenetic relationships. Phylogenies are constructed, usually with the aid of computer algorithms, such that conflict between assumed synapomorphies are minimized under a parsimony argument; thus trees with minimal length, which are those requiring the fewest character-state changes and therefore assumptions about convergence or homoplasy, or apparent loss of apomorphies, are favoured. As such, cladistic analyses can also be viewed as tests of character-state homology: assumed synapomorphies that fail to diag-
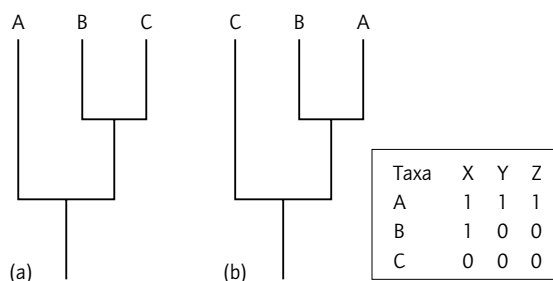

Fig. 2.1 Matrix of three characters (X, Y and Z) for three taxa and the relationships inferred using (a) phenetic and (b) cladistic methods. 0, Plesiomorphic character states; 1, apomorphic character states.

nose monophyletic groups (see below) are non-homologous; conversely, those that do diagnose monophyletic groups are homologous (Patterson 1982, 1988; de Pinna 1991; G.J. Nelson 1994).

Cladistic classifications differ from phenetic ones in that only monophyletic taxa (clades) are recognized: these can be viewed as groups that include an ancestor and all of its descendants. In contrast, pheneticists may also recognize paraphyletic taxa (grades) in their classifications: these are groups that exclude one or more of an ancestor's descendants such as a taxon consisting of B and C in Fig. 2.1. In short, cladistic methods effectively equate the terms 'synapomorphy', 'homologue', 'relationship' and 'taxon'.

The third method, evolutionary taxonomy, is more difficult to describe because it is not a unified method. Usually, evolutionary taxonomists employ cladistic methods for inferring phylogenetic relationships, though often invoking assumptions about the evolution of character states, but depart from cladistics in often recognizing paraphyletic taxa. Such taxa are recognized to reflect perceived gaps in evolution. Thus, an evolutionary taxonomist may infer the same relationships as a cladist for the example given in Fig. 2.1, but may conclude the same classification as a pheneticist (i.e. two taxa: A, B + C) if the autapomorphies of A were perceived as sufficient to place it in a different taxon from B + C. Recently, in discussing the classification of tunas and billfishes, Carpenter et al. (1995) defended the use of evolutionary taxonomic methods, arguing that they led to greater stability of taxonomic nomenclature.

In short, the primary objectives of systematics are to (i) discover characters; (ii) investigate their distributions; (iii) determine the phylogenetic relationships (hierarchical pattern) implied by (i) and (ii); and (iv) establish classifications that reflect the relationships in (iii). These objectives represent significant challenges. Our understanding of character distributions is often hampered by traditional classifications and views of relationships as illustrated in our discussion of acanthomorph fishes. In some sense assumptions are always made about the distribution of characters, because we lack the resources to investigate their real geo-graphical, temporal and ontogenetic distribution. We are also limited in our understanding by the historical basis of the characters under investigation. Most systematists have concluded that cladistic methods presently offer the best solution for both inferring phylogeny and constructing classifications. Our treatment of fish classification in this chapter reflects this cladistic approach.

2.2.1 Types of characters in fish systematics

For fishes, osteological and external characters have dominated historically, at least in part because they are most easily studied, particularly in fossil specimens. It is therefore not surprising that most higher taxa are diagnosed mainly or entirely by such characters. The modern discovery and survey of osteological characters has been greatly enhanced by the relatively recent development of improved methods for preparing specimens (Taylor 1967; Dingerkus and Uhler 1977; Taylor and Van Dyke 1985).

Muscles, particularly those operating the jaws, have received a reasonable level of investigation for character analyses, and have also played a role in determining topographical relationships of osteological features, an important step in refining our definition of such characters. Other systems associated with soft anatomy, such as neural anatomy, heart and blood vessel anatomy, have not been as comprehensively studied, though they are of considerable potential, both as characters in their own right and for refining our understanding of characters for osteological and other studies. For example, Parenti and Song (1996) studied innervation patterns in an attempt to define more carefully the character 'pelvic-fin position', which has had a long history in systematic ichthyology. Other morphological systems that have been important sources of characters include egg morphology (e.g. White et al. 1984; Mooi 1990; Britz 1997), scale ultrastructure (e.g. Roberts 1993) and spermatozoan morphology (e.g. Jamieson 1991). Behavioural characters has also been employed in phylogenetic studies. For example, the Ostariophysi are distinctive in possessing an

alarm reaction to alarm substance (see below) and McLennan et al. (1988) employed behavioural characters to investigate relationships among gasterosteids.

Finally, recent years have seen a strong bias towards the use of biochemical characters, such as isozyme and sequence data. Despite tremendous technological advances in methods of, for example, DNA extraction and sequencing and their demonstrated utility at lower taxonomic levels, biochemical characters have yet to contribute in a significant way to our understanding of the higher relationships of fishes. This, in part, reflects our poor understanding of biochemical characters, their distribution and homology, in short the lack of an appropriately comprehensive historical basis. Studies of higher relationship in which one or a few exemplars from huge clades are surveyed, which is the current norm in molecular studies of higher relationships of fishes, are unlikely to produce a realistic understanding of characters, their distribution, or the relationships they imply. For example, Rasmussen and Arnason's (1999) conclusion from an analysis of mitochondrial DNA sequences that cartilaginous fishes are nested within bony fishes is flawed, because the eight fish species surveyed do not meaningfully represent 25 000 or so fish species. Similar concerns about taxonomic sampling were expressed by Hennig (1966, p. 103) in his discussion of early studies of serum characters. Nevertheless, it is likely that this situation will improve as our historical basis for biochemical characters improves and more taxa are surveyed. As these challenges are overcome, molecular characters will provide fish systematists with valuable information that, along with continued analysis of morphological data, will significantly advance higher-level phylogeny construction.

2.2.2 Taxonomic ranks and species

A hierarchical system of taxa is currently used in biological classification (Table 2.1). Thus, a phylum consists of one or more classes, each of which consists of one or more orders, and so on through less inclusive taxa such as families, tribes, genera

Table 2.1 Classification of the Eurasian perch (*Perca fluviatilis*).

Phylum	Chordata
Class	Actinopterygii
Order	Perciformes
Family	Percidae
Tribe	Percini
Genus	*Perca*
Species	*fluviatilis*

and species. Additional divisions are also often recognized within these by adding a 'super', 'sub' or 'infra' prefix to these ranks. Examples are 'superfamily' between the order and family level, and 'subfamily' between the family and tribe level. An alternative is to slot in less commonly used ranks, such as 'division' and 'cohort'. The hierarchical structure of these ranks is convenient for reflecting nested phylogenetic relationships, but their use has resulted in considerable confusion about the reality of rank.

The artificial nature of ranking is immediately obvious when one examines the phylogeny of extant fish order provided in Fig. 2.2. Clearly the orders of fishes are not comparable, either in the sense of relative age as indicated by their relative position in the branching sequence, or in the sense of taxonomic diversity as perhaps indicated by the number of families or species. They are a necessary, though uncomfortable, compromise in communicating concepts of phylogenetic relationship within the framework of traditional Linnaean classification. However, the observation that ranking is arbitrary extends to all taxonomic levels, including – perhaps disturbingly for many biologists – species. The latter observation is at odds with various practices involved with the tallying of species, usually in the manufacture of indices of diversity; because species are not comparable, such tallies allow, at best, only gross comparison although we continue this tradition below in discussing such things as 'sizes' of orders.

The species issue deserves further discussion, if only in respect for the substantial baggage associated with that rank. More so than any other taxo-

Fig. 2.2 Interrelationships among extant fish orders. Numbers refer to supraordinal taxa: 1, Craniata; 2, Vertebrata; 3, Gnathostomata; 4, Chondrichthyes; 5, Elasmobranchii; 6, Galeomorphii; 7, Squalea; 8, Osteichthyes; 9, Sarcopterygii; 10, Dipnoi; 11, Actinopterygii; 12, Teleostei; 13, Osteoglossomorpha; 14, Elopomorpha; 15, Clupeocephala; 16, Clupeomorpha; 17, Ostariophysi; 18, Otophysi; 19, Protacanthopterygii; 20, Neoteleostei; 21, Eurypterygii; 22, Cyclosquamata; 23, Ctenosquamata; 24, Acanthomorpha; 25, Paracanthopterygii; 26, Smegmamorpha; 27, Atherinomorpha.
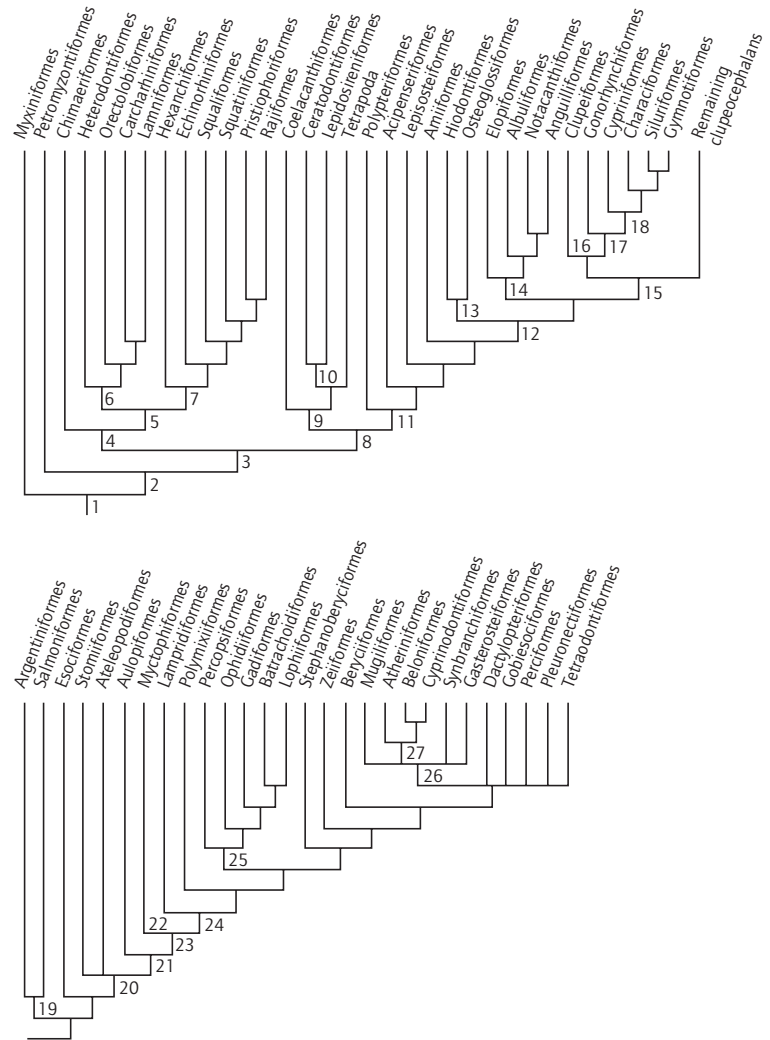
nomic rank, the species rank has been debated and usually seen as having a special reality or properties that uniquely distinguish it from all other taxonomic ranks. For example, species are often viewed as the 'building blocks' of biological diversity, the 'fundamental units' of evolution, unlike higher taxa, which are seen as the arbitrary units resulting from such evolution. Because of this view that species have some sort of special reality, many biologists feel qualified to make judgements

about species. However, there is little consensus among biologists concerning species concepts, not even among systematic biologists, the people who routinely describe and revise species. For example, Mayden (1997) listed some 22 different species concepts (Table 2.2), which variously address different interests and processes and thus attributes of biological diversity. For example, the biological species concept places emphasis on the reproductive interactions between individuals.

Table 2.2 Species concepts compiled by Mayden (1997).

Agamospecies concept
Biological species concept
Cladistic species concept
Cohesion species concept
Composite species concept
Ecological species concept
Evolutionary significant unit
Evolutionary species concept
Genealogical concordance concept
Genetic species concept
Genotypic cluster definition
Hennigian species concept
Internodal species concept
Morphological species concept
Non-dimensional species concept
Phenetic species concept
Phylogenetic species concept
    Diagnosable version
    Monophyly version
    Diagnosable/monophyly version
Polythetic species concept
Recognition species concept
Reproductive competition concept
Successional species concept
Taxonomic species concept

De Queiroz (1998) has argued that there is really only one species concept, that of species as an evolutionary lineage, and that the arguments concerning 'concepts' as listed by Mayden are really criteria, i.e. ways to identify whether or not a group of organisms is indeed a separate lineage. As systematists, we find G.J. Nelson's (1989a; see also Nelson and Hart 1999) argument compelling that species are taxa and are nothing more nor nothing less. Moreover, we believe that this concept, which places emphasis on pattern rather than process, will ultimately lead to discovery about process. Although some systematists argue for the recognition of subspecies and other intraspecific ranks (e.g. Randall 1998), we for various reasons (some of which are summarized by Gill 1999; Gill and Kemp, in press) argue against the use of intraspecific ranks, and that species should be the least inclusive monophyletic taxa identifiable. As such, species are hypotheses of relationships that

can be tested and modified by the collection of more data and their congruence as interpreted by cladistic analysis.

We do not expect the reader to agree with the view that species are merely taxa – the smallest taxa identifiable – and that taxa of the same rank are not comparable. Regardless, we do hope that the reader will appreciate that species are not directly comparable given that divergent species concepts are in use. A recent summary of views on the species concept in fish biology can be found in Nelson and Hart (1999).

2.3 FISH DIVERSITY AND PHYLOGENY

Phylogenetic relationships among fishes are perhaps better known than any other animal group of comparable size. This partly reflects the early and important contributions of several ichthyologists including G.J. Nelson, Patterson, Rosen and Wiley in the development and popularizing of cladistic theory and methods, and of the general influence of these individuals on the ichthyological community. However, it also reflects the cumulative effects of a very long history of endeavour in fish classification and anatomy, and the important contributions of a long line of dedicated ichthyologists. A small sample of these would include the French anatomist Georges Cuvier (1769–1832), the Swiss anatomist Louis Agassiz (1807–1873), the American ichthyologists Theodore Gill (1837–1914) and David Starr Jordan (1851–1931), and the British ichthyologists Albert Günther (1830–1914) and C. Tate Regan (1878–1943). Equally important has been the associated development of museum collections of both specimens and literature, which form the basis of our understanding of fish systematics (Pietsch and Anderson 1997). Despite this, however, there is much disagreement among ichthyologists regarding even interordinal relationships of fishes, particularly among the more 'advanced' taxa, and the same holds true for the classification of fishes.

Comprehensive classifications of fishes are provided in Greenwood et al. (1966, 1973), G.J. Nelson

(1969), J.S. Nelson (1976, 1984, 1994), Lauder and Liem (1983), Eschmeyer (1990), and Paxton and Eschmeyer (1994, 1998). Other publications that deal with the classification and relationships of one or more major fish taxa include Moser et al. (1984), Cohen (1989), Johnson and Anderson (1993), Stiassny et al. (1996) and Malabarba et al. (1998).

The following discussion of fish phylogeny and classification (Fig. 2.2; Table 2.3) is not intended to provide new hypotheses. Rather, the intention is to describe higher fish taxa based on recent literature, including aspects of taxonomic diversity, habits and general distribution, and to direct the reader to literature that details interrelationships and intrarelationships and associated character evidence among such taxa. We have also attempted to identify major areas of controversy and lack of resolution.

2.3.1 Extant fish orders and their interrelationships

The Myxiniformes (hagfishes) is a small order with about 45 extant species of marine fishes found mainly in temperate waters throughout the world. They are scavengers, feeding mainly on the insides of dying or dead fishes and invertebrates. They are sometimes classified with the lampreys (Petromyzontiformes) in the superclass Agnatha, but the characters for this grouping are primitive and thus not informative of a close relationship. Moreover,

other characters suggest that the lampreys are more closely related to the remaining extant craniates than they are to the hagfishes, with the main evidence being the presence of embryonic or rudimentary vertebral elements, and cladistic classifications place the lampreys in a monophyletic Vertebrata that excludes the hagfishes (Janvier 1981).

The Petromyzontiformes (lampreys) is a small order with about 40 species of freshwater and anadromous fishes found in cool temperate areas around the world. One extant family (Petromyzontidae) is restricted to the Northern Hemisphere; the remaining two extant families (Geotriidae and Mordaciidae) are restricted to the Southern Hemisphere. There is disagreement about the rank of these taxa, with some authors recognizing a single family (Petromyzontidae) with three extant subfamilies (e.g. J.S. Nelson 1994).

The remaining extant fishes are classified in a taxon called the Gnathostomata (jawed vertebrates). Character evidence for monophyly of this group includes presence of biting jaws derived from gill arches, spinal nerve roots united, semicircular canal horizontal, and gill arches jointed and medially placed (Janvier 1996). Living gnathostomes are divisible into two main groups, Chondrichthyes (cartilaginous fishes) and Osteichthyes (bony fishes and tetrapods).

The Chondrichthyes is divided into two taxa: the Holocephali, with a single extant order (Chimaeriformes), and the Elasmobranchii (sharks

Table 2.3 Classification of extant fishes. Orders and families are listed in phylogenetic and alphabetical sequences respectively. Commonly used synonyms of certain orders and families are indicated in parentheses. Families that include important commercial and recreational fisheries species are indicated in bold.

Myxiniformes [**Myxinidae**]
Petromyzontiformes [Geotriidae, Mordaciidae, Petromyzontidae]
Chimaeriformes [Callorhynchidae, Chimaeridae, Rhinochimaeridae]
Heterodontiformes [Heterodontidae]
Orectolobiformes [Brachaeluridae, **Ginglymostomatidae**, **Hemiscylliidae**, **Orectolobidae**, Parascylliidae, Rhincodontidae, **Stegostomatidae**]
Carcharhiniformes [**Carcharhinidae** (Sphyrnidae), **Hemigaleidae**, Leptochariidae, Proscylliidae, Pseudotriakidae, Scyliorhinidae, **Triakidae**]
Lamniformes [**Alopiidae**, **Cetorhinidae**, **Lamnidae**, Megachasmidae, Mitsukurinidae, **Odontaspididae**, Pseudocarchariidae]
Hexanchiformes [Chlamydoselachidae, **Hexanchidae**]
Echinorhiniformes [Echinorhinidae]
Squaliformes [Centrophoridae, **Dalatiidae**, **Squalidae**]

Table 2.3   *Continued*

Squatiniformes [**Squatinidae**]

Pristiophoriformes [**Pristiophoridae**]

Rajiformes [Dasyatidae (Gymnuridae, Myliobatidae, Mobulidae), Hexatrygonidae, Hypnidae, Narcinidae, Narkidae, Platyrhinidae, Plesiobatidae, Potamotrygonidae, **Pristidae**, **Rajidae**, Rhinidae, **Rhynchobatidae** (Rhinobatidae), Torpedinidae, Urolophidae, Urotrygonidae, Zanobatidae]

Coelacanthiformes [Latimeriidae]

Ceratodontiformes [Neoceratodontidae]

Lepidosireniformes [Lepidosirenidae (Protopteridae)]

Polypteriformes [Polypteridae]

Acipenseriformes [**Acipenseridae**, Polyodontidae]

Lepisosteiformes [Lepisosteidae]

Amiiformes [Amiidae]

Hiodontiformes [Hiodontidae]

Osteoglossiformes [Gymnarchidae, Mormyridae, Notopteridae, Osteoglossidae (Pantodontidae)]

Elopiformes [**Elopidae**, **Megalopidae**]

Albuliformes [**Albulidae**, Pterothrissidae]

Notacanthiformes [Halosauridae, Notacanthidae (Lipogenyidae)]

Anguilliformes [**Anguillidae**, Chlopsidae (Xenocongridae), Colocongridae, **Congridae**, Cyematidae, Derichthyidae, Eurypharyngidae, Heterenchelyidae, Monognathidae, Moringuidae, Muraenesocidae, Muraenidae, Myrocongridae, Nemichthyidae, Nettastomatidae, Ophichthidae, Saccopharyngidae, Serrivomeridae, Synaphobranchidae]

Clupeiformes [Chirocentridae, **Clupeidae** (Sundasalangidae), Denticipitidae, **Engraulidae**, Pristigasteridae]

Gonorynchiformes [**Chanidae**, Gonorynchidae, Kneriidae, Phractolaemidae]

Cypriniformes [Balitoridae (Gasteromyzontidae, Homalopteridae), Catostomidae, Cobitidae, **Cyprinidae** (Psilorhynchidae), Gyrinocheilidae]

Characiformes [Acestrorhynchidae, Alestiidae, Anostomidae, Characidae, Chilodontidae, Citharinidae, Crenuchidae, Ctenoluciidae, Curimatidae, Cynodontidae, Distichodontidae (Ichthyboridae), Erythrinidae, Gasteropelecidae, Hemiodontidae (Anodontidae), Hepsetidae, Lebiasinidae, Parodontidae, **Prochilodontidae**]

Siluriformes [Akysidae (Parakysidae), Amblycipitidae, Amphiliidae, Anchariidae, Andinichthyidae, **Ariidae**, Aspredinidae, Astroblepidae (Argidae), Auchenipteridae (Ageneiosidae, Centromochlidae), Austroglanididae, Bagridae (Olyridae), Callichthyidae, Cetopsidae (Helogeneidae), Chacidae, **Clariidae**, Claroteidae (Auchenoglanididae), Cranoglanididae, Diplomystidae, Doradidae, Erethistidae, Heteropneustidae (Saccobranchidae), **Ictaluridae**, Loricariidae, Malapteruridae, Mochokidae, Nematogenyidae, **Pangasiidae**, **Pimelodidae** (Heptapteridae, Hypophthalmidae, Pseudopimelodidae), **Plotosidae**, Schilbidae, Scoloplacidae, **Siluridae**, Sisoridae, Trichomycteridae]

Gymnotiformes [Apteronotidae (Sternarchidae), Hypopomidae, Gymnotidae (Electrophoridae), Rhamphichthyidae, Sternopygidae]

Argentiniformes [Alepocephalidae (Leptochilichthyidae), Argentinidae, Bathylaconidae, Microstomatidae (Bathylagidae), Opisthoproctidae, Platytroctidae]

Salmoniformes [**Coregonidae**, **Galaxiidae** (Aplochitonidae, Lepidogalaxiidae), **Osmeridae** (Plecoglossidae, Salangidae), Retropinnidae (Prototroctidae), **Salmonidae** (Thymallidae)]

Esociformes [**Esocidae**, Umbridae]

Stomiiformes [Gonostomatidae, Photichthyidae, Sternoptychidae, Stomiidae (Astronesthidae, Idiacanthidae, Malacosteidae, Melanostomiidae)]

Ateleopodiformes [Ateleopodidae]

Aulopiformes [Alepisauridae (Omosudidae), Aulopidae, Bathysauridae, Chlorophthalmidae, Evermannellidae, Giganturidae, Ipnopidae (Bathypterodidae), Notosudidae (Scopelosauridae), Paralepididae (Anotopteridae), Pseudotrichonotidae, Scopelarchidae, **Synodontidae** (Harpadontidae)]

Myctophiformes [Myctophidae, Neoscopelidae]

Lampridiformes [Veliferidae, Lamprididae, Stylephoridae, Lophotidae, Radiicephalidae, Trachipteridae, Regalecidae]

Polymixiiformes [Polymixiidae]

Percopsiformes [Amblyopsidae, Aphredoderidae, Percopsidae]

Ophidiiformes [Aphyonidae, Bythitidae, Carapidae (Fierasferidae), Ophidiidae (Brotulidae), Parabrotulidae]

Gadiformes [Bregmacerotidae, Euclichthyidae, **Gadidae** (Gaidropsaridae, Lotidae, Phycidae, Ranicipitidae), Macrouridae (Bathygadidae, Trachyrincidae), Melanonidae, **Merlucciidae** (Macruronidae, Steindachneriidae), **Moridae** (Eretmophoridae), Muraenolepididae]

Batrachoidiformes [Batrachoididae]

Table 2.3 *Continued*

Lophiiformes [Antennariidae, Brachionichthyidae, Caulophrynidae, Centrophrynidae, Ceratiidae, Chaunacidae, Diceratiidae, Gigantactinidae, Himantolophidae, Linophrynidae, **Lophiidae**, Melanocetidae, Neoceratiidae, Ogcocephalidae, Oneirodidae, Thaumatichthyidae]

Stephanoberyciformes [Barbourisiidae, Cetomimidae, Gibberichthyidae, Hispidoberycidae, Megalomycteridae, Melamphaidae, Mirapinnidae, Rondeletiidae, Stephanoberycidae]

Zeiformes [Caproidae, Grammicolepididae, Macrurocyttidae, Oreosomatidae, Parazenidae, **Zeidae**]

Beryciformes (Trachichthyiformes) [Anomalopidae, Anoplogastridae, **Berycidae**, Diretmidae, Holocentridae, Monocentridae, **Trachichthyidae**]

Mugiliformes [**Mugilidae**]

Atheriniformes [**Atherinidae**, Atherionidae, Atherinopsidae, Melanotaeniidae (Bedotiidae, Pseudomugilidae, Telmatherinidae), Notocheiridae (Isonidae), Phallostethidae (Dentatherinidae, Neostethidae)]

Beloniformes [Adrianichthyidae, **Belonidae**, **Exocoetidae**, **Hemiramphidae**, **Scomberesocidae**]

Cyprinodontiformes [Anablepidae, Aplocheilidae, Cyprinodontidae, Fundulidae, Goodeidae, Poeciliidae, Profundulidae, Rivulidae, Valenciidae]

Synbranchiformes [Chaudhuriidae, Mastacembelidae, Synbranchidae]

Gasterosteiformes (Indostomiformes, Pegasiformes, Syngnathiformes) [Aulorhynchidae, Aulostomidae, Centriscidae, Elassomatidae, Fistulariidae, Gasterosteidae, Hypoptychidae, Indostomidae, Macroramphosidae, Pegasidae, Solenostomidae, Syngnathidae]

Dactylopteriformes [Dactylopteridae]

Gobiesociformes [Gobiesocidae (Alabetidae, Cheilobranchidae), Callionymidae, Draconettidae]

Perciformes (Scorpaeniformes, Zoarciformes) [Abyssocottidae, **Acanthuridae**, Acropomatidae, Agonidae, Amarsipidae, **Ammodytidae**, Anabantidae, **Anarhichadidae**, Anoplomatidae, Apistidae, Aploactinidae, Aplodactylidae, Apogonidae, Ariommatidae, Arripidae, Badidae, Banjosidae, Bathyclupeidae, Bathydraconidae, Bathylutichthyidae, Bathymasteridae, **Belontiidae** (Luciocephalidae, Osphronemidae, Polyacanthidae), Bembridae, Blenniidae, Bovichtidae (Bovichthyidae), Bramidae, Butidae, Caesioscorpididae, Callanthiidae, Caracanthidae, **Carangidae**, Caristiidae, Centracanthidae, **Centrarchidae**, Centrogeniidae, Centrolophidae, **Centropomidae**, Cepolidae (Owstoniidae), Chaenopsidae, Chaetodontidae, Champsodontidae, Chandidae (Ambassidae), Channichthyidae (Chaenichthyidae), Channidae, **Cheilodactylidae**, Cheimarrhichthyidae, Chiasmodontidae, Chironemidae, **Cichlidae**, Cirrhitidae, Clinidae (Ophiclinidae, Peronedysidae), Comephoridae, Congiopodidae, **Coryphaenidae**, Cottidae, Creediidae (Limnichthyidae), Cryptacanthodidae, Cyclopteridae, Dactyloscopidae, Dichistiidae (Coracinidae), Dinolestidae, Dinopercidae, Drepanidae, Echeneidae, Eleotrididae, Embiotocidae, Emmelichthyidae, Ephippidae (Chaetodipteridae, Platacidae, Rhinoprenidae), Epigonidae, Enoplosidae, Ereuniidae, **Gempylidae**, **Gerreidae**, **Girellidae**, **Glaucosomatidae**, Gnathanacanthidae, Gobiidae (Amblyopidae, Cerdalidae, Gobioididae, Gobionellidae, Gunnellichthyidae, Kraemeriidae, Microdesmidae, Oxudercidae, Oxymetapontidae, Periophthalmidae, Ptereleotridae, Schindleriidae, Trypauchenidae), Grammatidae, **Haemulidae** (Plectorhynchidae, Pomadasyidae), Harpagiferidae (Artedidraconidae), Helostomatidae, Hemitripteridae, **Hexagrammidae**, Hoplichthyidae, Icosteidae, Inermiidae, **Kuhliidae**, Kurtidae, **Kyphosidae**, Labracoglossidae, **Labridae** (Callyodontidae, Scaridae, Odacidae), Labrisomidae, Lactariidae, **Latidae**, **Latridae**, Leiognathidae, Leptobramidae, Leptoscopidae, **Lethrinidae**, Liparidae, Lobotidae (Coiidae, Datnioididae), Lutjanidae (Caesionidae), **Luvaridae**, Malacanthidae (Branchiostegidae, Latilidae), Menidae, Microcanthidae, Monodactylidae, **Moronidae**, **Mullidae**, Nandidae, Nematistiidae, **Nemipteridae**, Neosebastidae, Nomeidae, Normanichthyidae, **Nototheniidae**, Odontobutidae, Opistognathidae, Oplegnathidae, Ostracoberycidae, Parabembridae, Parascorpididae, Pataecidae, Pempheridae, Pentacerotidae, **Percichthyidae** (Gadopsidae, Nannopercidae, Perciliidae), **Percidae**, Percophidae, Peristediidae, Pholidae, Pholidichthyidae, Pinguipedidae (Parapercidae), **Platycephalidae**, Plectrogeniidae, Plesiopidae (Acanthoclinidae, Notograptidae), **Polynemidae**, **Polyprionidae**, Pomacanthidae, Pomacentridae, **Pomatomidae**, Priacanthidae, Pristeolepidae, Pseudochromidae (Anisochromidae, Congrogadidae, Pseudoplesiopidae), Psychrolutidae, Ptilichthyidae, **Rachycentridae**, Rhamphocottidae, Rhyacichthyidae, Scatophagidae, **Sciaenidae**, **Scombridae**, Scombrolabracidae, Scombropidae, Scorpaenidae (Pteroidae), Scorpididae, Scytalinidae, **Sebastidae** (Sebastolobidae), **Serranidae** (Anthiidae, Niphonidae, Grammistidae, Pseudogrammatidae), Setarchidae, **Siganidae**, **Sillaginidae**, Sinipercidae, **Sparidae**, **Sphyraenidae**, Stichaeidae, **Stromateidae**, Symphysanodontidae, Synanceiidae (Inimicidae, Choridactylidae, Minoidae), **Terapontidae**, Tetragonuridae, Tetrarogidae, Toxotidae, Trachinidae, Trichiuridae, Trichodontidae, Trichonotidae, **Triglidae**, Tripterygiidae, Uranoscopidae (Xenocephalidae), Xenisthmidae, **Xiphiidae** (Istiophoridae), Zanclidae, Zaniolepididae, Zaproridae, Zoarcidae]

Pleuronectiformes [Achiropsettidae, Archiridae, Bothidae, Citharidae, Cynoglossidae, Paralichthyidae, Paralichthodidae, **Pleuronectidae**, Poecilopsettidae, Psettodidae, Rhombosoleidae, Samaridae, Scophthalmidae, **Soleidae**]

Tetraodontiformes [Balistidae, Diodontidae, Molidae, **Monacanthidae**, Ostraciidae (Aracanidae, Ostraciontidae), Triacanthidae, Triacanthodidae, Tetraodontidae (Canthigasteridae), Triodontidae]

and rays). They are readily distinguished from other fishes in having a cartilaginous skeleton with distinctive superficial calcification, called 'prismatic' calcification, and males with pelvic claspers, which are inserted into the female cloaca and oviduct during copulation. Synapomorphies diagnosing the group are listed by Didier (1995, table 1).

The Chimaeriformes (chimeras and allies) is a small order of about 50 or so species of mainly deepsea fishes that have a worldwide distribution. They have soft, scaleless bodies with prominent sensory canals on the head, a prominent spine in front of the first dorsal fin, three pairs of beak-like teeth in the mouth, two in the upper jaw and one in the lower jaw, spiracle absent in adults, and a fleshy operculum over the four gill openings. This means they have only one external opening. Males are distinctive in having, in addition to pelvic claspers found in other chondrichthyans, spiny retractable appendages in front of the pelvic fins and on the head. These are used to clasp or stimulate the female during copulation. Classification and relationships within the order are reviewed by Didier (1995) based on an extensive array of morphological characters.

All extant elasmobranchs belong to the Neoselachii. Characters supporting monophyly of this group are discussed by de Carvalho (1996, p. 39). The composition and interrelationships of the orders of Neoselachii are controversial. The classification and relationships presented herein follows de Carvalho (1996), who also reviews previous hypotheses. The reader is referred to that work for details of character support and named supraordinal taxa. Thus, ten orders are recognized: Heterodontiformes, Orectolobiformes, Carcharhiniformes, Lamniformes, Hexanchiformes, Echinorhiniformes, Squaliformes, Squatiniformes, Pristiophoriformes and Rajiformes. The orders are arranged into two major groups by de Carvalho (1996; see also Shirai 1992, 1996), Galeomorphii (= Galea of Shirai 1996) for the first four orders, and Squalea for the remaining six orders.

The Heterodontiformes (hornsharks or Port Jackson sharks) is a small order of nine species of benthic shark in one family, which live in coastal waters less than 300 m deep. They are readily distinguished from all other extant sharks in having, in combination, an anal fin and spines present at the front of each dorsal fin.

The Orectolobiformes (carpet sharks and allies) is a small but diverse order of about 30 species of mainly coastal, bottom-dwelling sharks. However, it also includes the pelagic, plankton-feeding whale shark (*Rhincodon typus*), the world's largest fish, which attains a length of at least 12 m but can purportedly grow to 18 m and weigh 12 tonnes. Orectolobiforms are distinctive in having a short, broadly arched to nearly straight mouth that is entirely in front of the eyes, and distinctively formed nasal flaps and barbels. Other characters defining the group and supporting internal relationships are discussed by Dingerkus (1986), Compagno (1988), Shirai (1996) and de Carvalho (1996).

The Carcharhiniformes (requiem sharks and allies) is a moderate-sized order of about 230 species of mainly marine sharks found throughout the world. There are several species that enter or are confined to fresh water. The order includes many of the most familiar large predatory sharks, including the tiger shark (*Galeocerdo cuvier*), whaler or requiem sharks (*Carcharhinus*) and hammerhead sharks (*Sphyrna* and *Eusphrya*), as well as many smaller bottom or near-bottom dwelling sharks, such as the catsharks (Scyliorhinidae) and houndsharks (Triakidae). Carcharhiniforms are distinguished from other sharks in having a nictitating lower eyelid or fold, a transparent movable membrane or inner eyelid that protects the eye during feeding and helps keep it clean. Other characters diagnosing the group and relationships within it are discussed by Compagno (1988) and Shirai (1996).

The Lamniformes (mackerel sharks and allies) is a small order of 16 species of coastal marine and oceanic sharks. It is a very diverse group that includes, among others, the bizarre goblin shark (*Mitsukurina owstoni*), the notorious great white shark (*Carcharodon carcharias*), the filter-feeding basking shark (*Cetorhinus maximus*, the world's second largest fish, attaining sizes of at least 10 m), the unusual thresher sharks (Alopidae) and the

filter-feeding megamouth shark (*Megachasma pelagios*). Considering that the latter grows to lengths of over 5 m, it is remarkable that the first specimen was not collected until 1976. Lamniforms are distinguished from other sharks in having a distinctive tooth pattern, and uterine cannibalism. Other characters diagnosing the group are discussed by Compagno (1988). Relationships among lamniform families are controversial (cf. Maisey 1985; Compagno 1990; Shirai 1996; de Carvalho 1996).

The Hexanchiformes (frill shark and cow sharks) is a small order of five species of mainly deepsea sharks found in cold waters throughout the world. They are distinguished from other sharks by the presence of six or seven gill slits and a single, spineless, posteriorly positioned dorsal fin. Other characters supporting monophyly of the group are discussed by de Carvalho (1996, p. 46).

The remaining five squalean orders form a monophyletic group, which is diagnosed by, among other characters, the absence of an anal fin (de Carvalho 1996). The Echinorhiniformes (bramble sharks) is a small order of two species of large (2.6–4 m), bottom or near-bottom dwelling sharks found in deep water throughout tropical and temperate seas. They are characterized by the presence of two relatively small, spineless dorsal fins positioned well behind the pelvic origin, and coarse denticles or enlarged thorns on the skin. Additional characters supporting monophyly of the order are discussed by de Carvalho (1996).

The Squaliformes (dogfishes and relatives) is an order of about 70 species of mainly bottom or near-bottom living sharks found in all the world's oceans. Although some occur in relatively shallow water, most species live in deep water down to depths exceeding 6 km. They vary considerably in morphology, ranging from species 16 cm long to the Greenland shark (*Somniosus microcephalus*), which at 6.4 m is one of the largest sharks. The bizarre, 45-cm long, pelagic cookie-cutter shark (*Isistius brasiliensis*), which feeds by removing a plug of flesh from larger fishes and cetaceans, is also in the order. Many of the deepwater species are bioluminescent. Some squaliforms are important fisheries species, harvested either for food or for a high-quality oil, squalene, which is stored in the liver. Characters supporting monophyly and interrelationships of the order are discussed by de Carvalho (1996).

The Squatiniformes (angelsharks) is an order of about 15 species of benthic sharks found in tropical to temperate seas at depths ranging from a few metres to 1300 m. They are flattened ambush predators with laterally placed gill slits, pectoral fins that are free from the head, and the lower caudal lobe longer than the upper. They are commercially fished for their flesh, oil and leather (Last and Stevens 1994).

The Pristiophoriformes (saw sharks) is an order with seven or so species of mainly marine temperate to tropical sharks found throughout the West Pacific, the southwestern Indian Ocean and the tropical West Atlantic. They are distinctive fishes, though they superficially resemble the rajiform family Pristidae (sawfishes), with a shark-like body, an elongate snout with enlarged tooth-like denticles on each side and a pair of barbels on the underside, and four to six pairs of gill slits placed laterally on the head.

The Rajiformes (= Batoidea; rays and relatives) is a moderately large order with over 450 species of mainly benthic marine fishes found worldwide. There are also some freshwater species. It is a diverse order and many workers advocate dividing it into four or more orders. It includes various bottom or near-bottom species such as the shark-like rhynids (shark rays) and pristids (sawfishes), disc-shaped rajids (skates), and the electric torpedinids, hypnids, narcinids and narkids (collectively called electric rays), as well as the huge pelagic *Mobula* and *Manta* (devil and manta rays; up to 6 m across and weighing over 1300 kg). Members of the order are distinguished from other elasmobranchs in having ventrally positioned gill slits. Characters supporting monophyly of the order (as the superorder Batoidea) are discussed by McEachran et al. (1996). The familial classification of the order is controversial; the one presented here largely follows McEachran et al. (1996), who also review relationships within the order.

The remaining vertebrates are classified in the Osteichthyes, which includes two extant groups,

the Sarcopterygii and Actinopterygii. Characters diagnosing the Osteichthyes include the presence of ossified dermal opercular plate(s) covering the gills laterally, branchiostegal rays, and an interhyal bone (Lauder and Liem 1983). Some authors (such as J.S. Nelson 1994) use the term 'Teleostomi' for the group we here call Osteichthyes, instead using the latter as a term for a phenetic grouping that includes only the bony fishes.

The Sarcopterygii includes three extant fish orders (Ceratodontiformes, Lepidosireniformes and Coelacanthiformes) and the tetrapods. Monophyly of the Sarcopterygii is supported by numerous synapomorphies, particularly associated with the structure of the skull and pectoral girdle (Cloutier and Ahlberg 1996). Relationships of the numerous fossil sarcopterygian fish taxa to each other and to the tetrapods is still in a state of flux, resulting particularly from an imprecise but improving knowledge of fossils and their characters (Cloutier and Ahlberg 1996; Ahlberg and Johanson 1998). However, there is consensus regarding the positions of the living sarcopterygian fish orders relative to each other and to the tetrapods (Fig. 2.2): the Ceratodontiformes and Lepidosireniformes belong to a monophyletic Dipnoi (lungfishes), which is more closely related to the Tetrapoda than it is to the final extant sarcopterygian order, Coelacanthiformes (Cloutier and Ahlberg 1996).

Monophyly of the Dipnoi, a group best known for its 270 or so fossil species, is based mainly on synapomorphies associated with dentition and skull morphology (reviewed by Cloutier and Ahlberg 1996). The Ceratodontiformes (Queensland lungfish) includes a single extant species from fresh waters of southeastern Queensland, Australia. The Lepidosireniformes (South American and African lungfishes) includes five extant freshwater species, one from South America and four from Africa. Unlike the Queensland lungfish, the South American and African lungfishes are able to tolerate environmental desiccation by aestivating, either in a moist burrow (South American lungfish) or a dry cocoon (African lungfishes). A collection of papers on the biology, systematics

and evolution of lungfishes is given in Bemis et al. (1987).

The order Coelacanthiformes (coelacanths) has just two extant species of deepwater reef fishes, one found in the western Indian Ocean off the coast of East Africa, and the other off northern Sulawesi, Indonesia. They are remarkable for the recency of their discovery, highlighting our poor understanding of deep-reef fishes in the Indo-Pacific: the African species (*Latimeria chalumnae*) was discovered in 1938, whereas the Indonesian species (*L. menadoensis*) was discovered 60 years later in 1998 (Erdmann et al. 1998). Forey (1998) provides a monograph on the systematics, evolution and biology of living and fossil coelacanthiforms.

The Actinopterygii (ray-finned fishes) is a huge diverse clade of fishes defined mainly on the basis of synapomorphies involving the morphology of the pelvic and pectoral girdles, scales, and median fin rays, although most are secondarily lost or modified in higher actinopterygians. These characters are reviewed by Lauder and Liem (1983). There has been considerable debate regarding the interrelationships of the basal actinopterygian orders Polypteriformes, Acipenseriformes, Amiiformes and Lepisosteiformes, and their relationships to the Teleostei. For example, the Holostei, a taxon based on the Amiiformes and Lepisosteiformes and various fossil taxa, has been recognized historically. Gardiner et al. (1996) presented morphological evidence to conclude that it is paraphyletic, forming a series of sister groups to the Teleostei as indicated in Fig. 2.2. Conversely, however, they also presented molecular evidence for a monophyletic Holostei. Discussions concerning the relationships of basal actinopterygians and supporting character evidence are provided by Grande and Bemis (1996, 1998) and Gardiner et al. (1996).

The order Polypteriformes (= Cladistia; bichirs or featherfins) consists of about 10 species in a single family of small freshwater fishes from West Africa, although fossils are also known from North Africa and possibly Bolivia. They have an unusual dorsal fin consisting of a number of finlets. These are composed of a single spine to which one or

more soft rays are attached, leading to the common name 'featherfin'. Other characters diagnosing the order are summarized by J.S. Nelson (1994). Some workers have considered the order to belong in the Sarcopterygii, particularly based on their pectoral-fin structure, but current consensus favours a basal position within the Actinopterygii (Gardiner and Schaeffer 1989).

The order Acipenseriformes (sturgeons and paddlefishes) includes 27 species in two families of Northern Hemisphere freshwater and anadromous fishes. They include some of the largest of fishes, with several species purportedly reaching lengths in excess of 7 m, though confirmed records are around 4–5 m. Many acipenseriforms are, or have been, commercially important, harvested either for food (particularly their caviar), or for their swimbladders, which yield isinglass, used for making special glues and historically for clarifying white wines. Well over half the acipenseriform species are now considered endangered. Characters supporting the monophyly and interrelationships of the Acipenseriformes, both fossil and recent, are reviewed by Grande and Bemis (1996). Diversity, biology and conservation of the order are reviewed by Birstein et al. (1997) and Secor et al. (2000).

The Lepisosteiformes (= Ginglymodi; gars) is a small order (seven species in one family) of large freshwater and estuarine but rarely marine fishes from eastern North America, Central America and Cuba. Fossil species are also known from South America, West Africa, Europe and India. They are heavily scaled, predatory fishes with elongate snouts; unlike other fishes with elongate snouts, such as belonids and sturgeons, the nostrils are located near the tip of the snout rather than near the eyes. Characters supporting monophyly of the Lepisosteiformes and relationships among its included species, both fossil and extant, are provided by Wiley (1976).

The Amiiformes (bowfins and allies) includes a single extant species from fresh waters of eastern North America. However, fossil amiiforms are known from freshwater and marine deposits in North America, South America, Eurasia and Africa. A treatise on the systematics, anatomy,

evolution and biogeography of fossil and extant amiids is provided by Grande and Bemis (1998), who also investigate relationships among amiiforms and other halecomorphs.

All remaining fishes belong to a huge taxon called the Teleostei. For most people, teleosts are the typical fishes. Characters supporting monophyly of the Teleostei are reviewed by de Pinna (1996). There are two competing hypotheses of relationships among basal extant teleosts. In one (see Patterson 1998; Fig. 2.2), the Osteoglossomorpha is the sister group of a clade consisting of all other teleosts, of which the Elopomorpha is the basalmost clade. In the other hypothesis (see Arratia 1998), the phylogenetic positions of the Elopomorpha and Osteoglossomorpha are reversed relative to other teleosts.

The Osteoglossomorpha is a small yet diverse group of freshwater fishes, characterized by the primary bite being between the parasphenoid bone on the lower part of the skull and the tongue. Monophyly of the group and interrelationships of included taxa both extant and fossil are reviewed by Li and Wilson (1996). Two extant orders are currently recognized: the Hiodontiformes (mooneyes), a small order with two extant species from fresh waters of North America, although fossil forms are also known from China; and the Osteoglossiformes (bonytongues, Old World knifefishes and elephantfishes), a moderately small order with over 200 species from tropical fresh waters of South America, Africa, Southeast Asia, Australia and New Guinea. Fossil osteoglossiforms are also known from North America. The Osteoglossiformes includes the South American arapaima (*Arapaima gigas*), one of the world's largest freshwater fishes, as well as the elephantfishes (Mormyridae), an African family of weakly electric fishes.

The Elopomorpha is a diverse group of mainly marine fishes that are characterized by an unusual leaf-like larval stage (leptocephalus) and a distinctive sperm morphology. Molecular and morphological characters supporting monophyly of the Elopomorpha and the composition and interrelationships of the four included orders are discussed by Forey et al. (1996). About eight species are

included in the Elopiformes (tarpons and allies), which are mainly marine herring-like fishes, although some enter fresh water. They are found throughout tropical and subtropical regions. The tarpon (*Megalops atlanticus*) is an important gamefish. The Albuliformes (bonefish and allies) includes about six species of mainly marine fishes found throughout tropical and subtropical regions. About 25 species of elongate deepsea fishes make up the Notacanthiformes (halosaurs and spiny eels). The final order, Anguilliformes (eels and gulpers), includes over 700 species of mainly marine (some freshwater) elongate fishes. Relationships and classification within the Anguilliformes are controversial. For example, the deepsea gulpers and allies (suborder Saccopharyngoidei) and the eels (suborder Anguiloidei) are sometimes classified as separate elopomorph orders, but evidence presented by Forey et al. (1996) suggests that some anguiloids are more closely related to saccopharyngoids than they are to other anguilloids (however, see Robins 1997). The familial classification of the Anguilliformes has not been cladistically demonstrated.

The remaining teleosts, collectively termed the Clupeocephala, are diagnosed by synapomorphies associated with the lower jaw and caudal skeleton (Patterson and Rosen 1977, p. 130). The following taxa are usually recognized in the Clupeocephala: Clupeomorpha, Ostariophysi, Protacanthopterygii, Esociformes and Neoteleostei. Relationships among these taxa are controversial. Thus, the relationships presented (Fig. 2.2) are likely to be unstable. We follow Lecointre and Nelson (1996) in recognizing a sister relationship between the Clupeomorpha and the Ostariophysi. This relationship is mainly supported by molecular characters, although these have not been extensively surveyed in basal clupeocephalans. Morphological evidence possibly bearing on the relationship, such as fusion of various bones in the caudal skeleton and morphology of the sensory canal in the skull, is ambiguous. An alternative to this relationship is one in which the Clupeomorpha is the sister group of a clade, called the Euteleostei, made up of ostariophysans and the remaining clupeocephalans (Patterson and Rosen 1977). We follow

Johnson and Patterson (1996) in the composition of the Protacanthopterygii (Salmoniformes and Argentiniformes; see below), and in recognizing a sister relationship between the Esociformes and Neoteleostei. The latter relationship follows Parenti (1986) and is based on the mode of tooth attachment and the presence of acellular bone.

The Clupeomorpha includes a single extant order, Clupeiformes (herrings, anchovies and relatives), of freshwater and coastal marine fishes found globally in temperate to tropical areas. There are about 360 or so extant species included in the order, among them some of the world's most important commercial species. They are typically silvery fishes with a pelvic scute, which is sometimes inconspicuous, usually a median row of scutes (often few in number or absent) along the abdomen in front of and behind the pelvic fins, and primitively with an additional median row of scutes in front of the dorsal fin. Anatomically they are characterized by a distinctive connection between the ear and the swimbladder. Additional characters supporting monophyly of the group are discussed by Lecointre and Nelson (1996), who also summarize internal relationships. The neotenic Southeast Asian freshwater genus *Sundasalanx* was recently placed with the clupeiform family Clupeidae by Siebert (1997). Previously it had been assigned to its own family in the Salmoniformes (Roberts 1981). We have adopted a conservative, though cladistically defensible, familial classification largely following J.S. Nelson (1994) (Table 2.3). Other authors have recognized additional families (see J.S. Nelson 1994 for review).

The Ostariophysi is a huge group of mainly freshwater teleosts that includes nearly 75% of all freshwater fishes; new species continue to be discovered at a rapid rate, particularly in Southeast Asia and the Neotropics (Lundberg et al. 2000). Ostariophysans are distinctive in possessing epidermal alarm substance cells and an alarm reaction. A wounded fish releases alarm substance into the surrounding water, which triggers alarm reactions such as scattering behaviour in adjacent fishes. Interestingly, alarm substance and alarm reaction are lacking in the electrocommunicating gymnoti-

form ostariophysans. Other characters supporting monophyly of the Ostariophysi and relationships among the five included orders are reviewed and discussed by Fink and Fink (1996). The interordinal relationships summarized in Fig. 2.2 follow Fink and Fink. The Gonorynchiformes (= Anotophysi; milkfish and allies) is a small order of about 35 species of Indo-Pacific marine and African freshwater fishes. Reviews of relationships within the Gonorynchiformes are provided by Fink and Fink (1996) and Johnson and Patterson (1997). The remaining ostariophysan orders are grouped into a taxon called the Otophysi. This is one of the best circumscribed higher fish taxa, which is defined in part by a complex of modifications of the anterior vertebrae and associated elements that are collectively called a Weberian apparatus. The carps, loaches and suckers belong to the Cypriniformes, a large order of about 2700 species of freshwater and rarely brackish water fishes found throughout North America, Africa and Eurasia. Interrelationships of the five cypriniform families are reviewed by Fink and Fink (1996). The Cyprinidae is worthy of mention, as it is one of the largest of all fish families (with about 2000 species), and includes such familiar species as *Brachydanio rerio*, the zebra danio or zebrafish, an important subject for genetic and development studies, *Carassius auratus* (the goldfish) and *Cyprinus carpio* (the carp); the latter two species are remarkable in that they have been introduced widely throughout the world's fresh waters. The Characiformes (characins, tetras and allies) is a large order with around 1400 species of Neotropical and African freshwater fishes. Relationships and familial classification of characiforms are controversial (see review by Vari 1998); the familial classification presented here (Table 2.3) follows Buckup (1998). The Siluriformes (catfishes) is a large order of about 2500 species of mainly freshwater and some marine fishes found throughout the tropics and some temperate areas. The familial classification and interrelationships of siluriforms are controversial; the classification in Table 2.3 follows Ferraris and de Pinna (1999), although this latter work does not exactly match the cladistic scheme outlined by de Pinna (1998). About 150

species of compressed or cylindrical eel-like Neotropical fishes make up the Gymnotiformes (American or electric knifefishes), although it is sometimes classified as a suborder of the Siluriformes (e.g. Fink and Fink 1981). These fishes are remarkable in possessing an organ system for producing and receiving electrical impulses; the electric eel (*Electrophorus*) is a famous, though atypical, example. A phylogeny and classification of the order, based on morphological and behavioural characters, including some from electric organ morphology and discharge patterns, is presented by Albert and Campos-da-Paz (1998).

The Protacanthopterygii includes two orders, Argentiniformes and Salmoniformes. There has been considerable debate over the composition of these two orders and relationships of the fishes included in them (reviewed by Johnson and Patterson 1996). Particular controversy has centred around the positions of the Northern Hemisphere osmeroids, the Southern Hemisphere galaxioids and the enigmatic Western Australian salamanderfish (*Lepidogalaxias*). The Protacanthopterygii as defined by Greenwood et al. (1966) was a much larger, poorly defined group that included, in addition to the above, taxa now assigned to the Gonorynchiformes, Esociformes, Stomiiformes, Ateleopodiformes, Aulopiformes, Myctophiformes and Stephanoberyciformes; some of these were placed within the Salmoniformes. Even as currently recognized, character support for the Protacanthopterygii is relatively weak, being based on two non-unique characters associated with the structure of intermuscular bones (Johnson and Patterson 1996, p. 314).

The Salmoniformes, containing the trouts, salmons, smelts and relatives, is a small order of about 175 species of marine, freshwater, anadromous and diadromous fishes. Kottelat (1997) provided justification for the recognition of many additional species of European coregonids and salmonids. They include some of the most important commercial and recreational fisheries species in the world; *Salvelinus fontanalis* (brook trout), *Salmo trutta* (brown trout) and *Onchorhynchus mykiss* (rainbow trout) have been introduced almost the world over for these purposes.

Salmoniforms are distinguished by various synapomorphies, including scales without radii and absence of epipleural bones. Additional characters supporting monophyly and relationships within the order are reviewed by Johnson and Patterson (1996).

The Argentiniformes (deepsea smelts, slickheads and relatives) is a small order of oceanic and deepsea fishes found throughout the world's oceans, and contains about 170 species. They are distinguished by the presence of a crumenal organ, a unique bilaterally paired pouch-like structure derived from the upper part of the posterior two gill arches and the front part of the oesophagus (Greenwood and Rosen 1971). Other characters supporting monophyly and relationships within the order are reviewed by Johnson and Patterson (1996).

The Esociformes is a small order of about 12 species of Northern Hemisphere freshwater fishes. It includes just two families, the Esocidae (pikes) and Umbridae (mudminnows), and is characterized by posteriorly positioned dorsal and anal fins. Characters supporting monophyly of the order are reviewed by Johnson and Patterson (1996). The phylogenetic position of the Esociformes is controversial, and it is often included in the Salmoniformes.

The remaining fish taxa are placed within the Neoteleostei. Characters supporting monophyly of this huge taxon are discussed by Johnson (1992). It can be divided into three taxa, Stomiiformes, Ateleopodiformes and Eurypterygii. Relationships among these three taxa are unresolved (Olney et al. 1993; Fig. 2.2).

The Stomiiformes (dragonfishes and relatives) includes over 320 species of midwater and deepwater oceanic fishes found worldwide. It is a very diverse group, ranging from darkly pigmented, slender-bodied, large-fanged fishes, such as the dragonfishes (Stomiidae), to the silvery, deep-bodied hatchetfishes (Sternoptychidae). The group also includes tiny fishes of the genus *Cyclothone*, delicate plankton dwellers, and considered by some scientists to be the most abundant vertebrate genus in the world (see Miya and Nishida 1996). All but a single species of the order have light

organs, and these have a distinctive structure that distinguishes stomiiforms from all other fishes with light organs. Other characters supporting monophyly of the order, as well as relationships within it, are reviewed by Harold and Weitzman (1996).

About 12 species of bottom-dwelling deepsea fishes comprise the Ateleopodiformes (snotnose or jellynose fishes). They are found worldwide, and are elongate flabby fishes with a weakly ossified skeleton, a long anal fin continuous with the caudal, a short dorsal fin positioned near the head, an inferior mouth and a pronounced jelly-like snout. The largest species grow to nearly 2 m. They have been classified near the lampridiform fishes, but Olney et al. (1993) removed them from the Acanthomorpha.

The Eurypterygii was diagnosed by Johnson (1992) on the basis of several synapomorphies associated with the gill arches, such as the toothplate fused to epibranchial 3, presence of an interoperculoid ligament in the jaws, and fusion of the ventral hemitrich of the medial pelvic ray to the medial pelvic radial. It includes two groups, the Aulopiformes (= Cyclosquamata) and the Ctenosquamata.

There are about 220 species of marine benthic and pelagic fishes in the Aulopiformes (lizardfishes and relatives). They occur worldwide in habitats ranging from coastal areas and estuaries to the abyss. The diversity of their habits is matched in their morphology, ranging from small (10 cm) sand-diving pseudotrichonotids to large (2 m) pelagic alepisaurids (lancetfishes). Despite this diversity, the monophyly of the order is well supported by various synapomorphies, mainly associated with gill-arch morphology. Characters supporting aulopiform monophyly, intrarelationships and familial classification are detailed by Baldwin and Johnson (1996). Historically, aulopiforms have been incorrectly classified with the Myctophiformes.

The myctophiforms and acanthomorphs, the remaining teleosts, are grouped into a large taxon called the Ctenosquamata. Characters supporting monophyly of this group are reviewed by Stiassny (1996).

The Myctophiformes (= Scopelomorpha; lanternfishes and relatives) is a moderate-sized order of about 250 species of small, mainly mesopelagic fishes found in oceanic and coastal waters worldwide. Characters supporting monophyly and interrelationships of the order are discussed by Stiassny (1996).

The Acanthomorpha is an immense grouping of fishes that includes about 60% of all fish species, and thus nearly one-third of all vertebrates, or about 14 700 species. It is diagnosed by a number of osteological features, the most conspicuous of which is the presence of true fin spines (unsegmented, bilaterally fused anterior rays) in the dorsal and anal fins (Johnson and Patterson 1993), though these are secondarily absent in some acanthomorphs. About 20 or so acanthomorph orders are usually recognized at present. We recognize 21 here: Lampridiformes, Polymixiiformes, Percopsiformes, Ophidiiformes, Gadiformes, Batrachoidiformes, Lophiiformes, Stephanoberyciformes, Zeiformes, Beryciformes, Mugiliformes, Atheriniformes, Beloniformes, Cyprinodontiformes, Synbranchiformes, Gasterosteiformes, Dactylopteriformes, Gobiesociformes, Perciformes, Pleuronectiformes and Tetraodontiformes.

Relationships among acanthomorphs are controversial and represent one of the major challenges facing vertebrate systematics. As G.J. Nelson (1989b, p. 328) put it when commenting on our understanding of relationships among teleost fishes: 'recent work has resolved the bush at the bottom [relationships among basal teleosts], but the bush at the top [the acanthomorphs] persists'. The most recent comprehensive treatment of acanthomorphs was by Johnson and Patterson (1993), who on the basis of a large array of morphological characters, particularly those associated with the configuration of the ribs and associated intermuscular bones, suggested a novel scheme of relationships among acanthomorphs. Johnson and Patterson's phylogeny is largely followed here (Fig. 2.2). Among their major conclusions were that, based on mainly osteological characters, such as the first intermuscular bone (epineural) originating at the tip of the transverse process on the first

vertebra, the Atherinomorpha (Atheriniformes, Beloniformes and Cyprinodontiformes), Gasterosteiformes, Mastecembeloidei and Mugilidae (which are both usually classified in the Perciformes), Synbranchiformes, and the genus *Elassoma*, which was previously classified in the North American perciform family Centrarchidae, form a monophyletic group, the Smegmamorpha. Johnson and Patterson's Smegmamorpha has not been cladistically tested, but Parenti and Song (1996) noted that some smegmamorphs (*Elassoma* and mugilids) share a unique derived pattern of pelvic innervation with higher acanthomorphs (such as Perciformes), but that atherinomorphs and gasterosteiforms possess a primitive arrangement. This suggests that the Smegmamorpha is not monophyletic. In contrast, however, Johnson and Springer (1997) have concluded that *Elassoma* is a gasterosteiform.

Johnson and Patterson (1993) also proposed that the Beryciformes of previous authors represents two distinct lineages, the Stephanoberyciformes and the Beryciformes. Moore (1993) agreed that the traditional Beryciformes is not monophyletic, but proposed a radically different arrangement in which the vast majority of the traditional taxa, including Johnson and Patterson's Stephanoberyciformes, were classified in a separate order, the Trachichthyiformes, which is not recognized here.

It is likely that debate over the relationships of acanthomorphs will continue. In addition to the need for testing the relationships and characters proposed by Johnson and Patterson (1993), there is a need to tackle major questions not addressed by these authors. In particular, the monophyly and intrarelationships of the Paracanthopterygii and Perciformes (see below), and the influence of their probable non-monophyly on Johnson and Patterson's scheme of relationships, represent significant challenges for systematic ichthyology (Gill 1996).

The oarfishes and allies form a small order of about 20 species of oceanic fishes called the Lampridiformes. Although very different in biology and form, ranging from the deep-bodied lampridids (opah) to the very elongate regalecids

(oarfishes), lampridiforms are characterized by a unique mouth structure. Other characters supporting monophyly of the order and relationships among the seven families included are discussed by Olney et al. (1993). The oarfish (*Regalecus glesne*) is the longest bony fish, purportedly reaching lengths of up to 17 m, although confirmed reports are to only 8 m. It is almost certainly responsible for early accounts of sea serpents, particularly those that refer to monsters having 'the head of a horse with a flaming red mane' (Norman and Fraser 1937, p. 113).

The Polymixiiformes (beardfishes) is a small order with 10 species in one family, the Polymixiidae (Kotlyar 1996), and occurs on outer continental slopes in tropical and subtropical waters of all major oceans. They are distinctive in having a pair of hyoid barbels, which leads to their common name of beardfishes. Polymixiids have been variously classified in the Beryciformes (J.S. Nelson 1984; Kotlyar 1996) or the superorder Paracanthopterygii (Rosen and Patterson 1969), but they are generally seen now as basal acanthomorphs (Rosen 1985; Stiassny 1986; Johnson and Patterson 1993).

Five acanthomorph orders, the Percopsiformes, Ophidiiformes, Gadiformes, Lophiiformes and Batrachoidiformes, were grouped into a diverse assemblage called the Paracanthopterygii by Patterson and Rosen (1989), who also postulated interordinal relationships. This superorder was originally proposed by Greenwood et al. (1966), but at that time also included several additional taxa. However, even as redefined by Patterson and Rosen and later supported by Murray and Wilson (1999), there is equivocal support for monophyly of the Paracanthopterygii (Gill 1996) and ordinal interrelationships and composition are controversial (cf. Markle 1989; Patterson and Rosen 1989; Murray and Wilson 1999). It is unlikely that paracanthopterygian interrelationships will be resolved without first resolving the question of monophyly of the group.

The Percopsiformes (troutperches, pirate perch and cavefishes and allies) is a small order of North American freshwater fishes, with nine extant species in three families. However, some authors

have concluded that the order is not monophyletic. For example, Rosen (1985; see also Patterson and Rosen 1989) was unable to find characters to diagnose the order but provided synapomorphies, such as a thoracic anus and segmented premaxilla, to link the families Aphredoderidae (pirate perches) and Amblyopsidae (cavefishes) into a monophyletic group, the Aphredoderoidei. More recently, Murray and Wilson (1999) proposed a different arrangement in which aphredoderids were grouped with the Percopsidae (troutperches) and several fossil taxa in the Percopsiformes, and amblyopsids were placed in their own order (Amblyopsiformes) within the Anacanthini, a group that also included gadiforms, ophidiiforms, lophiiforms and batrachoidiforms.

The Ophidiiformes (cusk-eels, pearlfishes and relatives) is a moderately large order with about 370 species in five families of mainly marine coastal to abyssal fishes, although there are a few brackish water or freshwater species (Nielsen et al. 1999). They are characterized by pelvic fins, when present, anteriorly positioned beneath the head and long-based dorsal and anal fins. However, monophyly of the order and its included families is questionable; for example, Patterson and Rosen (1989) concluded that the order is paraphyletic with some ophidiiforms more closely related to a clade consisting of the Gadiformes, Lophiiformes and Batrachoidiformes than they are to other ophidiiforms. Murray and Wilson (1999) also concluded that the order is not monophyletic, but divided the group differently. An alternative view of ophidiiform intrarelationships and classification is discussed by Howes (1992).

With about 500 species (Cohen et al. 1990), the Gadiformes (cods and relatives) is a moderately large order. They are mainly marine fishes found in temperate or deepsea habitats worldwide, and include the commercially important family Gadidae and the large mainly benthopelagic family Macrouridae. A very entertaining history of the Atlantic cod (*Gadus morhua*) fishery is provided by Kurlansky (1997). Monophyly of the Gadiformes is supported by various osteological and larval characters (Markle 1989), but relationships and familial classification within the order are

controversial (e.g. see papers in Cohen 1989). Table 2.3 follows Cohen et al. (1990) with parenthetical families (synonyms) as recognized by Howes (1991), who provided systematic and distributional summaries for each.

The Batrachoidiformes (toadfishes) includes one family and about 70 species of mainly marine coastal fishes, with a few species confined to fresh water. The order has a worldwide distribution. As the scientific and common names suggest (*batrachos* is Greek for frog), they resemble frogs and toads. They have smooth slimy skin with scales absent or small and cycloid, prominent forward-pointing eyes, ambushing predatory tactics, a large flattened head with a broad mouth, and the ability to produce croaking or grunting sounds. Some members of one subfamily (Porichthyinae) have rows of bioluminescent light organs, or photophores, along the sides of their head and body. Members of another subfamily, the Thalassophryninae, possess venomous spines on the dorsal fin and gill cover.

The Lophiiformes (anglerfishes and relatives) is a moderately small, worldwide order with about 300 species of marine shallow to deepsea fishes. Among the taxa included in the order are the commercially important lophiids (monkfishes and goosefishes), the reef-dwelling antennariids (frogfishes), the endangered southern Australian brachionichthyids (handfishes), and the deepsea ceratioids (deepsea anglerfishes). The latter group are distinctive in showing extreme sexual dimorphism; in some, the males are very reduced in size and have denticular teeth for attaching to and parasitizing females (Bertelsen 1984). Monophyly of the Lophiiformes is supported by various synapomorphies; most notably the anterior dorsal-fin ray, if present, is modified into an illicium ('rod and line') and esca ('bait'), devices for attracting prey to the mouth. They also produce eggs 'spawned embedded in a continuous ribbon-like sheath of gelatinous mucous' (Pietsch 1984, p. 320). Additional characters supporting monophyly of the order and interrelationships among its included suborders are discussed by Pietsch (1984) and Pietsch and Grobecker (1987).

The Stephanoberyciformes (pricklefishes,

whalefishes and allies) is an order of about 90 species of small deepsea fishes found throughout the world's oceans. They are distinguished by a number of osteological characters, such as the absence of a subocular shelf on the infraorbital bones and the presence of a uniquely hypertrophied extrascapular bone (Johnson and Patterson 1993). Other characters supporting monophyly and intrarelationships of the group are discussed by Moore (1993). Moore classified the taxon as one of two suborders in the Trachichthyiformes, the other suborder being the Trachichthyoidei; we follow Johnson and Patterson (1993), however, in including the latter in the Beryciformes.

The Zeiformes (dories and allies) is an order with only about 40 species of deep-bodied fishes found throughout the world's oceans, mainly on the continental slope and around seamounts, usually at depths of 600 m or less. They have highly protrusible jaws, and dorsal and anal fins with spines anteriorly and unbranched segmented rays posteriorly. The soft and spinous portions of the dorsal fin are separated by a notch. Monophyly of the order is questionable; in particular, the inclusion of the Caproidae is doubtful (see Johnson and Patterson 1993, p. 592). Rosen (1984) classified zeiforms within the Tetraodontiformes and proposed that the Caproidae is the sister of a clade consisting of all other members of the redefined Tetraodontiformes, which in turn is divisible into two sister taxa, Zeomorphi (traditional Zeiformes minus Caproidae) and Plectognathi (traditional Tetraodontiformes).

There are about 150 species in the Beryciformes (squirrelfishes and allies). These are shallow to deepsea fishes found throughout the world's oceans. Monophyly of the order is supported by the presence of Jakubowski's organ, a uniquely innervated portion of the laterosensory system on the snout (Johnson and Patterson 1993). However, the composition of the order is controversial (see Stephanoberyciformes above). Most members of the order avoid light; the shallow-water representatives, such as the squirrelfishes (Holocentridae) and most flashlight fishes (Anomalopidae), are nocturnal, inhabiting caves or deeper waters during the day. There are several commercially

important species in the order, most notably the orange roughy (*Hoplostethus atlanticus*).

The Mugiliformes (grey mullets) is a small order with one family containing about 80 species of coastal marine and freshwater fishes found throughout the world. They have two widely separated dorsal fins, a small triangular mouth, and pelvic fins positioned well behind the pectoral fins. Many species are commercially important for their flesh and roe.

The following three orders (Atheriniformes, Beloniformes and Cyprinodontiformes) are grouped together in a taxon called the Atherinomorpha. Monophyly of the Atherinomorpha is supported by a range of reproductive and osteological characters (reviewed by Parenti 1993). They are remarkable for their diversity of reproductive modes. Although most are oviparous, viviparity has evolved independently several times. Development is relatively slow, making atherinomorphs ideal subjects for embryological and associated studies. In certain species, such as the 'annual killifishes' of the families Rivulidae and Aplocheilidae, eggs enter diapause during periods of desiccation. The moderately large order Cyprinodontiformes (killifishes and allies) contains about 800 species found throughout freshwater and coastal marine areas of the New World, Africa, southern Europe and Asia. Monophyly of the order and interrelationships of its included genera were investigated by Parenti (1981) and Costa (1998). The Beloniformes (needlefishes and allies), at around 200 species, is a moderately small order of freshwater, coastal marine and oceanic fishes found throughout tropical to temperate areas of the world. It is a relatively diverse order, with such distinctive fishes as needlefishes (Belonidae), slender predators with elongate jaws; flying fishes (Exocoetidae), pelagic fishes with enlarged pectoral and sometimes pelvic fins for gliding flight; and the ricefishes (Adrianichthyidae), small killifish-like species from east Asia. Beloniforms are distinctive in having more fin rays in the lower lobe of the caudal fin than the upper lobe, and the upper jaw fixed and non-protrusible. Additional characters supporting monophyly of the order and relationships within it are discussed by Rosen and Parenti (1981), Collette et al. (1984) and Lovejoy (2000). The Atheriniformes (silversides, rainbowfishes and allies) is a moderately small order of about 300 species of freshwater and coastal marine fishes found throughout tropical to temperate waters of the world. They are small fishes, usually with two dorsal fins with the anterior one having spines, a weak spine at the front of the anal fin, no lateral line and a silvery stripe along the side of the body, which gives the common name. There has been considerable debate about the monophyly and relationships of atheriniform fishes in recent years. This has particularly centred around the various taxa included here in the Melanotaeniidae (Bedotiidae, Pseudomugilidae and Telmatherinidae), Dentatherinidae and Phallostethidae, and their relationships to other atherinomorphs (e.g. Allen 1980; Parenti 1984; Stiassny 1990; Saeed et al. 1994; Dyer and Chernoff 1996; Aarn and Ivantsoff 1997; Aarn et al. 1998). We tentatively follow Dyer and Chernoff (1996) in accepting a monophyletic Atheriniformes. This is in contradiction to Stiassny (1990), who proposed that the Bedotiidae is the sister of a clade consisting of all atherinomorphs. We also follow Dyer and Chernoff (1996) in the familial classification presented (Table 2.3), but anticipate that debate is likely to continue.

The Synbranchiformes (swamp eels and allies) is a small order of about 90 species of freshwater and estuarine fishes found throughout the tropics. They are characterized by an eel-like body shape and a distinctive configuration of the anterior vertebrae (Johnson and Patterson 1993). Two suborders are currently included in the order. The Synbranchoidei (swamp eels) are found throughout the Neotropics, Africa, Asia and the Indo-Australian area, and have highly reduced fins and a single ventral gill opening. Most are burrowers and many are amphibious, able to remain active out of water for up to six months (Liem 1998). The Mastecembeloidei (freshwater spiny eels) are found throughout Asia and Africa, and are also burrowing fishes, though most are fully aquatic. Until recently, the Mastecembeloidei were classified as a perciform suborder.

The Gasterosteiformes (pipefishes, stickle-

backs and allies) is an order of about 280 species of freshwater and coastal marine fishes found throughout the world. It is a morphologically diverse group that includes some of the most bizarre fishes, such as seahorses, seadragons and pipefishes (Syngnathidae), ghost pipefishes (Solenostomidae), shrimpfishes (Centriscidae), sea moths (Pegasidae), paradox fishes (Indostomidae) and sticklebacks (Gasterosteidae). The latter family includes some of the most intensively studied of all fishes, with many works devoted to their biology, ethology and geographical variation (e.g. Bell and Foster 1994). There is consensus neither on the composition of the order nor its internal relationships. Debate has in particular concentrated on whether the sea moths and the paradox fishes should be included in the order (see Johnson and Patterson 1993). As noted above, the Elassomatidae, previously classified in the Perciformes, has also been recently added to the order by Johnson and Springer (1997).

There are about 300 species in the Gobiesociformes (clingfishes, dragonets and allies), a small order of mainly shallow marine fishes, though a few enter fresh water. They are found throughout tropical to temperate areas of the world, and are distinctive in lacking scales and in having the pectoral and pelvic fins connected by a membrane and the infraorbital bone series represented only by a single anterior element, the 'lachrymal'. Other characters diagnosing the order are summarized by Gill (1996). The three families comprising the order have been variously classified in the Perciformes or Paracanthopterygii, and not always associated with each other. For example, many classifications place the gobiesocids in their own order, Gobiesociformes, within or near the Paracanthopterygii, while placing the draconnetids and callionymids in their own perciform suborder, Callionymoidei. Prior to Springer and Fraser (1976), the relationships of the Australian gobiesocid genus *Alabes* were particularly confused. On the basis of its eel-like body form and single ventral gill opening, most previous authors had classified it in its own family in the Synbranchiformes.

The Dactylopteriformes (flying gurnards) is a small order (about seven species in a single family,

Dactylopteridae) of bottom-living fishes, found throughout shallow to moderate-depth waters of warm-temperate to tropical seas. They are distinctive in having a bony head, with a large conspicuous preopercular spine, and enlarged pectoral fins, with the upper five to seven rays short and separated from the remaining rays. Other characters diagnosing the group are discussed by Gill (1890) and Eschmeyer (1997). Most recent authors have classified the Dactylopteridae in the order Scorpaeniformes (here grouped with the Perciformes), which they superficially resemble; dactylopterids bear, in particular, a striking resemblance to the family Triglidae (gurnards). However, we follow Mooi and Gill (1995) in rejecting a close relationship between 'scorpaeniforms' and dactylopteriforms. Imamura (2000) has recently proposed that dactylopterids are nested within the perciform family Malacanthidae.

The Perciformes (perches and allies) is a huge order of fishes found throughout fresh and marine waters of the world. With over 11 000 species, it is by far the largest vertebrate order; it is also one of the most diverse, ranging from tiny gobiids, including the 10-mm *Trimmatom nanus*, the shortest vertebrate, to the 4.5-m pelagic black marlin (*Makaira indica*), and, in particular, includes the vast bulk of the diversity of coastal and reef fishes worldwide (Johnson and Gill 1998). However, such claims are empty, as there is no evidence that perciforms form a monophyletic group. Moreover, not only are there no synapomorphies to unite the order, it is not diagnosable even on the basis of shared primitive characters. Thus the Perciformes has its basis in tradition rather than characters, and it is possible that the nearest relatives of some or many perciform taxa lie elsewhere in the Acanthomorpha. Relationships and classification within the Perciformes are likewise dubious. Although some suborders (e.g. Acanthuroidei, Anabantoidei, Blennioidei, Gobioidei, Notothenioidei, Scombroidei and Stromateoidei) and many families are demonstrably monophyletic, the monophyly of many others, such as the suborders Labroidei and Tachinoidei, is dubious, and the Percoidei, which is the largest suborder with about 3000 species, is effectively a wastebasket for perci-

form taxa that have not been assigned to other sub-orders (Gill and Mooi 1993; Johnson 1993; Mooi and Gill 1995; Mooi and Johnson 1997). We follow Mooi and Gill (1995) in including the Scorpaeniformes in the Perciformes; not only is there no justification for excluding scorpaeniforms, but they share a specialized arrangement of the epaxial musculature with certain traditional perciforms (including *Perca*, type genus of the order) that is not found in other Perciformes. Families listed in Table 2.3 follow Imamura and Shinohara (1998) and Johnson and Gill (1998) with some minor updates.

The Pleuronectiformes (flatfishes), with about 570 species, is a moderately large order of mainly marine fishes found worldwide. The order contains many important commercial fishes, including halibuts, flounders and soles. Pleuronectiforms are characterized by a unique synapomorphy: ontogenetic migration of one eye to the opposite side of the head. Adult flatfishes lie on their blind side, often with the body partially or completely covered with sand or silt; many are well known for their ability to rapidly alter their coloration to match the substrate. Additional characters supporting monophyly of the order and familial relationships within it are discussed by Chapleau (1993) and Cooper and Chapleau (1998). The Pleuronectiformes is sometimes stated as being derived from a perciform or percoid ancestor (e.g. J.S. Nelson 1994). However, there is no character evidence for a relationship with or within perciforms.

The Tetraodontiformes is a moderately large order of about 340 species of mainly marine fishes found throughout tropical to warm-temperate areas of the world. There are also species found in fresh water. It is a relatively diverse order, ranging from the 2.5-cm diamond leatherjacket (*Rudarius excelsus*, Monacanthidae) to the at least 3-m long, 2000-kg ocean sunfish (*Mola mola*, Molidae). Tetraodontiforms are distinctive in having a small slit-like gill opening, and scales usually modified as spines, shields or plates. Additional characters defining the order and relationships within it are variously discussed by Winterbottom (1974), Tyler (1980), Leis (1984) and Tyler and Sorbini (1996).

Tetraodontiforms are often regarded as perciform derivatives and, in particular, are often associated with the perciform suborder Acanthuroidei. However, Rosen (1984) considered and rejected such a relationship in favour of one between the Tetraodontiformes and Zeiformes (see above).

2.4   CONCLUSIONS

Systematic ichthyology is an active and important field. Our understanding of the relationships of fish taxa and their associated classification continues to develop as new characters are investigated and as our understanding of character distribution improves. Our appreciation of the diversity of fishes also continues to develop, as new species are described either through discovery of forms new to science or through refinement of species concepts. Other fields of fisheries biology, such as ecology, biogeography, genetics, development, physiology and conservation, are recognizing that an understanding of the systematics of fishes can often be necessary for clarifying concepts and frequently crucial to forming coherent and complete hypotheses. The rest of the *Handbook* will illustrate the significance of this.

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3 Historical Biogeography of Fishes

R.D. MOOI AND A.C. GILL

3.1 INTRODUCTION

Biogeography is the study of the distribution of life on Earth, or which organisms live where and why. It is fundamental to understanding the evolution of species, the development of diversity, and the composition and interaction of organisms within the environment. At its most basic, biogeography provides distributional and faunal composition data that directly impact fishery biologists and conservationists, where understanding of distribution and species limits will determine resource use. In this chapter we convey a more complete view of biogeography as a dynamic and exciting conceptual science that generates hypotheses and makes testable predictions about the natural world.

Biogeography is divided into two components. Historical biogeography reconstructs the historical influences on the distribution of organisms over long temporal and often large spatial scales, thereby identifying patterns of distribution and processes that might explain them. Ecological biogeography accounts for distribution in terms of the interaction of organisms with their physical and biotic environment over short temporal and small spatial scales, thereby exploring processes that limit distribution and examining patterns of species richness. Myers and Giller (1988) proposed that a complete understanding of distributions of organisms cannot be attained without knowledge of the full spectrum of ecological and historical processes. Their book is an attempt to integrate the two approaches. Brown and Lomolino (1998) provide an excellent university-level text for all aspects of the field (historical and ecological). The chapter by Jones et al. (Chapter 16, this volume) deals with ecological biogeography, but here we focus on the historical aspect of biogeography as a companion to the preceding chapter on the phylogeny of fishes. We briefly outline the concepts and methods before summarizing fish distributions, faunal composition, and historical biogeography of freshwater and marine regions.

3.1.1 What is historical biogeography?

Historical biogeographers rely on accurate distributional information, good taxonomy and well-corroborated phylogenies to identify distribution patterns and form robust hypotheses. Comprehensive knowledge of distributions of most organisms, including fishes, is not generally available. Hence, biogeographic hypotheses are often built on incomplete data. Our understanding of fish diversity and distribution has changed dramatically over the last three decades with increased collecting effort and improved methods. The number of described fish species increases by about 200 per year (Eschmeyer 1998), due to more thorough exploration of poorly known areas or habitats, and recognition of what were formerly widespread 'species' as pairs or complexes of allopatric species with separate evolutionary histories (Gill 1999). In either case, distributional ranges are altered and

patterns change. This emphasizes the importance of continued broad faunal surveys, museum collections and monographic work. Effective biogeographic studies are based on a synthesis of the distributions of several groups or repeating distributional patterns within a taxon; historical biogeography relies on common patterns.

3.2   CONCEPTS AND METHODS

3.2.1   *Past influences on today's approaches*

The history of biogeography is fascinating, and is required background to comprehend present-day polemics. Detailed accounts can be found in Nelson (1978) and Humphries and Parenti (1986, 1999) (cladistic perspective), and Mayr (1982, pp. 439–55) (classical perspective). Brown and Lomolino (1998) provide a balanced account of the development of ecological and historical biogeography. A summary of the last 20 years can be found in Holloway and Hall (1998).

Early biogeography was dominated by the identification of faunal realms, some of which are still recognized. Sclater (1858) divided the Earth into six regions based on the distribution of birds (Fig. 3.1a), later applied to animals in general by Wallace (1876), and Forbes (1856) produced a map dividing the oceans into provinces. Until the late 20th century, the geography of the Earth was considered stable over the evolution of distributions. Hence, biogeographers had no mechanism other than dispersal to explain them. Higher taxa were hypothesized to arise in a centre of origin from which new species disperse as widely as their abilities and suitable environment allow, displacing more primitive species towards peripheral areas. A comprehensive dispersalist summary of freshwater fish distribution was provided by Darlington (1957).

Fish biogeography became dominated by Myers' (1938) concept of primary, secondary and tertiary freshwater fishes, a scheme that identified the degree of salt tolerance of fish taxa, with primary being intolerant. The implication that primary freshwater fishes, being confined to particular watersheds, provided the most important data for biogeography continues to influence taxon choice in fish biogeographic studies.

The modern era of biogeography, beginning about 1960, has as a fundamental principle that Earth and life have evolved together. This concept was bolstered by the simultaneous re-emergence among geologists of support for continental drift and plate tectonic theory. This new, unstable Earth required that the foundations of historical biogeography be examined closely. Through a reinterpretation of Croizat's (1964) work in a phylogenetic framework, Nelson, Rosen (ichthyologists) and Platnick (arachnologist) revolutionized biogeography. They developed a method where cladistic summaries of organismal relationships and their distributions could be compared for congruence with geological area relationships as formulated by geologists; biotic data could provide a direct means to test hypotheses of geohistory (Platnick and Nelson 1978; Nelson and Platnick 1981). Ichthyologists played a leading role in the biogeography revolution (e.g. G. Nelson, Rosen, Patterson, Parenti, Wiley).

3.2.2   *Pattern and process: congruence and the roles of vicariance and dispersal*

Historical biogeography is essentially a search for an explanation of some form of endemic distribution: why is a taxon restricted to a particular geographic area? The field's development can be traced through the philosophical dominance of one of two main processes to explain endemism: vicariance and dispersal. In a vicariance explanation, taxa are endemic because their ancestors originally occurred in an area and their descendants remain. An ancestral population is divided when a barrier appears that individuals cannot negotiate (Fig. 3.2a). Eventually, the two groups differentiate into taxa that are then endemic to either side of the barrier. Here, the barrier is a cause of the disjunction and the barrier and the taxa are of equal age. In a dispersal explanation, endemic taxa arise as the result of the dispersal into new areas by
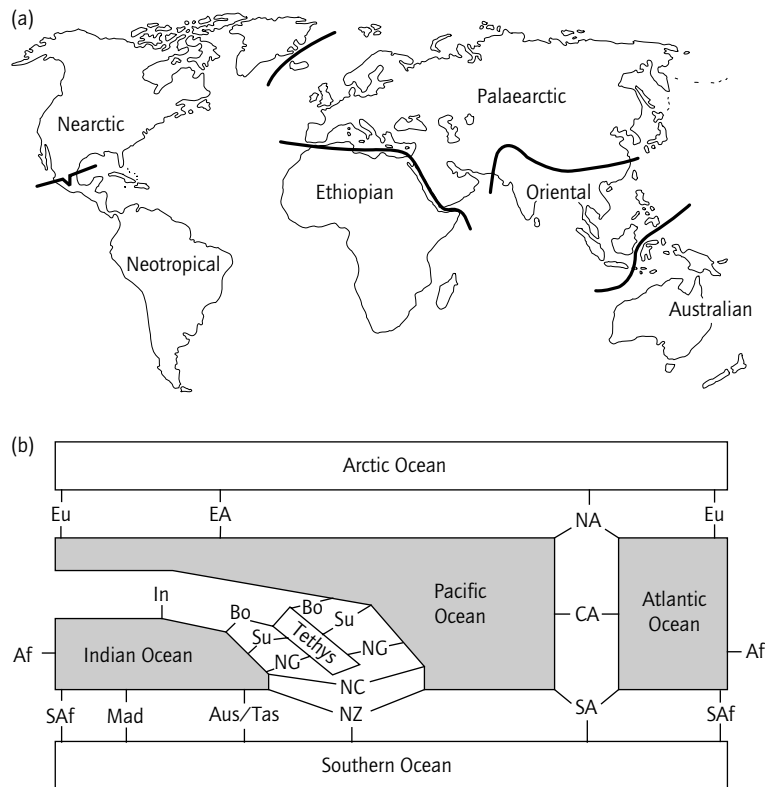
Fig. 3.1 Biogeographic realms. (a) World map showing the limits of Wallace's six terrestrial biogeographic regions, still in use today. (b) A schematic of biogeographic regions based not on landmasses but ocean basins; each continent is inferred to be composite because it is part of the biogeographic regions of the oceans it contacts. The Tethys Sea is a body of water that separated the portions of Borneo, Sulawesi and New Guinea that later came in contact. This Tethys should not be confused with the larger Tethys hypothesized to have separated India from Asia. Af, Africa; Aus, Australia; Bo, Borneo; CA, Central America; EA, East Asia; Eu, Europe; In, India; Mad, Madagascar; NA, North America; NC, New Caledonia; NG, New Guinea; NZ, New Zealand; SA, South America; SAf, South Africa; Su, Sulawesi; Tas, Tasmania. (Source: a, from Nelson and Platnick 1984; reprinted by permission of Carolina Biological Supply Company. b, from Parenti 1991.)

ancestors that originally occurred elsewhere (Fig. 3.2b). In this case, the range of the ancestor is limited by a previously existing barrier that is later crossed by chance dispersal by some members of the population. Over time, surviving colonizers in the new area would evolve into a distinct taxon. Here, the barrier is older than the endemic taxa.

The central theme of modern historical biogeography, discovering congruent patterns of species and area relationships, has often been overshadowed by a focus on the relative importance of the roles of dispersal and vicariance in organismal distribution. Early comments of Platnick and Nelson (1978, p. 8) should have made the process debate unnecessary:

the first question we should ask when confronted with the allopatric distribution of some group is not 'Is this pattern the result of vicariance or dispersal?' but 'Does this pattern correspond to a general pattern of area interconnections (and thus reflect the

Vicariance
(a)

Ancestral population

Barrier appears

A1   A2

Subsequent speciation

Dispersal
(b)

Ancestral population and barrier

Dispersal across barrier

A1   A2

Subsequent speciation
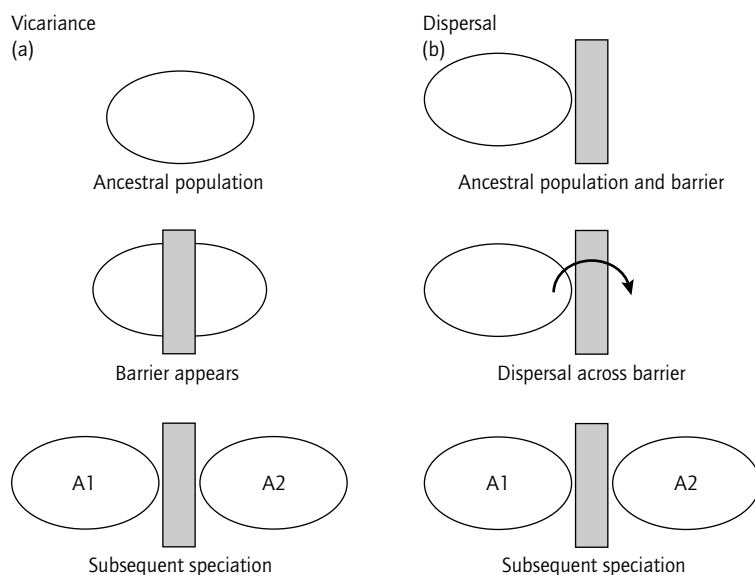
Fig. 3.2 Schematic of a vicariance explanation (a) and a dispersal explanation (b) of the disjunct distribution of two taxa (A1, A2). (Source: modified from Nelson and Platnick 1984; reprinted by permission of Carolina Biological Supply Company.)

history of those areas) or not? . . . After a hypothesized general pattern is corroborated, we may be able to ascribe it to vicariance or dispersal by the use of independent evidence of earth history.

The development of methods to detect patterns of distribution and underlying history has been the focus of theoretical biogeographers for the last 30 years.

3.2.3   Methods

There is no consensus on a preferred method of analysis; some workers have described historical biogeography as a subject looking for a method (Tassy and Deleporte 1999). Most workers agree in principle that such a method should include hypothesis testing based on a phylogenetic systematic framework using area cladograms. Space does not permit even a brief overview of the main methods in historical biogeography. Three that are not discussed further are dispersalism, largely discredited but some principles such as 'centres of origin' continue to be invoked implicitly, and even explicitly (e.g. Bremer 1992; Briggs 1999a,b); par-

simony analysis of endemicity, introduced by Rosen (1984) and critiqued by Humphries (1989, 2000); and panbiogeography, reviewed by Craw et al. (1999), with many critics (e.g. Seberg 1986; Platnick and Nelson 1989; Mayden 1992a). For more detailed discussion of all methods, see Myers and Giller (1988), Morrone and Crisci (1995) and Humphries and Parenti (1999). Humphries (2000) provides a historical perspective on biogeographic methods with a useful reference list. Two common methods used by ichthyologists are introduced below.

Phylogeography

Phylogeography is a new subdiscipline that examines the distribution of gene lineages within and among closely related species (Avise 2000). Usually, genetic divergence is used to estimate relationships among populations and molecular clocks to date lineages, with resulting unrooted similarity networks, called phenograms, used to hypothesize species relationships, directions of dispersal, number of invasions and vicariance (e.g. Bowen and Grant 1997; Bowen et al. 2001).

The recent surge in interest in biogeography is

an important contribution of phylogeography, and as methods are refined it will undoubtedly advance understanding of fish distribution. Others will disagree but we recognize some fundamental issues which have yet to be fully resolved or addressed by practitioners:

1 distributions are often examined on a case-by-case basis, emphasizing process over pattern, often imposing dispersal/centre of origin explanations;

2 use of molecular clocks remains controversial, since it has yet to be established that rates are constant;

3 frequent reliance on similarity matrices for phylogeny reconstruction is problematic (Farris 1981; Murphy and Doyle 1998);

4 the dichotomous branching forced on the data by tree-building algorithms does not reflect the reticulate nature of gene exchange at the population level, hence the trees will not necessarily portray history of the populations or of their distributions.

Despite these caveats, phylogeography has and will contribute important data and hypotheses for historical biogeography. This will be particularly true if it continues to move in the direction outlined by Arbogast and Kenagy (2001) in using more comparative approaches, and more closely complementing or even incorporating cladistic biogeographic methods. Phylogeographic studies of fishes are summarized in Avise (2000, pp. 180–96).

Cladistic biogeography

Cladistic biogeography was introduced by Platnick and Nelson (1978), with complete expositions of the method in Nelson and Platnick (1981) and Nelson and Rosen (1981) and a newer review in Humphries and Parenti (1986, 1999). Cladistic biogeography uses organismal history reconstructed using cladistics (see Gill and Mooi, Chapter 2, this volume) to imply area relationships which reflect geological and ecological history. This method uses implied area relationships to search for general patterns among taxa. General patterns speak to common processes, which are usually sought among vicariant events initiated by geol-

ogical or climatic episodes. However, Page (1989) and Page and Lydeard (1994) have argued that common patterns can be used to explore dispersal.

There are two basic steps in cladistic biogeography, the construction of area cladograms from taxon cladograms and the integration of these into a general area cladogram (Fig. 3.3). Area cladograms are constructed by replacing terminal taxa on an organismal cladogram with their distributions. This is simple if each taxon has a unique distribution, but realistic situations with widespread taxa (those found in more than one area) and redundant distributions (where two taxa occur in the same area) become complicated. Comparing area cladograms is equally problematic. Attempts to address these problems have filled the pages of several journals without consensus.

General area cladograms can be constructed several ways, the common methods being component analysis, three-area statements, reconciled trees and Brook's parsimony analysis (for details see Myers and Giller 1988; Brooks and McClennan 1991; Morrone and Crisci 1995; Humphries and Parenti 1999). A fifth promising method is analysis of paralogy-free subtrees (Nelson and Ladiges 1996).

3.3 DISTRIBUTION, FAUNAL COMPOSITION AND HISTORICAL BIOGEOGRAPHY BY REGION

The number of valid, named species of living fishes is about 25 000, accounting for just over half of vertebrate diversity. The actual number of species is expected to approach 33 000 or more with thorough investigation of relatively unsurveyed localities and habitats (Vari and Malabarba 1998) and reappraisal of widespread species. Hence, specific numbers reported here will quickly become dated, although the general character of the remarks will remain reliable.

Somewhat less than 60% of fishes can be considered marine and almost 40% are principally
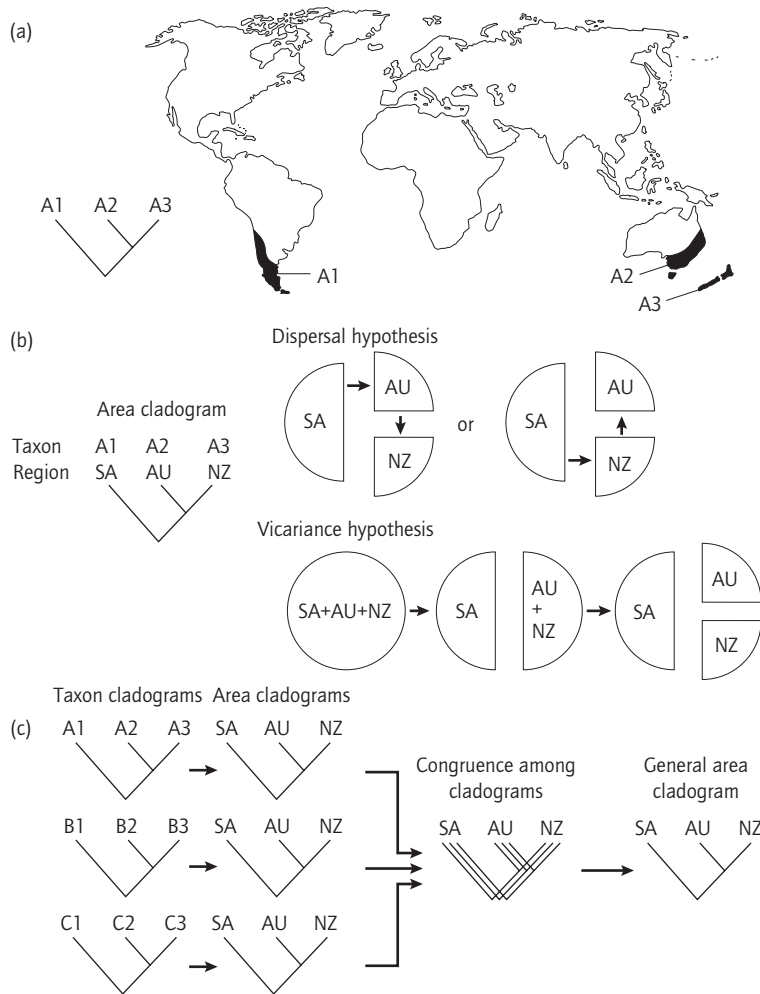
Fig. 3.3 Historical explanations in biogeography. (a) Geographical distribution and cladogram of three species, A1, A2 and A3. (b) The cladogram can be translated into an area cladogram by replacing the taxa with their distributions. Corresponding dispersal and vicariance hypotheses are shown to account for the distribution. Note that even in the simplest instance (no ad hoc extinction or multiple colonization events), there are two dispersal hypotheses that account equally well for the known phylogenetic and area relationships but only one vicariance hypothesis. Even so, neither the dispersal nor vicariance hypothesis can be favoured; a unique example can have a unique distribution and history. (c) A cladistic biogeographic analysis with the construction of area cladograms for several taxonomic groups and derivation of a general area cladogram. A common pattern of history and distribution has been discovered that suggests a general explanation; the vicariance hypothesis of (b) best provides this explanation. (Source: a, modified from Morrone and Crisci 1995, reprinted by permission; b, modified from Brown and Lomolino 1998; c, modified from Morrone and Crisci 1995, reprinted by permission.)

freshwater residents. Less than 1% (about 250 species) normally migrate between fresh and salt water (see Metcalfe et al., Chapter 8, this volume). Many people have remarked on the incredible bias of fish diversity in favour of fresh water, with about 10 000 of 25 000 species found in only 0.01% of the world's water. This is indeed impressive, but it should be remembered that most marine taxa are restricted to a relatively narrow photic zone that hugs coastlines and that marine habitats have been much less thoroughly surveyed than those of fresh water. The little exploration of marine habitats below normal SCUBA depths using submersible or unconventional diving techniques suggests that there remains considerable unsampled diversity, exemplified by the recent discovery of a second species of coelacanth from Sulawesi (Erdmann et al. 1998). Even among deeper-water groups, estimates of diversity are increasing dramatically. For example, the number of species of Indian Ocean grenadiers (Macrouridae; Gadiformes), found at depths of 200–2000 m, has increased from 30 known species in 1987 to 114, and is expected to far exceed that number (Iwamoto and Anderson 1999).

Our brief review of fish distribution is continent-based for freshwater taxa, roughly equivalent to the classic zoogeographic regions of Wallace (1876) (Fig. 3.1a), and ocean-based for marine taxa (Table 3.1). The historical reality of these regions is suspect, with most of them likely to be composite, meaning that they are composed of faunas that have separate evolutionary histories. Other ways of describing zoogeographic regions have been suggested (Fig. 3.1b), but we have no space to describe them.

3.3.1 Freshwater regions

A review of general freshwater fish distribution and faunal composition, along with recent and expected developments, can be found in Lundberg et al. (2000). Each section below provides additional sources for particular regions. With the exceptions of Europe and North America, faunas are generally poorly known. Thorough survey and systematic work is sorely needed if historical biogeog-

Table 3.1 Estimates of numbers of fish species for freshwater and marine biogeographic regions. Freshwater regional names follow Fig. 3.1. Marine estimates are for shorefishes only (defined as fishes occurring from shore to 200 m depth). Almost all counts are underestimates. Note that the historical reality for many of these regions, freshwater and marine, has not been adequately tested.

Freshwater regions	
Nearctic (North America)	1060
Neotropical (South and Central America)	8000
Palaearctic (Europe, excluding former USSR)	360
Ethiopian (Africa)	2850
Oriental (Southeast Asia)	3000
Australian (Australia and New Guinea)	500
Marine regions	
Western North Atlantic	1200
Mediterranean	400
Tropical western Atlantic	1500
Eastern North Pacific	600
Tropical eastern Pacific	750
Tropical Indo-West Pacific	4000
Temperate Indo-Pacific	2100
Antarctica	200

raphy is to make headway. Unfortunately, for many areas it is too late to obtain original distributional data because native faunas have been modified or obliterated through overexploitation, introduction of alien species, or other environmental mismanagement (Stiassny 1996; see Reynolds et al., Chapter 15, Volume 2).

Europe (western Palaearctic)

The Palaearctic has the most depauperate freshwater fauna. About 360 species are known in Europe proper, excluding the former USSR (Kottelat 1997). Almost 36% of the diversity is accounted for by the Cyprinidae, and another 35% by the Salmonidae, Coregonidae and Gobiidae combined. Cobitidae, Petromyzontidae, Clupeidae and Percidae make up an additional 15%, and the remainder is composed of several poorly represented families (Lundberg et al. 2000). Diversity generally

decreases northwards as recently glaciated regions are encountered. Endemic fishes of international interest include carp (*Cyprinus carpio*), goldfish (*Carassius auratus*) and brown trout (*Salmo trutta*), all widely introduced. Lake Baikal of Siberia has a unique fauna derived from the cottoids (about 50 species), with several endemic genera of Cottidae and two endemic families (Abyssocottidae, Comephoridae). The majority of the lake's diversity is found in the Abyssocottidae, with its species generally found below 170 m.

Europe, Asia and North America share many related taxa, including many fishes. These relationships have been explored by several workers. Patterson (1981) compared area cladograms for a variety of taxa (Lepisosteidae, osteoglossomorphs, percopsiforms, Amiidae, Esocoidei, Percidae) and found no strongly supported pattern, presenting nine alternative cladograms among Europe, Asia and eastern and western North America. However, as he pointed out, the fish cladograms available to him were tentative and it would be useful to compare these with cladograms from unrelated groups of vertebrates and invertebrates. Monographic biogeography treatments that investigate European relationships are uncommon, but include the Acipenseriformes (Bemis and Kynard 1997) and Amiidae (Grande and Bemis 1999). The difficulty in tracing biogeographic history of Europe, Asia and North America stems from the complicated geological history of Laurasia, the northern supercontinent sister to Gondwanaland, which began a separate history about 180 Ma. Laurasia's history involves the transient connection of Europe and Asia with North America several times during the Cretaceous and early Tertiary. The intermittent connections explain the general similarity and close relationship of these continental faunas, whereas the transient nature of the connections can provide an explanation for their more recent divergence. Patterns of internal biogeography of the European subcontinent have not been rigorously studied, although glaciation has undoubtedly had an impact. Individual case histories and some comparative work has been done using phylogeographic methods (Bernatchez and Wilson 1998; Bernatchez 2001).

North America and Mexico (Nearctic region)

The Nearctic fauna is extraordinarily well known, with over 1060 species of freshwater fishes described in North America and Mexico (Lundberg et al. 2000). Although relatively few new species are being described, better understanding of ecology and genetics with broader adoption of phylogenetic species concepts will undoubtedly add to the total. About 45% of all species belong to one of two families, the Cyprinidae (true minnows) with at least 305 species and the Percidae (perches and darters) with over 170 species. Other dominant families include the Poeciliidae (75 species), Catastomidae (68 species), Ictaluridae (48 species), Goodeidae (40 species), Fundulidae (37 species), Atherinopsidae (35 species), Centrarchidae (32 species), Cottidae (27 species) and Cichlidae (21 species). Over one-third of all species are found in the Mississippi Basin, with diversity declining away from this central drainage area. The western Great Basin and Colorado River faunas have the lowest diversity but exceedingly high endemism (over 50%). Northern areas are generally depauperate, having been glaciated until only 10,000 years ago. Fishes of particular interest include *Amia calva* (Amiidae; only living member of the family), *Polyodon spathula* (with its only living relative in China), *Hiodon* (two species, the only living hiodontiforms), Goodeidae (endemic; most species have internal fertilization and are euviviparous) and Cyprinodontidae (often restricted to particular springs).

Some of North America's fishes, such as amiids, polyodontids and acipenserids, are part of a relictual fauna, with distributions of related taxa that date back to the complicated history of Laurasia over 100 Ma (Early Cretaceous). Others are likely to postdate any connections with Eurasia, such as Centrarchidae which is endemic. The Atlantic Gulf Coast was submerged from the late Jurassic to the Eocene, so freshwater fishes have been in this region for no longer than about 40 million years.

The North American fauna has been subjected to far more rigorous phylogenetic study than fishes of any other region. Despite this, very few historical biogeographic studies that integrate area clado-

grams from several taxa have been attempted. An exception is Mayden (1989), who examined the cladistic relationships of fishes of the Central Highlands of eastern North America with the aim of examining historical influences on their distributions. He concluded that relationships among the fishes and their distributions were more congruent with a pre-Pleistocene drainage pattern than with the present-day drainages, suggesting a diverse and widespread pre-Pleistocene Central Highlands ichthyofauna. This is important for biogeographic studies in North America and other areas peripherally affected by glacial periods; distributions of organisms are not necessarily dictated by changes wrought by glaciation and subsequent dispersal, but have a more complex and longer history influenced by ancient distribution patterns as well as more modern influences.

However, fish distribution in some parts of North America (and Europe) are undoubtedly a product of postglacial dispersal. Much of Canada and parts of the northern USA are likely to have been scraped clean of fish fauna during the Wisconsinan glacial period. As the ice sheet receded from its maximum coverage (beginning 18 000 years ago), a series of temporary glacial lakes and outlets were formed along its southern edge. The meltwaters drained into larger basins and unglaciated drainages, providing dispersal corridors into the recently deglaciated areas. It is assumed that these colonizing fishes had been restricted to waters of unglaciated areas, called refugia. Five major refugia have been hypothesized for North America, with four southern and one northern (Hocutt and Wiley 1986). Studies of postglacial dispersal concern themselves with identifying the refugial origins of a species and the sequence of glacial waterways used to disperse to their present distributions (e.g. Mandrak and Crossman 1992). Possible dispersal routes have been examined by mapping present-day distributions on palaeogeological maps showing glacial outlets and water bodies (Mandrak and Crossman 1992). Phylogeographic methods have been used to suggest dispersal routes of individual species (Wilson and Hebert 1996) or to examine influence of drainage changes on population structure

(Kreiser et al. 2001). If population evolution of postglacial colonizers proves not to be overly reticulate (having a complex pattern of gene exchange), cladistic biogeography techniques would provide an effective tool to produce area cladograms of species and to search for congruence among species. Congruent area cladograms could be interpreted as common dispersal routes from glacial refugia and might form independent tests of glacial histories provided by geologists.

A summary of Nearctic biogeography can be found in Mayden (1992b), although Hocutt and Wiley (1986) remains an important reference. Patterson (1981) summarized area cladograms among northeastern and northwestern North America with Europe and Asia, but little rigorous study has been undertaken since. Several monographic studies have examined intercontinental biogeography on individual groups (Grande and Bemis 1991, Polyodontidae; Grande and Bemis 1999, Amiidae), although others have been of broader taxonomic scope (Bemis and Kynard 1997, Acipenseriformes).

Africa (Ethiopian region)

Africa is estimated to have 2850 species of freshwater fishes (Lundberg et al. 2000), although this is undoubtedly a considerable underestimate. Unlike North American and European faunas, new taxa continue to be described at high rates and distributions are poorly known. Leveque (1997) provided a recent review of African ichthyofaunal provinces. Diversity is highest in tropical areas, as northern and southern regions are quite arid. About two-thirds of the diversity is found in seven families: Cyprinidae (475 species); Characidae and Citharinidae (208 species); Clariidae, Clarioteidae and Mochokidae (345 species); and Cichlidae (conservatively 870 species). Fishes of particular interest include several unusual groups such as the Polypteridae (bichirs), *Protopterus* (lungfish), *Pantodon* (butterflyfish), Mormyridae (elephantfishes) and *Malapterurus* (electric catfishes). The diversity of cichlids has attracted most attention, with estimates for the three large East African lakes (Tanganyika, Malawi and Victoria) ranging

over 1000 species (Stiassny and Meyer 1999). These species flocks exhibit low genetic differentiation but highly diversified morphologies that evolved independently and rapidly in each lake (Fryer and Iles 1972; Meyer 1993). Lake Victoria was probably completely dry as recently as 12 000 years ago (Johnson et al. 1996), yet now supports almost 400 endemic cichlid species, and the small adjoining Lake Nabugabo is only 4000 years old but has five of seven *Haplochromis* endemic (Greenwood 1981). Lake Tanganyika, which is a deep rift lake, is believed to have had a succession of lowered lake levels of over 600 m, providing repeated isolation events and the opportunity for speciation. Sympatric speciation via sexual selection is also likely to have played a role (Seehausen et al. 1999).

With the extremely high level of endemism in African waters, approaching 100% at the species level and more than 40% at the family level, one would expect the relationships of the region to Europe, Asia and South America to be relatively transparent. However, phylogenetic work on African groups is sparse. The recognition of an African–South American biogeographic link is not new (Eigenmann 1909; Regan 1922), but it has been given considerable recent attention (e.g. Lundberg 1993; Grande and Bemis 1999). Many investigations take a simple view of area relations, with large complex geological entities assumed to behave as single units; essentially two-area cladograms are examined, with Africa and South America as the areas. Indeed, molecular phylogenies of cichlids (Farias et al. 1999) and aplocheiloids (killifish) (Murphy and Collins 1997) have hypothesized monophyletic African and South American sister clades. These patterns implicate rifting of Africa and South America from remaining Gondwanaland some 160 Ma, and the vicariance of Africa and South America beginning about 125 Ma. However, it would be surprising if each of these continents were not composites and their relationships not more complicated. Work by Ortí and Meyer (1997) and Buckup (1998) on characiforms supports this. Unlike cichlids and killifishes, neither South American nor African characiforms are monophyletic in and of themselves, but instead form a series of clades that often have separate elements in portions of both continents.

Special mention should be made of the island of Madagascar. Once considered to have a depauperate fauna, a new accounting of Madagascan fish species, including the discovery of several new taxa yet to be described, has put Madagascar more in line with other areas of similar size (Sparks and Stiassny, in press). The total number of freshwater species is estimated to be 127, with 76 of these endemic. Dominant families are the Gobiidae (26 species), Cichlidae (25 species) and Bedotiidae (23 species). Madagascar possesses a high number of endemic taxa, many of which appear to occupy basal phylogenetic positions (Stiassny and Raminosa 1994). Despite its geographic proximity to Africa, a preponderance of links with India and Sri Lanka have been suggested. Its cichlids (*Paratilapia*, *Ptychochromis*), along with south Asian genera (Etroplinae), appear to be basal to the African and South/Central American species (Stiassny 1991; Farias et al. 1999). The Madagascan *Pachypanchax* (Aplocheilidae) and *Ancharias* (Ariidae) are also considered basal taxa of their respective families. Recent work on cichlids (Farias et al. 1999) and aplocheiloids (Murphy and Collins 1997) suggested that Madagascan and Indian taxa form a monophyletic sister group to an African and South American clade. These patterns are congruent with the rifting of the African and South American landmass from remaining Gondwanaland about 160 Ma. The Madagascan genera *Bedotia* and *Rheocles* are perhaps most closely related to eastern Australian melanotaeniids (Aarn and Ivantsoff 1997), a pattern reflected by possible close affinities of the Madagascan eleotridid *Ratsirakea* and Australian/New Guinean *Mogurnda*. These relationships and distributions are congruent with the subsequent separation of Madagascar and India from the Antarctica–Australian landmass about 130 Ma. Hence, the freshwater fauna of Madagascar has a very ancient history.

South and Central America (Neotropical region)

The Neotropical region is estimated to have up-

wards of 8000 species (Vari and Malabarba 1998). The Amazon basin alone is home to well over 1000 species. The Neotropical fauna is dominated by five major groups: Siluriformes (catfishes, over 1400 species), Characiformes (characid-like fishes, about 1800 species), Gymnotiformes (New World knifefishes, about 100 species), Cyprinodontiformes (rivulines, livebearers and others, about 375 species) and Cichlidae (about 450 species) (Lundberg et al. 2000). Fishes of particular note are far too numerous to list exhaustively, but include *Arapaima gigas* (pirarucú, Osteoglossidae, the largest scaled freshwater fish, reaching 2.5 m), some of the smallest and largest catfishes in the world (*Micromyzon akamai*, Aspredinidae, 12 mm; *Brachyplatystoma*, Pimelodidae, 3 m), the electric 'eel' (*Electrophorus*, Gymnotidae, capable of producing up to 650 V), and parasitic catfishes or candirús (Trichomycteridae, famous for reported entry into the urethra of humans).

Central America shares the majority of its faunal elements with northern South America. Poeciliids and cichlids are especially well represented in the 350 species known from the region, with characids and siluriforms abundant only in the south. The best-known fauna is that of Costa Rica through the efforts of Bussing (1998), with 135 species recorded. The most diverse freshwater families in Costa Rica are Characidae (17), Poeciliidae (20), Cichlidae (24) and Eleotrididae (16). Central America can boast the most well-known application of modern biogeographic methods, that of Rosen (1978, 1979) and his hypothesis of congruent taxon and area cladograms for the middle American poeciliid genera *Heterandria* and *Xiphophorus* (live bearers). This study was the initial trial of Platnick and Nelson's (1978) cladistic biogeography and remains one of the convincing examples of geographic congruence for fishes. Nelson and Ladiges (1996) and Humphries and Parenti (1986, 1999) provide detailed reanalysis of Rosen's data. Although Myers (1938) is associated with dispersal scenarios because of Darlington's (1957) reliance on his ecological fish divisions, he was open-minded on distribution processes, and proposed 'continental drift to be the ultimate answer' (Myers 1966, p. 772) for origin of

South American freshwater fauna. Significant tests of this have yet to be provided.

Biogeographic patterns of South American freshwater fishes are summarized in Vari and Malabarba (1998). Available area cladograms are often contradictory or only partially congruent, although this should not be surprising given the relatively few studies available and the complex geohistory of the region. The best example involves common patterns among several groups involving northwestern South America and nearby Central America separated by the Andean Cordilleras. Malabarba (1998) with characiforms and Armbruster (1998) with loricariids provided area cladograms that suggested stream capture of the Río Tietê (Paraná drainage) by the Río Paraíba in southeastern Brazil during the early Tertiary. There are also repeated patterns of freshwater invasion by marine groups before the completion of the Panamanian Isthmus (Nelson 1984, Engraulidae; Lovejoy 1996, Lovejoy et al. 1998, Potamotrygonidae), placing in doubt the oft-cited Pacific origin suggested by Brooks et al. (1981; see Lovejoy 1997). Lovejoy and Collette (2001) used a phylogeny of the Belonidae to suggest four independent entries of fresh water by marine ancestors. In contrast, Dyer (1998) provided an example of secondary marine invasion by a freshwater group, sorgentinin silversides; the general assumption of marine to freshwater invasion clearly requires phylogenetic testing. These are only a few examples showing the potential for the explanation of diversity and faunal composition of South American fresh waters using historical biogeography. This is an incredibly complex geological system, as shown by Lundberg et al. (1998), that provides an almost endless source of possible processes and many of the histories will be difficult to tease out. Careful systematic work and the search for congruent historical and distributional patterns provide the best hope for uncovering the processes by which the unparalleled Neotropical diversity evolved.

Relationships of South America to Africa and to Australia are briefly explored under those sections. Although with somewhat different topologies, Ortí and Meyer (1997) and Buckup (1998) came to

the conclusion that characiforms had diversified into many of the currently recognized taxa long before the separation of South America and Africa about 125 Ma. Similarly for siluriforms, de Pinna (1998) has shown that South American taxa are interspersed in monophyletic clades that include African and sometimes Asian taxa. Much of siluriform diversity existed before the final break-up of Gondwanaland.

Southern Asia (Oriental region)

Numbers of freshwater species in the Oriental region range upwards of 3000, but this is likely an underestimate. Although this has been considered a single biogeographic unit for almost 150 years, differences in levels of endemism, diversity and faunal composition vary widely from one area to another. Overall, dominant families are the Cyprinidae (over 1000 species), Balitoridae (300 species), Cobitidae (100 species), Bagridae (100 species) and Gobiidae (300 species). The continental and peninsular portions of the region follow this faunal composition quite closely, but the islands (e.g. Philippines, Sulawesi) lose most if not all of the primary freshwater groups and are dominated by the Gobiidae (Lundberg et al. 2000). Many of the faunas are poorly known, with India and China in particular need of modern systematic work. Noteworthy fishes include the Adrianichthyinae, which carry eggs with the pelvic fins and whose distribution provides some evidence of the geologically composite nature of Sulawesi to which it is endemic, and extensive cave fish fauna of the karst regions of China, Laos, Vietnam, Thailand, Malaysia and India.

Biogeographic studies of fishes of the region are sparse. India's drift northwards through the Indian Ocean and its effect on its freshwater taxa has been debated in the literature (e.g. Briggs 1990; Patterson and Owen 1991). The boundary between the traditional Oriental and Australian regions for terrestrial organisms has been the topic of considerable debate, with a plethora of boundaries including and then excluding various islands of the Indonesian archipelago with one or the other region (Simpson 1977). Wallace's Line has been afforded favoured status among at least seven such lines, even for some marine fishes (Woodland 1986) and perhaps invertebrates (Barber et al. 2000). Although a zone of biotic contact exists in the Indonesian area, Parenti (1991, p. 143) logically noted that if we cannot place a biogeographic boundary to the west or east of a particular island, perhaps the line should be drawn through it. Acknowledging that the composite geological nature of several of the region's islands (Sulawesi, Borneo, New Guinea) is reflected by the evolutionary history of their taxa will greatly enhance our understanding of the biogeography of Wallace (see Fig. 3.1a). Parenti (1991, 1996) provided area cladograms based on phallostethids and sicydiine gobiids and compared these to those derived from bats and insects. These and other studies (Michaux 1991, 1996; Parenti 1998) emphasize the composite nature of many of the Oriental islands and the complex geological history underlying the animal distributions. Hall and Holloway (1998) present several papers outlining details of geology that will undoubtedly provide much fodder for biogeographic processes in the Southeast Asian region. Although they provide no fish examples, the terrestrial faunal studies offer phylogenetic patterns to which future fish cladograms and distributions can be compared.

Australia and New Guinea (Australian region)

The Australian region has well over 500 freshwater fish species. Australia is estimated to have 215 freshwater fish species, with 30 of these having been described in the last 10 years; the most recent review is by Allen (1989). New Guinea has 320 listed species (Allen 1991) with subsequent research boosting this to 350. These two major areas share about 50 species (Lundberg et al. 2000). The apparent lack of diversity is due in part to substantial arid areas in Australia, but perhaps more to taxonomic artefact. Many species regarded as widespread are very likely to comprise several unrecognized species with more restricted distributions. As an extreme example, the melanotaeniid *Melanotaenia trifasciata* has been divided into some 35 geographic forms, each with highly re-

stricted allopatric distributions, suggesting that the number of phylogenetically distinct species has been grossly underestimated for this and other species in the family. Similar though less dramatic 'geographic variation' has been reported for members of at least nine additional families. Dominant Australian taxa include the Eleotrididae and Gobiidae (over 50 species), superfamily Galaxioidea, Melanotaeniidae, Terapontidae and Percichthyidae (each with over 20 species), and Plotosidae and Atherinidae (each with over 15 species). Distinctive components of the fauna include *Neoceratodus forsteri* (Queensland lungfish), *Scleropages* (a bonytongue) and *Lepidogalaxias salamandroides* (salamanderfish), whose relationships have been greatly debated (Williams 1997) and whose behaviour includes aestivation (Berra and Pusey 1997). Unmack (1999, 2001) divided Australia into several provinces using similarity indices, although the historical reality of these needs to be tested by phylogenetic patterns not yet available. The highest endemism occurs away from the eastern and northeastern coastal drainages. In New Guinea, the most diverse families are the Eleotrididae and Gobiidae (about 115 species), Melanotaeniidae (about 70 species), Ariidae (21 species), and Terapontidae, Chandidae and Plotosidae (each with about 15 species). Melanotaeniids, the rainbowfishes, are well known in the aquarium trade.

Australia and New Guinea have been associated throughout much of their history, made evident by the shared taxa of these areas. As recently as 6000 years ago during the last glacial sea-level drop, the two were connected via the sea floor of the shallow Arafura Sea and Torres Strait. Streams of southern New Guinea and adjacent northern Australia were confluent at this time. However, Unmack (1999, 2001) suggested that freshwater faunal exchanges were unlikely during this time due to intervening brackish water and that the most recent viable freshwater connections likely date back to the late Miocene. Unfortunately, phylogenetic studies are scarce for most freshwater fishes of the region, making historical biogeographic hypotheses sketchy. Many discussions assume that the freshwater biota resulted from multiple invasions by marine taxa. An extreme, and unfounded, example is presented in Aarn and Ivantsoff (1997) who suggested that the Melanotaeniidae, based on the 'disparate distribution of the family' in Madagascar, eastern Indonesia, New Guinea and Australia, arose recently from a cosmopolitan marine atheriniform. Not only would this marine ancestor have had to have gone extinct, as there are no basal marine melanotaeniids, but their hypothesis intimates several independent marine invasions by the ancestor to explain the allopatric distribution of the family. A Gondwanan origin for this group would make a more parsimonious hypothesis (see section on Africa). It has long been acknowledged that the Australian–New Guinean fauna has a Gondwanan component, particularly through the relationships of galaxioids, *Neoceratodus* and the osteoglossid *Scleropages*. Other taxa, such as the Percichthyidae and Terapontidae, also appear to have Gondwanan distributions (Lundberg et al. 2000). Until more phylogenies are available, the general pattern will remain elusive and conclusions regarding biogeographic relationships unwarranted.

3.3.2 Marine regions

Marine regions are somewhat more fluid and their relationships more obscure than freshwater regions. Although some workers have tried to place specific boundaries on marine areas, we provide only very general geographic regions because so little work has been done to determine their historical reality. Taxonomy, distribution and phylogenies are more poorly known for marine groups than for freshwater groups. The following is only a brief introduction to some of the marine areas and is in no way exhaustive or presented as a definitive treatment. For example, we refer to McEachran and Fechhelm (1998) for the Gulf of Mexico. The emphasis here is on shorefishes which are those occurring from shore to a depth of 200 m; most pelagic groups are widely distributed, sometimes circumglobal, and deepsea families are usually poorly known both taxonomically and biogeographically (but see Miya and Nishida 1997 for an interesting example). Nelson (1986) discussed

problems and prospects for historical biogeography of pelagic fishes.

The application of historical biogeographic techniques to marine fishes was slow to materialize. Myers' (1938) observation that primary freshwater fishes are confined to particular drainage basins and will closely mirror geological history held the implication that marine fishes would have little to say concerning biogeography because of their capacity for dispersal. This dissuaded biogeographers from seriously examining marine fish distributions for almost half a century. Myers' notion of relative value of fishes for biogeography continues to have an impact on the choice of study taxa, despite the fact that taxon phylogeny and endemism are the final arbiters of biogeographical information content rather than little-known physiological tolerances and implied dispersal limitations (e.g. Dyer 1998, p. 528). With the identification of marine zoogeographic regions by Briggs (1974) and the recognition of areas with high endemism, wide dispersal could not be common to all groups. Springer's (1982) study of the biogeography of shorefishes on the Pacific tectonic plate, the first major work on marine fishes to espouse a modern approach, was the springboard that launched analytical marine fish biogeography. Hence, analytical marine biogeography is a very new science. Only over the last 15–20 years have the relatively restricted distributions of several groups, for example blennioids and pseudochromids, overcome some of the early hesitancy and lent credibility to the role of marine shorefishes in biogeographic studies.

Since Springer (1982), several authors have applied historical biogeographic interpretations to the distribution of marine shorefishes (e.g. White 1986, atherinids; Winterbottom 1986, pseudochromids; Springer 1988, *Ecsenius*, blenniids; Williams 1988, *Cirripectes*, blenniids; Springer and Williams 1994, *Istiblennius*, blenniids; Mooi 1995, plesiopids) and even to deep shelf forms (Harold 1998, sternoptychids). As in freshwater studies, rigorous methods for comparison among cladograms has not generally been undertaken (see Lovejoy 1997 for an exception), but the search for common distribution patterns has been useful in generating testable hypotheses for several regions (e.g. Nelson 1984 and White 1986, amphitropical/isthmian; Springer and Williams 1990, Indo-Pacific). Pattern congruence and phylogeny will also undoubtedly help to solve the vexing problem of antitropical distributions, where sister species or populations are found in higher northern and southern latitudes separated by a broad equatorial distributional gap.

Some recent ecological work supports the biogeographic evidence for restricted distributions and separate histories of some marine fishes. Swearer et al. (1999) and Jones et al. (1999) have shown, with different experimental protocols, that despite the production of planktonic eggs and larvae, offspring of some species remain close to their native shores or eventually settle back on to the reefs of their parents. The long-distance dispersal assumed for marine fishes is not universal, and populations of even presently assumed widespread species are unlikely to be panmictic (Cowen et al. 2000; Pogson et al. 2001). Consistent with these studies, Gill (1999) has questioned marine fish species concepts and the reality of widespread species, suggesting that many of these are likely to comprise two or more allopatric cryptic species each with more restricted distributions. These observations have clear taxonomic, systematic, biogeographic and conservation implications.

North Atlantic and Mediterranean

There are about 1200 species along the North American Atlantic coast including the northern Gulf of Mexico. Dominant families are the Serranidae and Gobiidae each with well over 50 species, although several families are represented by over 20 species (including Ophichthyidae, Muraenidae, Gadidae, Syngnathidae, Carangidae, Haemulidae, Sciaenidae, Scorpaenidae). It is estimated that about 600 species occur in the Mediterranean, with almost two-thirds of these considered shorefishes.

Humphries and Parenti (1999) use data from merluciids (hakes), *Lophius* (monkfishes) and two sponge groups to produce an area cladogram for

Fig. 3.4 Cladistic biogeographic analysis of real organisms from the North Atlantic. (a) Areas of endemism for chalinid sponges that are similar to those of northern species of the monkfish genus *Lophius*. 1, Arctic; 2, Boreal; 3, Mediterranean; 4, southeastern North Atlantic; 5, western North Atlantic; 6, Caribbean. (b) Taxa and area cladogram of northern *Lophius* species, with a line drawing of a typical member of the genus. Areas are numbered as in (a). (c) General area cladogram calculated from the combined data of *Lophius* and two chalinid sponge groups. (Source: after Humphries and Parenti 1999, reproduced by permission of Oxford University Press. *Lophius* outline from Nelson 1994; reproduced by permission of John Wiley & Sons, Inc.)
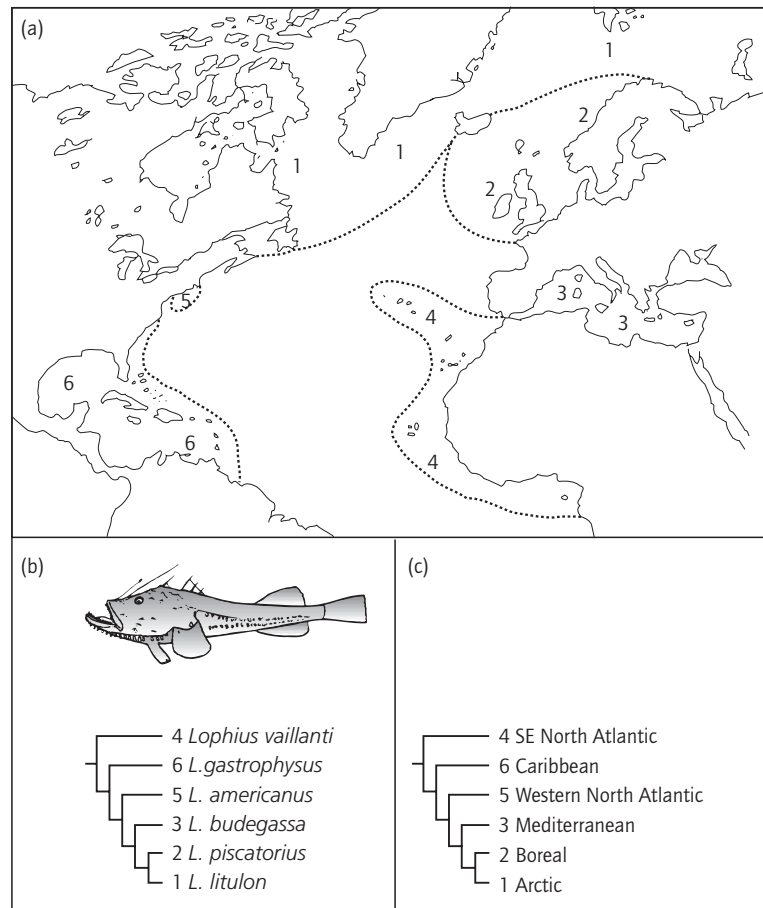
the northern and tropical Atlantic (Fig. 3.4). They found that the Mediterranean shared a more recent faunal history with the Arctic and Boreal regions than with any of the more tropical areas. The western North Atlantic (eastern USA), then Caribbean and finally the southeastern North Atlantic (western Africa, Azores, Canaries and Cape Verde Islands) are hypothesized as sequential outgroups to the Mediterranean and Arctic regions. Too few corroborative patterns have been suggested to imply plausible scenarios.

Tropical western Atlantic

There are no accurate estimates of numbers of species for the tropical western Atlantic. This is due in part to differences in defining the area, with early workers considering it a single area and later workers dividing it into the Caribbean including coastal tropical Mexico and Central and South America, a West Indian region covering the Greater and Lesser Antilles, and a Brazilian region. The latter has recently received attention resulting in recognition of additional endemic species and better understanding of its faunal history (Joyeux et al. 2001). Böhlke and Chaplin (1993) listed almost 600 species for the Bahamas. A comprehensive recent accounting for Bermuda (Smith-Vaniz et al. 1999) lists 365 nearshore species for what is recognized to be a relatively depauperate

fauna. Smith-Vaniz et al. (1999) also compares the composition of the Bermudan fauna with that of the Bahamas, Florida Keys and Carolinian Bight, comparing a total of over 800 species among these areas, which extend as far north as Cape Hatteras. However, this comparison was among selected families, so a total would be substantially higher for these areas and the Caribbean as a whole, perhaps as high as the 1500 species estimated by Lieske and Myers (1996). Dominant families with 30 or more species each include the Gobiidae, Serranidae, Labrisomidae, Apogonidae and Sciaenidae, although relatively strong representation is found in the Labridae, Syngnathidae, Carangidae, Chaenopsidae and others with about 20 species each. Endemic families of the western Atlantic include the Grammatidae and Inermiidae, but there is considerable endemism within most represented shorefish families. The Caribbean has received substantial attention by historical biogeographers. Rosen (1976, 1985) provides plate tectonic models to explain biotic distributions. Rauchenberger (1989) and Lydeard et al. (1995) used freshwater fishes to hypothesize area relationships, but marine groups have played very little part in examining Caribbean biogeography. Page and Lydeard (1994) summarize the requirements for advancing Caribbean biogeography. That the Caribbean and tropical eastern Pacific have a close biological connection with many amphi-American taxa has been known for well over a century. Briggs (1974, 1995) and Rosen (1976) provide summaries from differing perspectives on this connection. Fishes have provided numerous examples of amphi-American relationships including Atherinopsidae, Dactyloscopidae, Labrisomidae, Chaenopsidae and Centropomidae (*sensu* Mooi and Gill 1995), plus many others. Sister species and sister taxa at various supraspecific levels are known to be separated by the Isthmus of Panama. Kocher and Stepien (1997) provide some molecular examples, whereas Nelson (1984), White (1986) and Hastings and Springer (1994) provide morphological studies showing relationships among amphi-American and pan-Isthmian taxa.

Eastern North Pacific

The temperate to boreal areas of the North Pacific have a surprisingly diverse shorefish fauna. Along the North American coast alone, from California to Alaska, there are over 600 species in the top 200 m. The dominant families are in the Scorpaenoidei (*sensu* Mooi and Gill 1995), with scorpaenids (70 species), cottids (85 species) and agonids (over 20 species) making up most of these. The liparidids comprise about 15 species in water less than 200 m deep, the remaining 35 species being found at depths between 200 and 7600 m. Other dominant families of the eastern North Pacific include the zoarcids (40–50 species) although most are found below 50 m, stichaeids (25 species), pleuronectids (22 species) and embiotocids (20 species). The latter family is endemic to the North Pacific and is unusual in having internal fertilization and true viviparity. Various other taxa suggest a close relationship for North Pacific taxa. For example, additional North Pacific endemic families include the gasterosteiform aulorhynchids, the scorpaenoid Anoplopomatidae (two species) and Hexagrammidae (over a dozen species). Other North Pacific taxa of note are, of course, the Salmonidae with about 11 species, the most famous of which are anadromous and die after impressive migrations upriver to spawn, and the Pacific halibut (*Hippoglossus stenolepis*) growing to over 2.5 m and 360 kg.

Tropical eastern Pacific

There are about 750 species in the tropical eastern Pacific, which includes the Gulf of California to Ecuador and offshore islands, and over 80% of these are endemic (Allen and Robertson 1994). The dominant families are the Sciaenidae (80 species) and Gobiidae (80 species), with blennioids also forming a substantial part of the shorefish fauna with Chaenopsidae (30 species), Dactyloscopidae (24 species) and Labrisomidae (25 species). Other well-represented families include the Serranidae, Haemulidae and Labridae, all of which have about 30 species, and Ariidae, Muraenidae and Pomacentridae that each have about 20 species. All recorded

species of the Pomacentridae are endemic. Of the offshore islands, the Galapagos has the highest diversity with 300 species, of which about 17% are endemic; the Clipperton, Cocos, Revillagigedos and Malpelo islands have around 100 species each with between 5 and 10% endemic.

Tropical Indo-Pacific

Dividing this huge area, which includes the Red Sea and east coast of Africa to Hawaii and Easter Island, into identifiable subregions is difficult. Essentially all parts of this region require substantial sampling to produce a clear picture of the fauna. In addition relationships among the fishes remain obscure, and species limits and distributions are frequently poorly delimited. Springer (1982) made an estimate of 4000 species for this area, but this is likely to be too low. The following discussion of species numbers and endemism follows Randall (1998) and references therein.

The highest number of species is found in the East Indian region, which includes Indonesia, New Guinea and the Philippines, This region is estimated to be home to 2800 species of shorefishes. Because the region is so large, it is misleading to provide levels of endemism because many fish are restricted to smaller subregions. The diversity in this area is probably a result of its complex geological history. Several islands, including Sulawesi, New Guinea and others, are known to be composites with smaller pieces having accreted during a basically counterclockwise rotation of the Sahul Shelf into the Sunda Shelf over the last 30 million years, with significant tectonic change even over the last 3–5 million years (Burrett et al. 1991; Hall 1996, 1998; Moss and Wilson 1998). Significant fluctuations in sea level during glacial cycles are also hypothesized to have resulted in speciation. Shorefishes that appear to provide examples of patterns consistent with these geological models are discussed by Winterbottom (1986), Woodland (1986), Springer (1988), Springer and Williams (1990, 1994) and Springer and Larson (1996). The region also exhibits an incredible variety of habitats, including silicate and volcanic sands, muds, mangroves, estuaries, lagoons and protected and exposed reefs. The fauna is dominated by the perciforms, especially the Gobiidae (200+), Labridae (100+), Pomacentridae (100+), Serranidae (about 100) and Blenniidae (about 100). Other common and conspicuous families are the Apogonidae (about 80), Pseudochromidae (about 60), Chaetodontidae (about 50) and Acanthuridae (about 45). The only non-perciform families with 50 or more species are the Muraenidae and Syngnathidae.

Numbers of species in the Pacific decrease away from the East Indian region. To the north, Taiwan is estimated to have about 2200 species, with almost 14% of these not found to the south in the East Indian region. The Ryukyu Islands probably have about 2000 species. Almost 1600 species are expected to be found in Micronesia, but numbers decrease eastward through the archipelago (Palau 1400, Carolines 1100, Marianas 920, Marshalls and Gilberts 850). Myers (1989) provided an excellent review of the geography, geology and ecology of Micronesia and its shorefishes. Springer (1982) referred to Micronesia as the Caroline Islands conduit, forming a potential set of stepping stones on to the Pacific plate and discussed the biogeography of the Pacific in general. The oceanic island groups, of course, offer fewer habitats and have a less diverse fauna. However, endemism is often high. Hawaii has about 560 species, with over 130 not found elsewhere. The Great Barrier Reef of eastern Australia and New Caledonia have the greatest diversity of the South Pacific, both with about 1600 species. Randall et al. (1998) provide the only comprehensive summary of Great Barrier Reef fishes. To the east of New Caledonia, numbers of shore species decrease to about 900 in Samoa, 630 in the Society Islands, 260 in Rapa and 126 in Easter Island (Randall 1998). Highest endemism in the South Pacific is found at Easter Island, with 22% of its species found nowhere else. The Marquesas Islands have 10% endemism, but most island groups exhibit about 5%. Briggs (1995, 1999a) has attributed these diversity differences to centre of origin hypotheses and competitive exclusion. However, such explanations have been discredited and replaced by allopatric speciation models incorporating plate tectonics, sea-level

fluctuations and other geological mechanisms and parameters such as island age (e.g. Springer and Williams 1990, 1994). Woodland (1986) suggested that Wallace's Line, usually reserved as a boundary for terrestrial taxa (see section on Southern Asia), might be descriptive for some marine fish groups, and Barber et al. (2000) have found sharp genetic breaks for stomatopods in this same area.

West of the East Indian region, numbers of species are surprisingly similar among localities. The Chagos Archipelago has 784 reported species but is expected to approach the total of the Maldives at about 950 species (Winterbottom and Anderson 1999). Almost 900 species are reported from the Seychelles, a substantial underestimate of the Mauritius shorefish fauna sets its total at 670 species, and over 900 species are recorded for Oman (Randall 1998). At least 1160 species occur off the coast of southeast Africa and the Red Sea has a similar number of species but exhibits a much higher level of endemism at about 14%, although some families have much higher levels, for example almost 90% in pseudochromids. Unfortunately, there are no recent summaries of the fauna of India, although Anderson (1996) estimated over 1000 for Sri Lanka alone. Several authors have proposed that disjunct distributions among sister taxa across the Indian Ocean is a result of vicariance imposed by the movement of India northwards towards Asia (Winterbottom 1986; Hocutt 1987; Springer 1988; Mooi 1995). Briggs (1990) criticized these hypotheses based mostly on the proposed age of taxa, but Patterson and Owen (1991) effectively countered these arguments. Within the Indo-Pacific region, the western Indian Ocean exhibits considerable endemism. Several taxa, such as butterflyfish species pairs and pseudochromid genera, have sister-group clades with one member in the western Indian Ocean and the other in the eastern Indian Ocean/western Pacific Ocean (Winterbottom 1986; Gill and Edwards 1999).

Antitropical distributions

Most distributions do not fit classical regions because the regions themselves do not have a his-torical basis. Particularly striking examples are antitropical (antiequatorial) distributions, which are distributions of the same or closely related taxa that occur in southern and northern subtropical or temperate regions with an intervening equatorial disjunction. Briggs (1999a,b) continued to argue that such distributions are a result of competitive exclusion of newer taxa over older taxa. White (1989) succinctly discussed the numerous problems with Briggs' approach and noted several logical alternative hypotheses. As with many biogeographic questions, the solution lies in the recognition of pattern. If the antitropical distributions are truly congruent in time and space, then a common explanation can logically be sought and tested. However, if each antitropical distribution is unique, then any explanation of each pattern will also be unique and will remain speculative. White (1986, 1989) hypothesized a common process of global Eocene/Oligocene cooling followed by a mid-Miocene equatorial warming event as the main factor in shaping the repeating patterns of antitropical distributions of taxa, using atherinopsines (silversides) as a model. Humphries and Parenti (1986, pp. 84–6) described a novel explanation for antitropical patterns involving a north/south division of a pre-Pangaean continent called Pacifica. Nelson (1986, p. 216) provided an example from the Engraulidae that, if not supporting the Pacifica model, suggested taxonomic differentiation in a growing rather than shrinking Pacific Basin. Geological explanations that are not mainstream have been dismissed by some (Hallam 1994; Holloway and Hall 1998), but mainstream geologists do not have a stranglehold on truth; plate tectonics itself was dismissed as radical until recently.

Temperate Indo-Pacific (South Africa, southern Australia, New Zealand)

Although not recognized as a traditional region, this area deserves special mention because of the high diversity and endemism exhibited and its faunal connection. In total, this area is home to at least 2100 shorefishes, with about 900 of these found nowhere else. South Africa has over 2200

species representing over 80% of the world's fish families, with about 13% of species endemic (Smith and Heemstra 1986). Perhaps 1500 of these are shorefishes, with the highest endemism found in the Clinidae (38 endemics), Gobiidae (28 endemics) and Sparidae (25 endemics).

Wilson and Allen (1987) estimated that of 600 inshore species for southern Australian temperate seas an incredible 85% are endemic, far outstripping levels of endemism in any tropical region (peak of 23% in Hawaii). Families with 20 or more endemics are Clinidae, Gobiesocidae, Gobiidae, Labridae, Monacanthidae and Syngnathidae, which includes the famous seadragons. These are also the most speciose families, making up over one-quarter of inshore species. Other inshore families with five or more endemic species include Apogonidae, Antennariidae, Atherinidae, Callionymidae, Ostraciidae, Platycephalidae, Plesiopidae, Pleuronectidae, Rajidae, Serranidae, Scorpaenidae, Soleidae, Tetraodontidae, Uranoscopidae and Urolophidae. Gomon et al. (1994) listed 730 species for the southern coast of Australia, although the inclusion of species from the pelagic and deepsea realms and geographic coverage were arbitrary. Even from this source, southern Australia boasts well over 400 endemic species representing 100 families and over 60% endemism. Neira et al. (1998) estimated 1500 temperate Australian species including deepsea and oceanic taxa.

Paulin et al. (1989) listed just over 1000 species for New Zealand and adjacent islands, with 110 endemic species (11%). Paulin and Roberts (1993) split the New Zealand fauna into 'rockpool' and 'non-rockpool' fishes and determined that the 58 of the 94 species in the former group were endemic whereas 52 of the remaining 900+ fishes were endemic. Dominant rockpool endemic groups are Tripterygiidae (20 endemics), Gobiesocidae (9 endemics), Syngnathidae and Plesiopidae (four endemics each). Of non-rockpool species, dominant endemic families are the Galaxiidae (12 endemics; spawns in fresh water but at least part of the life cycle is marine), Macrouridae (about 12 endemics) and Pleuronectidae (eight endemics).

These localities have a surprising number of

taxa in common. Cool temperate New Zealand and Australia share over 80 species (in over 40 families) that are found nowhere else; an additional 70 or more species are shared by warm temperate environments in these areas (Paulin et al. 1989). Families endemic to this region include Arripidae (four species) and Chironemidae (four species). An additional 50 or more species are shared with Australia, South Africa and southern South America to the exclusion of other regions. Some of these latter species are from deep water and their apparent restricted distributions might be due to poor sampling. However, families such as the Aplodactylidae are found only in Australia, New Zealand, Peru and Chile. Detailed phylogenetic studies are necessary to test whether some marine fish distributions might support patterns shown by freshwater fishes that indicate a shared history among Australian, South American and African taxa and the implied Gondwanan origin.

Antarctic

The Antarctic Ocean is a well-defined body of water that is bounded by the continent of Antarctica to the south and by the Antarctic convergence, or polar front, which encircles the continent at 50–55° S and is where cold Antarctic surface water (2–6 °C) meets warmer Southern Ocean water (8–10 °C). Miller (1993) listed almost 300 species for the region, although over one-third of these are not shorefishes (they are pelagic or deepwater species). As would be expected, the fish fauna is dominated by those that can withstand exceedingly low temperatures. The Notothenioidei make up well over one-third of the total fauna and over half of the shorefishes, with Nototheniidae (over 40 species), Artedidraconidae (over 20 species), Channichthyidae (about 20 species), Bathydraconidae (16 species), Harpagiferidae (eight species) and Bovichthyidae (one species). Most of these species are endemic to the Antarctic and, given that some species live in water with an average temperature of about –2 °C, exhibit some incredible adaptations: they have special glycoproteins in the blood that lower its freezing point or lack haemoglobin altogether in the cold oxygen-

rich waters. This suborder is mostly benthic and without air bladders, but some species have entered the water column and have evolved lipid-filled sacs that help to provide neutral bouyancy. Bargelloni et al. (2000) hypothesized a phylogeny based on mitochondrial DNA; a candidate for sister taxon has yet to be established. The Liparidae (about 40 species) and Zoarcidae (about 25 species) are also common faunal elements but are mostly found deeper than 100 m, with some deeper than 7000 m.

3.4   CONCLUSIONS

Although biogeographers have been assembling taxon and area cladograms for about 25 years, there have been relatively few successful attempts to compare and evaluate potential congruence. New methods in biogeography are continually developed, and choosing which advance the field is difficult. Morrone and Crisci (1995, pp. 392–4) advocated an integrated approach that can take advantage of the merits of each method; such an approach is perhaps as likely to incorporate their various disadvantages. Despite the number of methods, there is consensus for reliance on phylogeny reconstruction, use of some form of area cladogram, and increased use of geology and palaeontology. A continuing serious challenge to biogeographers is the definition of the unit of analysis, the area of endemism (Harold and Mooi 1994; Morrone 2001). Most workers employ organismal distributions uncritically without regard to any historical component that underlies the identification of homologous areas. Platnick (1991, p. v) states that we should prefer 'taxa that are maximally endemic – those which include the largest number of species, with the smallest ranges'. He provides a succinct discussion of areas in an introduction to a volume that presents a wide range of applications of the term 'area' (Ladiges et al. 1991).

In this chapter, we emphasize the need to identify patterns of distribution and history before exploring process and mechanisms. There has been a return to process-orientated approaches, relying less on biological patterns (phylogeny) and more on geological hypotheses and environmental and dispersal assumptions (Holloway and Hall 1998; Avise 2000); some welcome this shift to a process/modelling approach (Heaney 1999) whereas others do not (Humphries 2000). Although an integration of the two paradigms (process and pattern) will advance the field, process narratives should be incorporated cautiously. Repeated historical patterns that can form the basis of robust mechanistic explanations are only very slowly coming to light but we should be patient in waiting for them to avoid the shortcomings of previous eras in biogeography.

Historical biogeography in ichthyology is a relatively new science and, with few exceptions (e.g. North America), quality data for pattern recognition remain scarce; opportunities to make contributions to the field abound. Future work in biogeography will continue to rely on excellence in taxonomy and phylogenetics, basic field data for complete distributional records, and a method to identify congruence among area cladograms. There are areas of the world for which a synthesis of phylogenies using rigorous techniques would help direct future ichthyological work, particularly Neotropical and Australian fresh waters and the Indo-Pacific.

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Part 2

Production and Population Structure

4 The Physiology of Living in Water

OLE BRIX

4.1 INTRODUCTION

About 25 000 living species, which include more than 50% of all living vertebrate species, belong to a very heterogeneous assemblage of aquatic animals called fish (Nelson 1994; Gill and Mooi, Chapter 2, this volume). They have been divided into three major groupings that have been separated during the last 500 million years of evolution. The Agnatha, or jawless vertebrates, are primitive fish that evolved in sea water about 350–500 million years ago. The ostracoderms, also an ancient lineage, are largely found in freshwater deposits. This line is today represented by the hagfishes (about 43 species) and lampreys (about 41 species). A major group of fishes includes the Chondrichthyes or cartilaginous fishes, with 800+ types of rays and sharks and about 50 or so species of chimeras, and the Osteichthyes, which includes the bony or teleost fishes and contains more than 20 000 species. The cartilaginous fishes evolved like the Agnatha in sea water. The teleost fish evolved in fresh water 50–100 million years ago. They proliferated into a huge number of species which today can be found in almost every conceivable aquatic habitat, ranging from hot soda springs where temperatures may exceed 40 °C to the polar regions under the ice sheet with temperatures below 0 °C. Despite salt water covering about 70% of the Earth's surface and comprising about 97% of all water (Horn 1972), as many as 10 000 fish species (nearly 40%) live in fresh water. The largest numbers of these are found in the tropical regions, especially the river drainages of Southeast Asia and South America. About 500 marine species enter fresh water during their life cycle (see Gill and Mooi, Chapter 2, Mooi and Gill, Chapter 3 and Metcalfe et al., Chapter 8, this volume).

The diversity of adaptation to these habitats is determined by the evolutionary background of the fish and the physical and chemical characteristics of water. These characteristics set a number of constraints on the functional design of fish, of which high density, low compressibility, solvent properties and transparency are the most important.

1 The high density of water reduces the effects of gravity and enables fish to remain suspended in the water column using a minimum amount of energy. Fish cope with buoyancy problems by applying either dynamic or static lift or a combination of both.

2 The low compressibility of water strongly influences the swimming performance of fish, who have to push large volumes of water aside to move through it. For this purpose they have developed different motor systems, reduced the drag forces and the cost of locomotion, and increased the efficiency of respiratory and cardiovascular adaptations during swimming.

3 The most important characteristic of water is that it is an almost universal solvent, containing complex mixtures of salts, organic compounds and gases. Many of these are essential for life and are taken up by fish using specialized organs in complicated processes of ion regulation, osmoregula-

tion, gas exchange and acid–base balance, or via digestion of food.

4 The transparency of water is very poor. In clear water, light can penetrate to a maximum of 1000 m; however, penetration is usually much less than this. Since most food production is within the photic zone, most fish reside in this region, where prey capture depends on good visibility and well-developed eyes. In the dark zone of the oceans, however, fish communicate and capture prey by producing their own light using photophores.

In the following sections the physiological mechanisms that fish use to cope with these four physical and chemical constraints upon life are dealt with in more detail.

4.2 BUOYANCY, OR COPING WITH PRESSURE

4.2.1 *Defining the problem*

Most fish have body densities slightly higher than the specific gravity of sea water (1.026 g cm^{-3}). Without any lift mechanism they will sink to the bottom. Neutral buoyancy allows fish to minimize the energetic cost of staying at a particular depth, and thus they are able to allocate more energy for other activities such as feeding, growth, reproduction, hiding and migration.

Fish achieve neutral buoyancy and float by using one or both of two physical principles: dynamic lift and static lift.

4.2.2 *Dynamic lift*

Dynamic lift is widely used by elasmobranchs and active teleosts such as mackerels and tunas, which have bodies that are heavier than water. Lift is generated by the caudal and pectoral fins acting as lifting foils at about the centre of gravity of the fish and depends on a minimum cruising speed to prevent the fish sinking. In scombrid and thunnid fish species a direct correlation exists between the density of body tissues and sustained long-term swimming speed. Swimming speeds of about 1 body length (BL) s^{-1} have been recorded for the Atlantic

mackerel (*Scomber scombrus*) which has a body just slightly heavier than sea water (1.02–1.06 g cm^{-3}), while the heavier bonito (*Sarda sarda*), skipjack tuna (*Katsuwonus pelamis*) and bullet mackerel (*Auxis rochei*) (body densities 1.08–1.09 g cm^{-3}) have swimming speeds of about 2 BL s^{-1}. None of these species have a functional swimbladder (Jobling 1998). Continuous effort to support the body by muscular effort alone would be energetically costly (Marshall 1966). Therefore, most other fish, except benthic species that rest on the bottom and only swim occasionally, use static lift as a solution to the problem of buoyancy.

4.2.3 *Static lift*

Fish reduce their specific gravity in a number of ways.

1 The ratio of heavy to light tissue is reduced by minimizing elements of the skeleton, which has a specific gravity of about 3 g cm^{-3}. Compared with terrestrial animals the skeletal elements of fish are very much reduced. For example, the skull of fish may contain up to 30% lipids, whereas that of mammals rarely contains more than 1% lipid by weight.

2 Replacement of heavy ions (Mg^{2+}, SO$_4^{2-}$) with light ions (H$^+$, Cl$^-$, NH$_4^+$) is not a very efficient solution for adult fish. However, it occurs during early development in pelagic eggs (Fyhn 1993; Terjesen et al. 1998). Elasmobranchs employ urea and trimethylamine oxide (TMAO) as organic osmolytes to reduce their density. During the early larval stages of pelagic marine bony fish, urea is produced via both the urea cycle and uricolysis (Chadwick and Wright 1999; Terjesen et al. 2000). Although present at considerably lower concentrations than in elasmobranchs, this urea could possibly lower the density of the larvae, which need to reach the upper photic zone where feeding begins.

3 A better solution to the problem is the removal of ions from the body fluids to the medium, a process called hypo-osmotic regulation. In the absence of gills, kidneys and gut, which are hypo-osmotic regulatory organs found only in the adult, ionic regulation requires the presence of other ap-

propriate structures. In pelagic eggs, fish larvae take up water into the rudimentary gut over the opercular pores just before hatching (Mangor-Jensen and Adoff 1987).

Fish obtain static lift by the use of two different materials: lipids and gas. Since gases are much more efficient than lipids with respect to providing lift, fish with swimbladders have no problems in supporting their heavy body components. Fish using lipids for static lift have to reduce their specific gravity as outlined above.

Lipids

The main advantage of using lipids as a means of static lift is that the lift provided varies very little with depth. Thus if a fish is neutrally buoyant at the surface of the sea, it will also remain close to neutral buoyancy at considerable depths. This allows the fish to perform fast vertical migrations. The main drawback in the long term is that fat and oils may also be used as fuel for sustained swimming or even as substrates for growth and development. Where lipid is the only source of static lift, fish will also have great problems adjusting buoyancy in response to short-term density changes due to feeding and parturition. The most important lipids are:

1 acylglycerol (fatty acid + glycerol, density 0.90–0.93 g cm^{-3});
2 wax esters (long-chain fatty acids + long-chain fatty alcohols, density ~0.87 g cm^{-3});
3 squalene (density ~0.86 g cm^{-3}).

In general, lipid stores may contribute relatively little to buoyancy in the majority of bony fish species. Triglycerides present in the muscles or mesenteric fat as a consequence of metabolic lipid storage may provide some lift for scombrids and herring (*Clupea harengus*). Wax esters in muscles, swimbladder and bones may play some role in many families of mesopelagic teleosts. Squalene, which is an extremely light unsaturated hydrocarbon, is very important for providing lift, especially in elasmobranchs and particularly pelagic sharks, which have large livers and small pectoral fins. Squalene is formed by the condensation of isoprene units in the metabolic pathway leading to

cholesterol. The liver of these fish contains up to 80% squalene and accounts for up to 25% of body weight. Eggs of these sharks also contain squalene. Some sharks use sub-neutral buoyancy: they maintain a constant lipid content, which provides some lift but not enough; they therefore have to swim to keep buoyant.

Gas

Gas is the most efficient material for providing lift, and most teleosts possess gas-filled swimbladders. Swimbladders have sizes that provide neutral buoyancy: about 5% of body volume for marine fish and about 7% of body volume for freshwater fish. Since the volume of gas is inversely proportional to the ambient pressure, which increases by 101 kPa (1 atm) for each 10 m of depth (Boyle's law), the swimbladder must have mechanisms for efficient filling and emptying at different depths. Volume changes are much larger near the surface than at greater depths. A fish at the surface (101 kPa) halves the volume of its swimbladder at 10 m depth (202 kPa), while a fish at 200 m (2020 kPa) has to descend to 400 m (4040 kPa) to halve the volume. Buoyancy control near the surface will thus be very difficult using a swimbladder, and the complete loss of the swimbladder or at least a reduction in its importance is often seen among surface-dwelling pelagic fish. A similar loss of the swimbladder is found among many bottom-dwelling species, where buoyancy control is of no importance.

The swimbladder arises during ontogeny from a diverticulum in the roof of the foregut. In the physostomatous (Greek *physa*, bladder; *stoma*, mouth) teleosts the connection between the foregut and the swimbladder is maintained, as in elopomorphs and clupeoids, and gas can enter or be released via this duct. In the more advanced physoclistuous (Greek *kleistos*, closed) teleosts this connection has been lost or, for some species, closed during development after allowing the larvae to fill the swimbladder for the first time.

Three major problems need to be solved before the swimbladder can be used for buoyancy regulation: (i) release of gas from the swimbladder;

(ii) maintaining gas inside the swimbladder; (iii) filling the swimbladder with gas. Gas can be released by two mechanisms: via the pneumatic duct into the gut whilst ascending/diving (physostomes), or into the circulation via oval chamber control by nervous stimulation (physostomes/physoclists).

The walls of the swimbladder are impermeable to gas due to a thin lining of overlapping guanine crystals and other purines. The density of purines varies from about $20 \mu g\, cm^{-2}$ in shallow waters ($<15\,m$) to nearly $400 \mu g\, cm^{-2}$ in deep water ($>1000\,m$, pressure $>10\,100\,kPa$). The oval chamber can be closed off by nervous control, and gas release via the circulatory system is regulated in an advanced countercurrent system called the rete mirabile (Fig. 4.1). The rete consists of a tight bundle of afferent and efferent capillaries surrounding each other. This system may be diffuse, such as the micro-rete in salmonids, or it may be at some distance from the gas gland as in physostomes. In physoclists the length of the rete is directly corre-
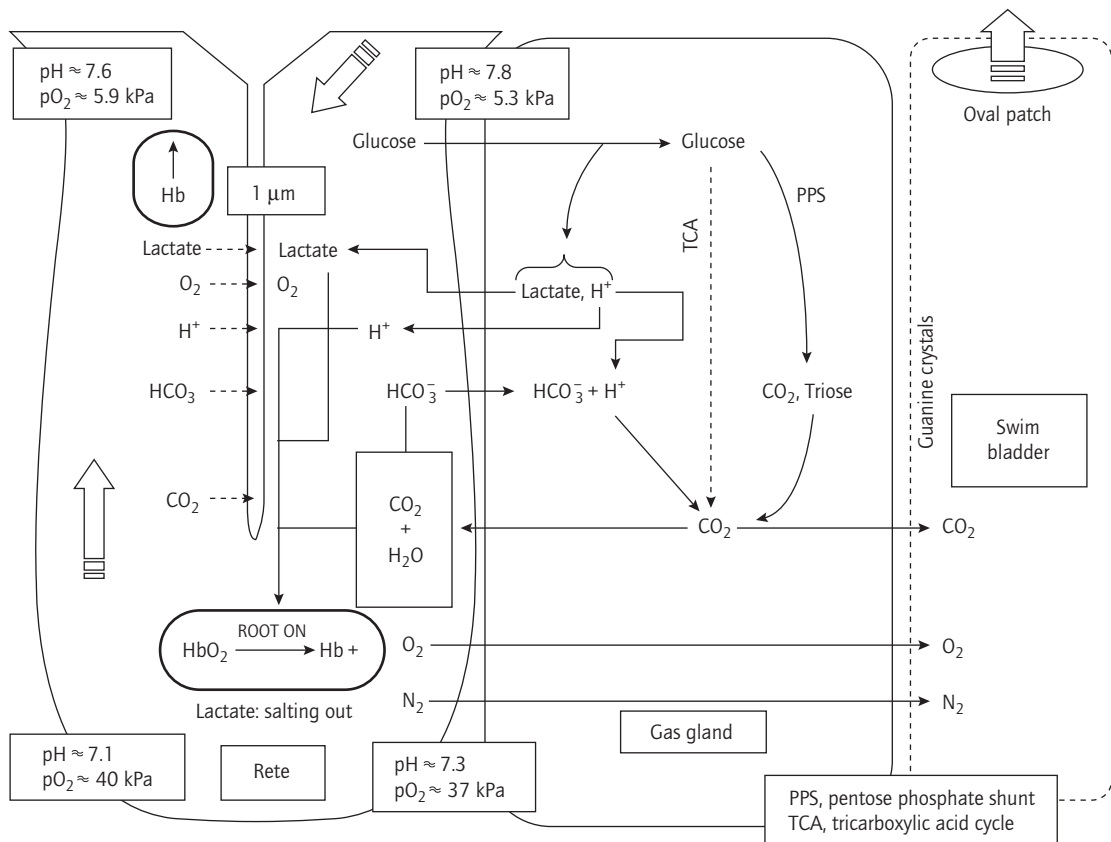
Fig. 4.1 Summary of the main processes involved in filling the swimbladder with gas. The blood entering the descending rete is acidified with lactate, H^+ and carbon dioxide from the gas gland. This causes the release of oxygen from haemoglobin via the Root effect (see text). Oxygen and nitrogen, which have been salted out, diffuse into the swimbladder. Multiplication of the solutes in the descending rete is obtained by diffusion from the ascending rete. Oxygen is retained in the rete because the process of binding oxygen is slower than the release of oxygen from haemoglobin (Hb).

lated with the depth at which the fish live and the gas pressure in the swimbladder.

Steen (1971) solved the puzzle of how the swimbladder of the eel (*Anguilla anguilla*) is filled with gas against huge pressure gradients. The gas-filling mechanism is linked to the countercurrent structure of the rete, which allows gas pressure, and therefore volume, to 'multiply' within the swimbladder (Fig. 4.1). Lactate and carbon dioxide secreted from the gas gland near the luminal end of the rete decrease blood pH, which results in a fast unloading of oxygen from a very pH-sensitive haemoglobin component in the blood and thus an increase in the oxygen partial pressure. This so-called Root-off mechanism is accompanied by a salting-out mechanism, which allows more oxygen, but also other gases like nitrogen, to accumulate. In this way oxygen, and also nitrogen, diffuse into the swimbladder. Since lactate and carbon dioxide diffuse from the efferent capillaries to the afferent capillaries by following a downhill gradient like oxygen, pH again increases in the efferent capillary leaving the rete. Oxygen now binds again to the haemoglobin component and the oxygen partial pressure decreases. However, this process, which is referred to as the Root-on mechanism, is much slower than the root-off mechanism, allowing a fraction of the oxygen content to remain within the system.

4.3 SWIMMING

Though some fish can fly, crawl on land, climb trees or burrow in mud, most fish swim primarily by oscillating their bodies. Some swim by moving just their paired and unpaired fins ('propellers'). The analysis of swimming is very complex, and certainly needs more space than can be given in this basic approach. There is of course great variation in how fish swim due to the large variability of their body shapes. These swimming methods can be divided into five basic types.

1 Anguilliform: whole body is flexed into lateral waves for propulsion. Typical for 'eel-like' species such as eel, marine gunnels and lampreys. Other species that use this type of swimming include nurse sharks and Atlantic gadoids when swimming slowly (Wardle and Reid 1977).

2 Subcarangiform: species that undulate their bodies into less than one full wavelength, yet more than one-half body length at speeds greater than $1\,\mathrm{BL\,s^{-1}}$.

3 Carangiform: species that undulate their bodies into a shallow wave up to one-half wavelength within the body length, with the amplitude increasing from head to tail. Typical for fast swimmers such as jacks, drums snappers, tunas and mackerels.

4 Ostraciform: these fish swim mainly by flexing the caudal peduncle. Typical for fish that need armour for protection like boxfishes, trunkfishes and cowfishes.

5 Swimming with fins alone: these fish swim by moving their ray-and-membrane fins individually rather than their bodies. An example in the lionfish (*Pterois volitans*).

In the following I concentrate on some of the features of the motors, the drag forces and the cost of speed, and efficiency of respiratory and cardiovascular adaptations during swimming.

4.3.1 Motors

Rhythmic undulations of the body or fins exert force on the relatively incompressible surrounding water and the fish will move either forward or backward. The undulations result from the contraction of the segmented axial musculature, which is divided into myotomes by the myoseptal–connective tissue partitions on which the muscle fibres insert. Since the vertebral column is incompressible, these alternating contractions in the myotomes on each side result in lateral bending of the body. The muscle fibres of the myotomes lie in a series of horizontal tubes of connective tissue, which run along the length of the fish. Most of the myotomes lie ventral to the vertebral column and form a characteristic pattern, which in amphioxus and fish larvae looks like the letter 'V' pointing towards the tail. In all other adult fish the overlapping myotomes are folded into 'W' shapes. In higher fishes, only the fibres just under the skin lie along the axis, while the deeper fibres in the

myotomes spiral up to 30° to the axis. This arrangement assures a near-isometric contraction at the lowest cost, since the deeper fibres all contract to a similar degree for a given bending of the trunk, so the longitudinally running fibres shorten about 10% during swimming while the deeper fibres only shorten about 2%. The more undulatory waves the fish can exert against the surrounding water, and the faster and more exaggerated the waves are, the more power can be generated, resulting in higher accelerations and swimming speeds, given that the resistance is held constant.

Slow and fast muscles

Just below the skin of the fish there is a thin layer of myoglobin-rich red fibres that covers most of the myotomes, which consist of white fibres. Fish use these red fibres, which are commonly referred to as slow fibres, for cruising. The main mass of white fibres is used for burst swimming. The main characteristics of red and white fibres are described in Table 4.1 (Bone 1978). Guppy and Hochachka (1978) showed how changes in muscle pH, oxygen pressure, temperature and biochemical substrates can reversibly alter aerobic and anaerobic enzyme activities in skipjack tuna white muscle. Thus some fish conform to the classical differentiation of white and red muscle function, for example

bluefish, striped bass and herring, while others, such as the chub mackerel, rainbow trout, coalfish and carp, show a broader range of white muscle activity (Freadman 1979).

4.3.2   Drag forces and the cost of speed

Swimming is retarded by two kinds of drag forces:
1 pressure drag, which is caused by the vorticity in the wave creating a higher pressure at the nose than at the tail and which is highest for unstreamlined fish; and
2 skin friction drag, which is caused by the viscosity of water and which makes it stick as a boundary layer to the fish surface.
Skin friction drag is the most important drag component for fish. For the fish to keep moving, the inertial forces of motion must be larger than the viscous forces of the surrounding water. The dimensionless Reynolds number, Re, describes the relationship for theses two forces in fish:

$$\mathrm{Re} = \frac{VL}{v}\,(\text{always} > 1), \qquad (4.1)$$

where V is main swimming velocity, L the length of the fish and v the coefficient of kinematic viscosity of the fluid (v = viscosity/density, and for

Table 4.1   Comparing slow red and fast white muscle fibres in fish myotomes.

Red fibres	White fibres
Diameter about 60–150 μm	Fibres more than 300 μm
Rich vascularized	Poorly vascularized
Abundant myoglobin, colour red	No myoglobin, colour white
Abundant large mitochondria	Few smaller mitochondria
Oxidative enzyme systems	Enzymes of anaerobic glycolysis
Low activity of Ca^{2+}-activated myosin ATPase	High activity of Ca^{2+}-activated myosin ATPase
Little low molecular weight Ca^{2+}-binding protein	Rich in low molecular weight Ca^{2+}-binding protein
Lipid and glycogen stores	Glycogen store, usually little lipid
Sarcotubular system has lower volume than in fast fibres	Relative larger sarcotubular systems
Distributed cholinergic innervation	Focal or distributed cholinergic innervation
No propagated muscle action potentials	Propagated action potentials; may not always occur in multiply innervated fibres
Long-lasting contractions evoked by depolarizing agents	Brief contractions evoked by depolarizing agents

water ≈ 0.001 and is constant at any given temperature). For fish swimming normally, Re is within the range 10^4–10^8. In this range viscosity effects are mostly confined to a thin boundary layer adjacent to the body surface. At $Re < 5 \times 10^5$, viscous forces dominate and the boundary layer on a flat plate will be laminar. At higher Reynolds numbers the boundary layer will be turbulent. Thus fast-swimming fish have to cope with a larger skin friction drag. This drag can be lowered by reducing the wetted area and lateral movements, but most importantly by a boundary layer control mechanism. These mechanisms mainly tend to delay the transition from a laminar layer to a turbulent layer so keeping Re low. A mucous coating acts in this way. It has also been suggested that opercular water flow may smooth the flow of boundary water next to the body. Sharks have denticles with low sharp-edged ridges parallel to the swimming direction that are believed to delay transition by reducing microturbulence in a laminar boundary layer. In addition many fast-swimming fish, such as scombrids and the blue shark, can save up to 20% of the energy needed for locomotion by using a so-called glide–power cycle, where 'propulsive' body movements are alternated with periods of gliding when the body is held rigid.

4.3.3 Efficiency of respiratory and cardiovascular adaptations during swimming

Traditionally the different taxonomic groups have been divided into 'cruisers' that mainly use red muscles, and 'burst swimmers'. However, in order to discuss efficiency of respiratory and cardiovascular adaptations during swimming we have to be more precise about defining the term 'swimming'. In fish physiology three main categories of swimming are defined (Jobling 1998).

1 Sustained swimming: speeds that can be maintained for 200 min or longer. Totally aerobic metabolism.

2 Prolonged swimming: speeds that can be maintained for 20 s to 200 min and result in fatigue.

Fuelled by anaerobic and aerobic metabolism. The so-called critical speed is calculated from the maximum speed achieved prior to fatigue in a tunnel respirometer, where the speed has been increased stepwise until fatigue is reached.

3 Burst swimming: burst speeds that can be maintained for less than 20 s. Characterized by an initial acceleration phase followed by a sprint phase of steady swimming defined as swimming in a given direction at constant speed. This type is predominantly fuelled by anaerobic metabolism.

Tunnel respirometry of fish calculates the cost of transport for swimming at a given speed in $J g^{-1} km^{-1}$ as well as its most efficient speed (Brett 1975). The locomotion of fish is very efficient compared with that of animals on land. Transport in water is thus about ten times less costly than transport in terrestrial animals (Schmidt-Nielsen 1997). However, with increased swimming activity, tissue demand may increase 5–15-fold, with about 90% of this increase being accounted for by elevated muscle metabolism. It is reasonable to believe that the efficiency of transferring momentum from the body and fins to the water in scombrids may be as high as 85% (Bone et al. 1996). Webb (1975) showed that rainbow trout expend 18% of the total work of acceleration to overcome frictional drag. A number of respiratory and cardiovascular responses are invoked in order to meet this demand for increased oxygen supply. Increased swimming rate results in a minor increase in breathing rate and a significant increase in ventilatory stroke volume. As a result ventilation volume may increase eightfold, and the contact time between water and respiratory exchange surface decreases from about 300 ms at rest to about 30 ms when active. At the same time, cardiac output is increased mainly by a 50–250% increase in stroke volume and a 20–40% increase in heart beat frequency. Though the blood transition time in the gill lamellae is reduced from 3 s to 1 s, gill recruitment is increased due to higher blood pressure. As a result of these respiratory and cardiovascular adjustments more oxygen is channelled to the muscles to meet the increased tissue demand.

4.4 OSMOREGULATORY PROBLEMS IN FRESH AND SALT WATER

4.4.1 *Defining the problem*

Fish live in many different environments, ranging from virtually distilled water to salt concentrations that are so high that living underwater may be difficult. Though most fishes are stenohaline, meaning that they live all their life in water of nearly constant salt concentration, many fish are able to move between fresh water and sea water. Such fish are euryhaline and/or diadromous. Catadromous species, such as eels, leave fresh water to spawn in the sea, while anadromous species, such as salmon, which are more numerous, make the reverse migration to spawn in fresh water (see Metcalfe et al., Chapter 8, this volume). The skin of fish is relatively impermeable to water and ions. The gills, however, have large areas of permeable epithelium, which are in contact with the surrounding water. The osmolality (number of undissociated solute molecules or ions per kilogram of solvent) of fresh water is <10 mosmol, and sea water falls within the range 800–1300 mosmol. The freshwater teleosts have blood osmolalities of about 260–330 mosmol kg^{-1}. Thus these fish will be subjected to a passive influx of water and efflux of ions. In marine fishes, which have blood osmolalities in the range 370–480 mosmol kg^{-1}, these fluxes will be reversed. In addition to osmoregulation, many fish regulate the ionic composition in their blood by active, energy-consuming processes. In the following sections I examine in more detail how different groups of fish regulate their blood osmolality and ionic composition to the surrounding water.

4.4.2 *How to regulate in fresh water*

Since all freshwater fish have blood osmolalities higher than the surrounding water, they have evolved mechanisms to (i) prevent the passive efflux of ions through diffusion over the body and loss from urine and faeces and (ii) remove excess water. In lampreys and teleosts, ion loss is com-pensated for by salt intake in the food and by a high-affinity salt-uptake mechanism at the gills, while water balance is maintained by the excretion of about 2–6 ml kg^{-1} h^{-1} of copious urine (10–80 mosmol). Drinking rate is kept low.

Processes in the gills

The gills are the site of many of the exchange processes that occur between the fish and its environment, such as gas exchange, ion regulation in the form of active uptake of sodium and chloride ions, acid–base regulation, and excretion of nitrogenous waste products of protein catabolism such as ammonia and ammonium ions. Since these various exchange mechanisms are coupled, the excretion of waste products may result in the uptake of sodium and chloride (Fig. 4.2). Thus chloride is taken up in exchange for bicarbonate, and sodium is taken up in exchange for protons and/or ammonium ions. In this respect the double exchange mechanisms seem to differ from those present in marine teleosts (i.e. Na$^+$/K$^+$/2Cl$^-$ cotransport, see Section 4.4.3). Thus, the double exchange mechanism provides for:

1 maintenance of appropriate internal [Na$^+$];
2 maintenance of appropriate internal [Cl$^-$];
3 elimination of toxic NH$_3$$^+$;
4 elimination of CO$_2$ as HCO$_3$$^-$;
5 adjustment of internal H$^+$/OH$^-$;
6 maintenance of internal ionic electrical balance.

Processes in the kidneys

The elongate teleost kidneys are, like adult lamprey kidneys, composed of typically segmented mesonephrons (Fig. 4.3). They consist of glomeruli in the posterior lobe of the kidney, which receives oxygenated blood from the dorsal aorta, and proximal and distal tubules in the more anterior part of the kidney that receive venous blood from the caudal vein.

The glomerular filtration rate (GFR) is high in freshwater teleosts. They produce about ten times more urine than marine teleosts. The urine is much more dilute than the plasma and as much as
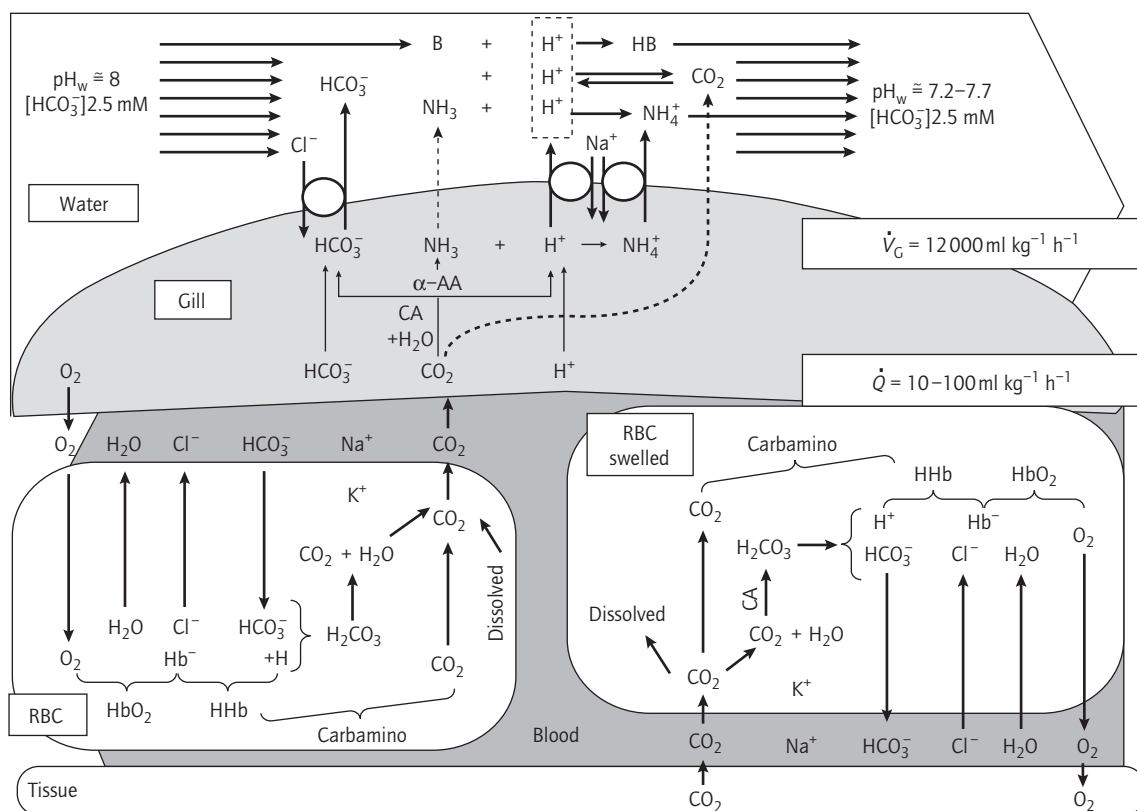
Fig. 4.2 Summary of the main ion transport and acid–base regulatory processes taking place in the gills in fresh water and its relation to the transport of oxygen to, and carbon dioxide from, the tissues. At the top, a secondary lamella is in contact with the water, which flows from left to right. Beneath is a blood vessel with red blood cells (RBC). The left cell illustrates the processes in the gills (loading O_2, releasing CO_2); the right cell shows the processes in the tissues (delivering O_2, loading CO_2). The gills are the main site of acid–base regulation mainly due to the high flow of water over the gills, resulting in a high buffer (B) capacity. The uptake of sodium and chloride ions is directly coupled to the excretion of carbon dioxide and ammonia. Most of the carbon dioxide is transported as bicarbonate in the blood, a minor fraction as physical dissolved carbon dioxide and some directly bound to the haemoglobin molecule. Some of the carbon dioxide entering the red blood cells diffuses out into the plasma. Electrical neutrality is maintained by the inward diffusion of chloride ions followed by water, which causes the cell to swell (referred to as the chloride shift). The binding of carbon dioxide and protons to haemoglobin facilitates oxygen release to the tissues, while the release of carbon dioxide over the gills facilitates the uptake of oxygen by haemoglobin. $\dot{V}_G$, flow of water over gills; $\dot{Q}$, cardiac output (blood flow); CA, carbonic anhydrase; α-AA, alpha amino acids. (Source: acid–base part based on Heisler 1984.)

99.9% of the sodium and chloride ions passing into the glomerular filtrate are resorbed. The resorption of organic solutes occurs primarily in the proximal tubules. This resorption is accompanied by some water uptake. Most of the resorption of the monovalent ions occurs in the distal tubules, which are impermeable to water. Urine production is proportional to GFR. The urine is collected in the urinary bladder and urination may occur at intervals of 20–30 min. This structural arrange-
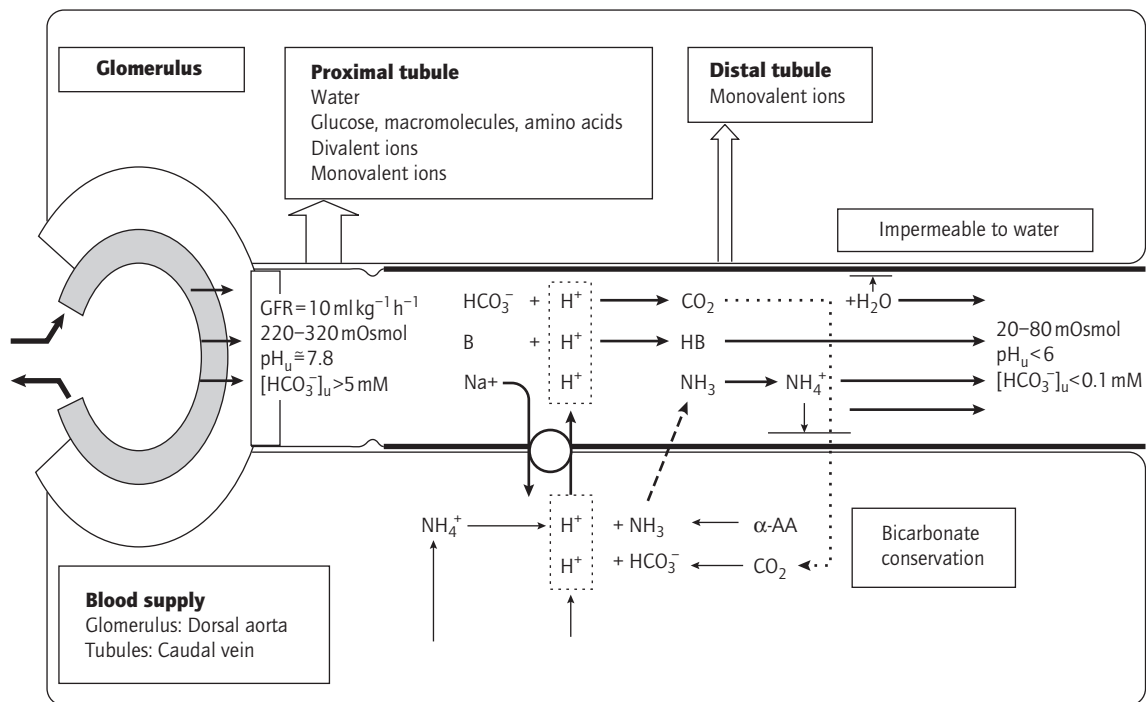
Fig. 4.3 Summary of the main functions of the kidney in freshwater fish, showing the major sites of absorption and water permeability. The kidney does not play the same role as the gills in acid–base regulation due to the considerably lower flow and thus buffer capacity. GFR, glomerular filtration rate; B, buffer; α-AA, alpha amino acids. (Source: based on Lahlou 1980; Heisler 1984.)

ment of the kidneys in freshwater teleosts allows considerable control of the composition of the glomerular filtrate, but little control over the final urine volume. The freshwater stingrays from the Amazon (*Potamotrygon* sp.), which live more than 4500 km from the sea, also have a very high GFR. Urea is reduced to only 1 mм, and sodium and chloride ions are reduced to similar levels (Bone et al. 1996).

4.4.3   How to regulate in sea water

Sea water has an osmolality of about 1000 mosmol. Among marine fish three different strategies for regulation of internal water and total solute concentrations can be distinguished:
1 same osmolality as sea water, no regulation at all (hagfish);

2 osmolality close to sea water, internal inorganic ion concentration about one-third of sea water (elasmobranchs, *Latimeria*);
3 osmolality of about 400 mosmol, internal inorganic ion concentration about one-third of sea water (marine teleosts).

Hagfish

Hagfish have a blood volume twice that of Gnathostomata. The blood is isosmotic to sea water and concentrations of sodium and chloride ions are the same as in sea water, but are slightly higher in the tissues due to high levels of intracellular amino acids. Osmotic water exchange is more or less absent, while water exchange rates may be as high as $2.3 \, l \, kg^{-1} \, h^{-1}$ (McInerney 1974) due to the free permeability to water. Urine pro-

duction is minimal, and chloride cells have been observed. Though hagfish are strictly marine (stenohaline), experiments by McInerney (1974) demonstrated that they have the ability to reabsorb sodium from the glomerular filtrate, a feature necessary for living in fresh water. This could be reminiscent of an original freshwater ancestry (Marshall and Smith 1930).

Marine elasmobranchs

Like the hagfish the elasmobranchs are not in danger of losing water because they are isosmotic to the medium. However, like the marine teleosts they are hypo-ionic to sea water. Plasma osmolarity is increased to seawater levels by the organic osmolytes, urea and TMAO. Urea is produced from the nitrogen waste product, ammonia, in the ornithine–urea cycle in the liver, from where it enters the plasma and other body fluids. Though urea is less toxic than ammonia, the levels seen in elasmobranch plasma would be fatal for other fish except *Latimeria*. Elasmobranchs have achieved higher tolerance to urea by retaining TMAO, which counteracts the effect of urea at a ratio of about 1 : 2 in their body fluids, and by having enzymes and proteins that appear to be less sensitive to disruption by urea. A special sodium chloride excretory organ has evolved in the elasmobranchs. This so-called rectal gland uses a $Na^+/K^+/2Cl^-$ cotransport mechanism to secrete excess sodium and chloride ion intake from ingested food. The secretion contains very little of the organic osmolytes and is isosmotic to the plasma. Energy for the cotransporter is provided by an abundance of Na^+/K^+ ATPase in the gland.

Marine teleosts

In contrast to marine elasmobranchs the marine teleosts, being hyposmotic to sea water, lose water to the medium primarily over the thin gill epithelium. They have to replace this water loss and drink between 10–20% and 35–40% of their body weight per day. In addition there is a constant passive influx of monovalent ions over the gills as well as dietary salt uptake. The kidneys are not able to produce urine more concentrated than the blood so that excess salts are removed and water is conserved. In fact many marine teleosts have evolved an aglomerular kidney to minimize water loss, and urine flow rate is as low as 1–2% of body weight per day. Marine fish have solved the osmotic problem as follows (Potts 1976; Kirsch et al. 1981). After drinking, the water passes into the oesophagus, which is impermeable to water but permeable to light monovalent ions. Sodium and chloride thus diffuse into the blood down their concentration gradients. When entering the intestine, which is permeable to water, the water has become hyposmotic to sea water and nearly isosmotic to the blood. A $Na^+/K^+/2Cl^-$ cotransport mechanism located in the apical brush border membrane transports the ions from the gut lumen into absorptive cells and water follows passively in a process called solute-linked water transport. Na^+/K^+ ATPase, which is present in the basal membrane of the absorptive cells, provides the energy for this active transport. The excess sodium, potassium and chloride ions are then transported in the blood to the gills where they are excreted via the 'chloride cells' (Fig. 4.4). The concentration of divalent ions is low in sea water; 80% of these ions that are taken up by drinking are expelled in the faeces. The remaining ions are excreted in the urine.

In order to become truly marine the teleosts had to solve the osmotic problems for the spawned egg. At spawning, marine fish eggs must contain a water reservoir to compensate for the passive water loss imposed by the hyperosmotic sea water (Fyhn et al. 1999). The high water content of the yolk of marine teleost eggs forms this water reservoir. Regardless of systematic affinities, most extant marine fishes spawn pelagic eggs. Yolk protein hydrolysis and increase in content of free amino acids during final oocyte maturation is part of the mechanism that brings water into the yolk before the eggs are spawned (Rønnestad et al. 1996; Thorsen & Fyhn 1996).

4.4.4 Antifreeze

For hagfish, marine elasmobranchs and freshwater teleosts, freezing is not a problem since they have
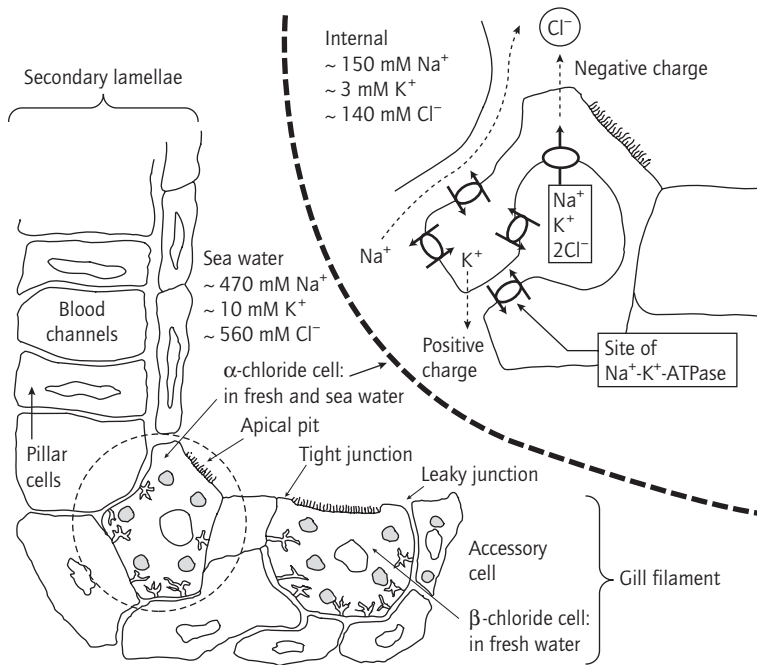
Fig. 4.4 Schematic illustration of part of secondary lamellae on a gill filament showing the two types of chloride cells involved in the active secretion of chloride ions. The process depends on Na^+/K^+ ATPase activity and causes polarization of the cell. Sodium ions may diffuse out via the leaky junctions.

body fluids that are either isosmotic or hyperosmotic to the surrounding water, as long as the water is not frozen. Marine teleosts, however, are hyposmotic to the ambient water and can freeze to death when the water temperature drops below 0 °C. To prevent freezing the fish may produce macromolecular 'antifreeze' compounds in their blood serum. The antifreeze consists of glycoproteins or proteins, which coat and isolate ice crystals forming in the blood by binding their hydroxyl groups to oxygen molecules on the surface of the ice crystals (DeVries and Wohlschlag 1969). The production of antifreeze is dependent on cold acclimation and short photoperiods (Duman and DeVries 1974a), and genetically based differences in antifreeze production have been described (Duman and DeVries 1974b). In the aglomerular kidneys of Antarctic fish the glycoproteins are conserved rather than filtered out of the blood, which lowers the energetic cost of osmoregulation in these fish (Dobbs et al. 1974; see also Section 4.5.4).

4.5 RESPIRATION AND SPECIAL ADAPTATIONS FOR LIVING IN LOW OXYGEN

4.5.1 The environment

Fish live in a dense and very viscous environment, which for a terrestrial animal would appear to be almost depleted of oxygen. At best, one volume of water contains a little less than 4% the amount of oxygen present in the same volume of air. In air the solubility of a gas would be roughly $1000\,ml/101.3\,kPa = 9.87\,ml\,l^{-1}\,kPa^{-1}$ (at 15 °C). In practice the respiratory gases are treated as ideal gases, which means that oxygen and carbon dioxide would dissolve more or less equally in air. In water, however, the solubility of gases depends on: (i) the nature of the gas, (ii) the pressure of the gas in the gas phase, (iii) the temperature and (iv) the presence of other solutes. Thus, while the solubility of oxygen in water is only about one-thirtieth the solubility in air, the solubility of carbon dioxide is

more or less the same in air and water depending on temperature and is similar at about 15 °C.

For calculating gas fluxes we use the concept of Ohm's law: flux = capacitance × potential difference, which gives the following three fundamental gas equations:

$$\dot{M}_{CO_2} = \dot{V}_m[\beta_m \cdot (P_e - P_i)]_{CO_2} \qquad (4.2)$$

$$\dot{M}_{O_2} = \dot{V}_m[\beta_m \cdot (P_i - P_e)]_{O_2} \qquad (4.3)$$

where $\dot{M}_{gas}$ is the volume of gas taken up (O_2) or produced/released (CO_2), $\dot{V}_m$ the flow of medium over the gills, β_m the capacitance coefficient (solubility) of the gas in the medium and P the partial pressure of gas (i, before gills; e, after gills). From these expressions, we may calculate:

$$\frac{\dot{M}_{CO_2}}{\dot{M}_{O_2}} = RQ \qquad (4.4)$$

where RQ is the respiratory quotient (R, the exchange ratio, is used when examining isolated parts of the fish). Rearranging equations 4.2–4.4 and ignoring P_i:

$$(P_e)_{CO_2} = \frac{(\beta_m)_{O_2}}{(\beta_m)_{CO_2}} \cdot (P_e - P_i)_{O_2} \qquad (4.5)$$

If the fish extracts all the oxygen in the water ($P_i \cong$ 21 kPa, $P_e = 0$ kPa), the partial pressure of carbon dioxide can, at a maximum, be about 0.7 kPa in the exhalant water. This means the maximum partial pressure of carbon dioxide in the arterial or postbranchial blood will not exceed this value, which is almost a factor of 10 lower than for air-breathing animals.

This low oxygen availability has undoubtedly contributed to the evolutionary development of:
1 large gill surface areas for extremely efficient gas exchange;
2 air-breathing organs and the necessary circulatory arrangements;
3 acid–base regulation depending more on ion than ventilatory exchanges.

4.5.2 Gas exchange over gills

All fish have a unidirectional flow of water over their gills, except for adult lampreys, which have tidal ventilation in and out of the gill sac via the valved branchial openings. The mouth cannot be open since the lamprey is likely to be attached to either rocks or hosts. Synchronous expansion and contraction of the buccal opercular cavities ventilate the gills. This provides a nearly constant flow of water over the gill surfaces. At a given swimming speed fish adopt ram ventilation to conserve energy. The branchial pump is switched off and the flow of water over the gills is regulated by the opening of the mouth in relation to the actual speed and oxygen demand. The gills consist of bony or cartilaginous arches to which one row of paired gill filaments are anchored. Numerous secondary lamellae protrude from both sides of each filament. A layer of thin epithelial cells covers the outside of the lamellae. Beneath the basement membrane are supportive pillar cells and blood vessels running in the opposite direction to the water flow (Fig. 4.4). This arrangement ensures very efficient gas exchange, with oxygen utilization as high as 80% and postbranchial oxygen partial pressures higher than in the water passing through the gill. The functional area of the gills can be changed by shunts in the secondary lamellae or by the action of an autoregulatory system, which reacts on blood pressure by increasing the tonus of the contractile elements in the pillar cells so re-routing blood flow (Laurent 1984). Intrinsic muscles in the gill filaments of most teleosts can change the angle of the filaments on each arch and thus alter the flow pattern over the secondary lamellae.

Other sites for gas exchange

An efficient gas exchange system should have the following characteristics: close contact to the medium, short diffusion distances, and a well-developed circulation that can transport oxygen efficiently from the site of gas exchange to the tissues. Cutaneous respiration may be of some significance in a few cases either when oxygen demand

is very low, as in some Antarctic fishes, or when the diffusion distance is very short, as for fish larvae. In adult fish, cutaneous respiration is less than 30% of routine metabolism (O. Brix, unpublished results). Its significance is still poorly investigated, but it may be of some importance for fish like eels when migrating short distances across land (Berg and Steen 1965). For air-breathing organs see Section Air breathing.

4.5.3   *Circulation and gas transport*

The main tasks of the circulatory system are to transport respiratory gases, nutrients and metabolic waste products, endocrine factors and heat. Most fish have a single circulatory system. The heart consists of the sinus venosus, atrium, ventricle and bulbus. In elasmobranchs, agnatha and holosteans the bulbus is replaced by the conus arteriosus. The conus does not increase the acceleration of blood, as does the bulbus in teleosts. The blood is pumped into the ventral aorta, where blood pressure is in the range 4.0–7.3 kPa. After passing the gills, which create ~30% of the total resistance to blood flow, the blood pressure has decreased to about 3.3–4.7 kPa in the dorsal aorta, which flows alongside the caudal vein in the haemal canal formed by fusion of vertebral processes. The haemal canal thus protects the caudal vein from the pressure waves that move to the caudal end of the fish as the myotomes contract during swimming. The pressure for venous return is generated in the segmental veins in the muscles in the caudal region by the so-called haemal arc pump, or in the caudal sinuses or caudal pump, which can be called caudal hearts, before entering the caudal vein. Back-flow is prevented by a series of valves. The caudal vein collects blood from the cutaneous circulation, the posterior muscles and the remainder of the caudal region (Satchell 1965, 1971). Hagfishes have no less than five accessory hearts. For circulatory adaptations in air-breathing fish see Section Air breathing.

Aneural and neural mechanisms control the heart and vascular system allowing for a wide range of circulatory adjustments to environmental or other changes. Aneural control is mainly effected by:

1 changes in blood volume and venous return by swimming movements and mobilization of blood into general circulation from the spleen, liver or blood sinuses in various species;

2 direct response of heart muscle (pacemaker) to temperature changes, which increase the heart rate (Randal 1970);

3 circulating catecholamines like adrenaline, which stimulates heart rate and stroke volume and dilates the gill vasculature (Nakano and Tomlinson 1967; Bennion 1968), and noradrenaline, which constricts systemic vascular beds (Wood and Shelton 1975).

The hearts of teleosts and elasmobranchs, but not hagfish and lungfish are innervated by the vagus nerve (Xth cranial nerve). Stimulation of the vagus causes a cholinergic effect, simulating the effects of acetylcholine, which slows the heart rate in teleosts and elasmobranchs producing bradycardia and increases the heart rate in lamprey (Randall 1970). Light flashes, sudden movements of objects or shadows, and touch or mechanical vibrations may increase vagal tone. The response can be blocked by injection of atropine. Some fish also have adrenergic or stimulatory fibres from the vagus.

The circulatory system may be linked to maximization of oxygen uptake in the gills and delivery to the tissues. In the following I examine in more detail some of the key factors in this process.

The significance of haemoglobins

Fish haemoglobins are mostly tetramers consisting of two α and two β polypeptide chains (141 and 146 amino acid residues, respectively). The basic function of the haemoglobins is to ensure an adequate supply of oxygen to all parts of the organism in which they occur. In order to accomplish this task they have developed, in the course of evolution, a common molecular mechanism based on the principle of ligand-linked conformational change in a multi-subunit structure (Wyman 1964). Within the framework of this common mechanism, however, different haemoglobins

Fig. 4.5 Blood perfusion requirements of fish in relation to blood haemoglobin concentrations. (Source: based on Wood and Lenfant 1979.)
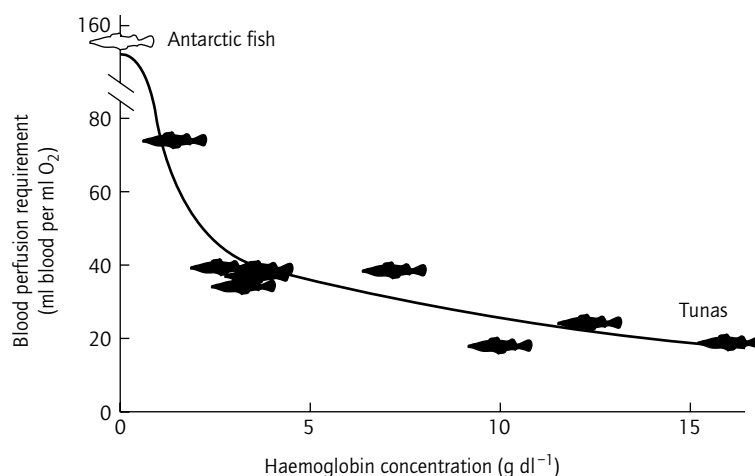
have acquired special features to meet special needs. The significance of haemoglobins is illustrated in Fig. 4.5, which shows the impact of haemoglobin concentration on perfusion requirement expressed as millilitres of blood pumped by the heart (cardiac output, $\dot{Q}$) for each millilitre of oxygen taken up by the cells ($\dot{V}_{O_2}$) for random examples of fish species. The perfusion requirement, which links cardiac output and blood oxygen transport to oxygen uptake, is calculated from the flux equations shown in Section 5.1:

$$\frac{\dot{Q}}{\dot{V}_{O_2}} = \left(\frac{1}{C_{aO_2} - C_{\bar{v}O_2}} \right), \tag{4.6}$$

where $C_{aO_2} - C_{\bar{v}O_2}$ is the difference in oxygen content between arterial and mixed venous blood. The Antarctic fish without haemoglobins thus have to pump almost ten times as much blood for the same amount of oxygen taken up as the tunas with the highest haemoglobin concentration.

Sites of control

Oxygen transport is based on conformational changes of the quaternary structure of the haemoglobin molecule that are caused by the binding and release of small solvent components, such as H^+, CO_2 and nucleotide triphosphates (NTP), called ligands (Brunori et al. 1985). Although the product of the central exon of the haemoglobin gene (the oxygen-binding site) is sufficient for accomplishing the primary function of haemoglobin, the products of the external exons (the ligand-binding sites) allow external modulation of the functional properties (Eaton 1982). Hence, oxygen binding at the haem groups is modulated to different extents in different species by interactions with ligands (Fig. 4.6). Haemoglobins exhibit a great deal of variation, in terms of absolute affinity for oxygen, in their susceptibility to metabolic effectors; these variations allow haemoglobin to fully meet the physiological requirements of a given species. This type of tuning is primarily based on the ability of effectors to preferentially bind to one of the two quaternary conformations. In particular, preferential binding of NTP, typically to the low oxygen affinity T-state, facilitates the unloading of oxygen to the tissues (Fig. 4.6). The decrease in oxygen affinity caused by protons is commonly referred to as the Bohr effect. When the binding of protons is so strong that the haemoglobin remains in the T-state, in which there is no transition to the R-state and thus no cooperativity, this is called a Root effect. This plays an important role in filling the swimbladder (see Fig. 4.1). Fig. 4.6 summarizes how the oxygen uptake of fish can be modified by
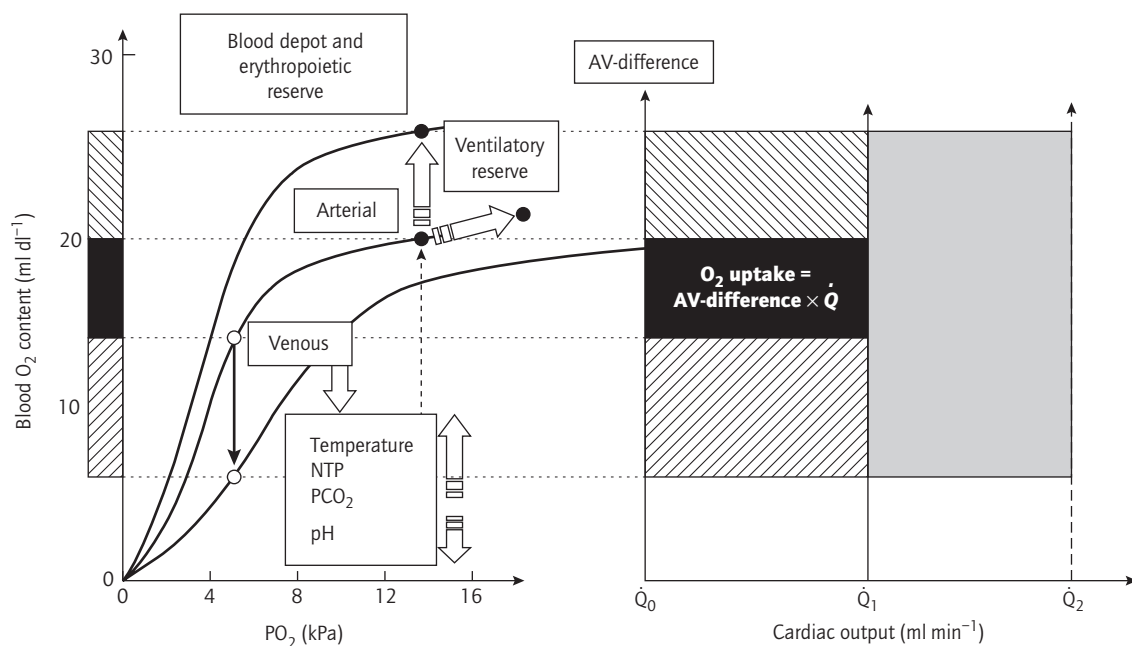
Fig. 4.6 The magnitude of oxygen uptake of fish is illustrated as a square, where one side is the arterial–venous difference in blood oxygen content (AV-difference) and the other side is the cardiac output ($\dot{Q}$). The arterial–venous difference can be increased by increasing ventilation and/or the release of more red blood cells into the blood from the spleen (stress response), or by increasing the unloading of oxygen to the tissues under the allosteric control of ligands and temperature (the most important nucleotide triphosphates (NTPs) in fish are GTP and ATP). Cardiac output is the product of stroke volume and heartbeat frequency, and will accordingly be changed in parallel with these parameters.

regulating haemoglobin oxygen transport and cardiac output.

The significance of haemoglobin multiplicity

The term 'haemoglobin multiplicity' means the occurrence of more than one haemoglobin component in the same or different developmental stages of a species. Vertebrate red blood cells typically contain more than one kind of haemoglobin. Commonly, multiple genes are expressed that code for different variants of these globins, resulting in 'isohaemoglobins'. Some species show haemoglobin 'polymorphism', the occurrence of different 'allohaemoglobins' in different individuals representing different genetic strains (Brix et al. 1998a; Samuelsen et al. 1999). The multiplic-

ity of haemoglobin components appears greatest in ectothermic animals, and in particular among fishes that may experience both rapid tidal or diurnal, and marked seasonal, changes in ambient oxygen and temperature. It has been suggested that both the number of isohaemoglobins and their functional heterogeneity is related to the constancy of physicochemical conditions in the environment (Brix et al. 1999). However, demonstrating this simple hypothesis has been hampered by phenotypic plasticity, which can produce for example an acclimatory response of the individual, and by phylogenetic divergence in physiological mechanisms.

The selective advantages of heterogeneous isohaemoglobins have been considered for very few, predominantly European and North Ameri-

can freshwater teleosts, including fish with atypical diadromous behaviour (Brix et al. 1998b). For example, trout (*Salmo trutta*) and eel (*Anguilla anguilla*) possess both anodic isohaemoglobins which are sensitive to temperature and pH and are characterized by strong Bohr and NTP effects, and high-affinity cathodal components with low sensitivity to pH and temperature (Binotti et al. 1971; Fago et al. 1995, 1997a). In addition the effects of temperature and hypoxia on the expression of specific isohaemoglobins (Murad and Houston 1991; Houston and Gingras-Bedard 1994) demonstrate the phenotypic plasticity of the haemoglobin system in trout. Functionally heterogeneous isohaemoglobins of many Amazonian fishes have been suggested to be adaptive to water oxygen tensions in the tropics (Powers 1974, 1980; Fyhn et al. 1979; Val et al. 1990). This feature is supported by the observation that haemoglobins from ten different species of African cichlids share an identical electrophoretic pattern and similar haemolysate oxygen-binding properties (Verheyen et al. 1986). However, the Antarctic notothenioid fishes have few isohaemoglobins present, which correlates with low activity levels and the stability of the polar marine environment (high dissolved oxygen and constant low temperature) (DiPrisco et al. 1990; DiPrisco and Tamburrini 1992). Differences in the functional properties of these simple haemoglobin systems is correlated not with environmental factors but with organismal factors such as swimming behaviour and body mass (Wells and Jokumsen 1982; Fago et al. 1997b). Haemoglobin is not expressed at all in the channichthyid fishes (Cocca et al. 1997). Brix et al. (1999) showed that triplefin fishes living in shallow, thermally unstable habitats possess a greater number of cathodal isohaemoglobins, haemoglobin components that migrate towards the negative pole during electrophoresis. These species have haemoglobins with higher oxygen affinity and reduced cooperativity and which are less sensitive to changes in pH compared with haemoglobins of species occurring in more stable, deeper water habitats (Fig. 4.7). The analysis of an assemblage of closely related species circumvents some of the difficulties inherent in studies where interpretation of experimental results is confounded by phylogeny.

4.5.4 Influence of environmental temperature and hypoxia on oxygen uptake and transport

Coping with environmental temperature

Critical temperature thresholds (Tc) have been defined as the transition to an anaerobic mode of mitochondrial metabolism, once temperature reaches low or high extremes, due to insufficient ventilation and/or circulation and aerobic energy provision (Zielinski and Pörtner 1996; Pörtner et al. 1998). The lower Tc is set by insufficient aerobic capacity of the mitochondria, while the upper Tc is set by a mismatch of excessive oxygen demand by mitochondria and insufficient oxygen uptake and distribution by ventilation and circulation (Pörtner et al. 2000a). In the cold, energy demand will be met by mitochondrial proliferation, which ultimately will cause an increase in oxygen demand that becomes detrimental at the upper Tc. Oxygen demand is not only related to cellular energy requirements but also to the number of mitochondria and their properties, specifically maintenance of the proton gradient. The relationship between this so-called proton leakiness and aerobic capacity appears to be constant. Pörtner et al. (2000a) suggest that metabolic cold adaptation may depend upon the extent of diurnal and seasonal temperature fluctuations, leading to higher costs of maintenance in eurythermal than in stenothermal fish. Thus in stenothermal fish aerobic capacity and energy expenditure is minimized as far as possible according to environmental and lifestyle requirements.

The haemoglobin polymorphism of Atlantic cod (*Gadus morhua*), which possesses the phenotypes HbI_{11}, HbI_{12} and HbI_{22}, was described more than 30 years ago (Frydenberg et al. 1965; Sick 1965a,b). The frequency of the two alleles HbI(1) and HbI(2) shows a north–south cline along the Norwegian coast: the frequency of the HbI(1) allele is about 10% in the Barents Sea in Arcto-Norwegian cod, 20–50% along the coast of north-
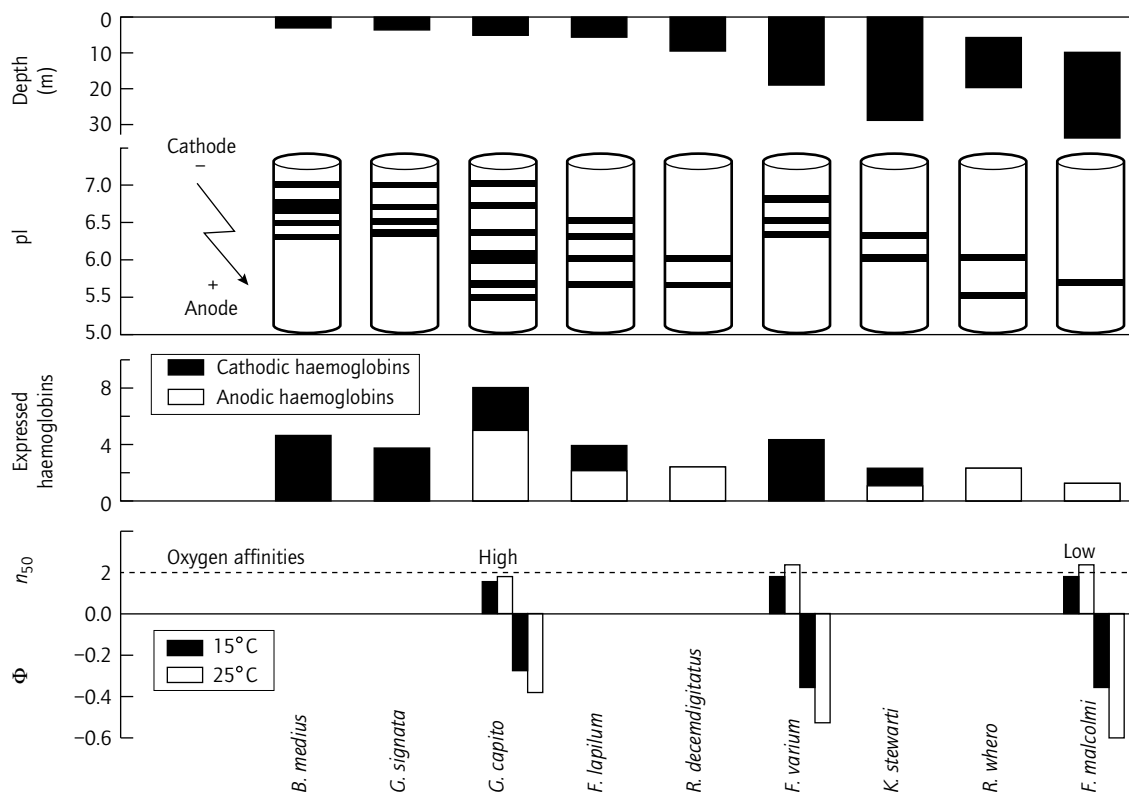
Fig. 4.7 Structural and functional properties of haemoglobins of nine species of triplefin (Blenniidae) in relation to their habitat (preferential depths). The species living in the unstable environment (i.e. rock pools) in the upper layers have a larger number of preferential cathodic haemoglobin components (those migrating towards the negatively charged cathode having isoelectric points, pI, >6.25), with higher oxygen affinities and lower cooperativity (expressed by the Hill coefficient, n_{50}) as well as a much lower pH sensitivity of oxygen binding (expressed by the Bohr coefficient

$$\phi = \frac{\Delta \log P_{50}}{\Delta pH},$$

where P_{50} is the partial pressure of oxygen at half saturation). Those species living in the deeper water, with less fluctuations in temperature and oxygen availability, had fewer haemoglobins. These were preferentially anodic (pI < 6.25), with a larger potential for allosteric regulation. The genera examined are *Bellapiscis* (*B.*), *Grahamina* (*G.*), *Fosterygion* (*F.*), *Ruanoho* (*R.*) and *Karalepis* (*K.*). (Source: Brix et al. 1999.)

ern and western Norway, and 70% in the Kattegat (Frydenberg et al. 1965). A similar, though less clear, cline can be seen along the North American east coast (Sick 1965b). According to these publications, genetic differences exist between Arctic cod and coastal groups as well as between populations of coastal cod. Karpov and Novikov (1980) reported on the functional properties of the HbI_{11}, HbI_{12} and HbI_{22} components. They suggested that the HbI_{22} molecule has the highest oxygen affinity and is the

most efficient oxygen carrier at low temperatures, while the HbI_{11} molecule has the highest affinity at about 20 °C. Brix et al. (1998a, submitted) and Pörtner et al. (2000b) clearly demonstrate that HbI_{22} is better fitted to cold temperatures than HbI_{11} because it is able to transport more oxygen from the environment to the tissues. This could result in a higher growth rate, a suggestion supported by length and weight data. However, while not excluding this possibility, it could also be a result of higher oxygen demand in response to cold adaptation, compensating for some of the energy loss caused by proton leakage in the mitochondria (see above). In both cases the HbI_{22} phenotype appears better fitted for life in cold environments. In the temperature range 8–12 °C, where maximal mean growth rates for all phenotypes have been reported, there are no differences with respect to oxygen-binding properties. Oxygen binding of all phenotypes is very sensitive to pH. Any temperature change would thus greatly affect oxygen affinities by indirectly changing pH (Brix et al. 1981). Brix et al. (submitted) further showed that the heterozygote, HbI_{12}, changed the concentration of haemoglobin components during long-term acclimation to either 4 °C or 12 °C, achieving similar oxygen-binding properties as HbI_{11} in the warmer water and vice versa. This clearly suggest that selection is very important for the evolution of cod. These results are supported by the work of Árnason et al. (1998), who found that the stock from both the Baltic and Barents Sea are more related to the North Atlantic stock than with each other, supporting the hypothesis of a transatlantic flow of genes (Árnason et al. 1992). More detail on the genetic structure of North Atlantic cod stocks is given by Ward (Chapter 9, this volume).

Temperature not only influences the metabolism of fish but also oxygen availability. At high temperatures the oxygen concentration in water will be markedly reduced, which makes it very difficult for fish to meet the extra oxygen demand. We refer to this condition as environmental hypoxia, and fish have to make significant circulatory and respiratory adjustments in order to extract sufficient oxygen from the water.

Coping with low oxygen availability

Environmental hypoxia causes a fish to maximize oxygen transport by cellular adjustments in the red blood cells combined with a reduced heartbeat (bradycardia), an increase in cardiac stroke volume, increased peripheral resistance, and enhanced efficiency of gas exchange linked to increased lamellar recruitment in the gills (Satchell 1971; Booth 1978). Hypoxia causes the following:

1 reduction of ATP (GTP) production in the cells, which in turn changes the Donnan equilibrium, the passive distribution of solutes over a semipermeable membrane, causing a decrease in the concentration of protons and thus an increase in intracellular pH;

2 increase in ventilation, causing increased plasma pH and thus intracellular pH;

3 increase in Hb/HbO_2 ratio (chronic hypoxia), causing an increase in intracellular pH.

The reduction in ATP (GTP) and the increase in intracellular pH increases oxygen affinity, which thus safeguards oxygen uptake (Weber et al. 1976). When oxygen availability in water becomes limited fish have to breathe air.

Air breathing   Various groups of fish have solved the problem of air breathing in different ways, ranging from simple modification of the gills that prevent them from collapsing in air to using the mouth, special parts of the gut, the swimbladder, or even the development of lungs. The role of the gills in oxygen uptake is reduced but they are still the most important site for carbon dioxide elimination. The air-breathing organs in bimodally breathing fish are well vascularized with an efficient blood supply. In species using modified gills, mouth or opercular cavities for air breathing, the air-breathing organs are parallel with the gills and the blood enters directly into the systemic circulation. For most other bimodal breathers, blood from the air-breathing organ passes the gills before entering the systemic circulation. The lungfish, Dipnoi, have separated the pulmonary and branchial circulation allowing them, unlike most other air-breathing fishes, to respire with their

lungs and gills simultaneously (Johansen et al. 1968). The tetrapods evolved from this ancient group of fish (see Gill and Mooi, Chapter 2, this volume).

As water dries up and becomes more and more muddy, the African lungfish (*Protopterus*) makes a bottle-shaped burrow lined by mucus secreted by the skin to form a cocoon and the fish becomes torpid. The nares becomes plugged with mud and the fish breathes air through its mouth about once an hour. The lungfish may remain aestivated for more than 6 months and may survive for years in this condition. During aestivation, when ammonia excretion over the gills is impossible, urea is formed in the liver and accumulates in the blood. Other species, like the western Australian *Lepidogalaxias salamandroides* and the New Zealand mudminnows (*Neochanna*), also aestivate during periods of drought.

4.6 DIGESTION AND ABSORPTION

4.6.1 Structure and function of the alimentary tract

Our knowledge of digestive physiology is based largely on studies conducted on carnivorous Northern Hemisphere species (Kapoor et al. 1975; Fänge and Grove 1979; Helpher 1988; Lovell 1989), most of which are freshwater or diadromous taxa such as salmonids (Christiansen and Klungsøyr 1987). Thus, the overall morphology and enzyme complement of the alimentary tract appears to be more or less 'hard-wired' to the 'normal' diet of the fish (Jobling 1998). However, many fish in the tropics and the Southern Hemisphere are herbivorous, a fact that has been very little considered in the physiological literature (Clements 1997). The low nutritional value of diets high in fibre requires the ingestion and processing of a large volume of food (Stevens 1988). The extra time necessary for microbial digestion of this refractory material requires the retention of food within the gut for extended periods of time, and the ability of herbivorous fish to triturate ingested food influences the rate and efficiency of fermentation (Bjorndal et al.

1990). The ability to triturate, contain, and retain plant material will therefore have a major impact on the structure and function of the alimentary tract, in particular the possible role of gastrointestinal microbes in digestion. The material in this section is complementary to the chapter on growth by Jobling (Chapter 5, this volume) and the chapter on the behavioural ecology of feeding by Mittelbach (Chapter 11, this volume).

4.6.2 Carnivorous fish

As in other vertebrates the alimentary tract in fish is divided into the mouth and buccal cavity, the pharynx, the oesophagus, the stomach, the intestine with the pyloric caeca and related organs (liver, gallbladder and pancreas), and the rectum and anus. The alimentary tract is lined by an inner epithelium called the mucosa, underneath which is the submucosa, a layer of circular and longitudinal muscles called the muscularis, and the serosa. The thickness of the different layers varies in the different parts of the alimentary tract.

Ingested food is sometimes broken down mechanically in the mouth and pharynx. In the oesophagus, which is highly distensible, the food is lubricated by mucus secreted from the mucosa before entering the stomach. The stomach in fishes can be a straight tube, U-shaped, or Y-shaped with a gastric caecum (Fänge and Grove 1979; Helpher 1988; Stevens 1988). Distension of the stomach activates a cholinergic response, which triggers secretion from the gastric mucosa of hydrochloric acid, which decreases pH, and protease enzymes such as pepsin that have a pH optimum of 2–4. In the foregut, the caecal tissue or the pancreatic tissue, which commonly envelops the caeca, produces a secretion with a pH of 7–9 that contains trypsin, an enzyme that digests protein at alkaline pH. The pancreatic tissue is also the primary site for the production of lipase and amylase, which digest fat and carbohydrate. Lipase activity has also been found in the caecal tissue and in the upper part of the intestine (Chesley 1934). The pyloric caeca may also secrete fluids that serve to buffer intestinal contents (Montgomery and

Pollak 1988). A muscular valve or sphincter, a fold in the mucous membrane, controls the flow of food into the intestine (Stevens 1988). Assimilation of digested food also takes place in the intestine.

The behaviour and ecology of predatory fish is described in detail in Juanes et al. (Chapter 12, this volume).

4.6.3   *Herbivorous fish*

Most marine herbivorous fish belong to the order Perciformes (Horn 1989; Choat 1991). They have typically a small gape for taking rapid small bites, and a row of small closely spaced mandibular teeth that serve to crop plant material or scrape it from the substratum. In some fishes these teeth have become fused into a parrot-like beak (Scaridae, Odacidae; Clements and Bellwood 1988). Some herbivorous fish have developed pharyngal teeth on the modified fifth gill arch, which does not carry gills (Helpher 1988; Horn 1989, 1992). Buccal teeth, which prevent the escape of prey, are not important in herbivorous fish. Some fish, like the surgeonfish (*Acanthurus*) and the girellids (*Ctenochaetus*), have developed gizzard-like stomachs similar to those in birds that serve to break down the cell walls of bacteria, blue-green algae, diatoms and filamentous red and green macroalgae, which are ingested along with some sedimentary material (Payne 1978; Lobel 1981; Horn 1992). The stomach may be absent in many herbivorous fishes like cyprinids, odacids and scarids. These fish typically have a pharyngeal apparatus for processing food before it enters the intestine (Fänge and Grove 1979; Stevens 1988). Most species containing high concentrations of short-chain fatty acids (SCFA) in the gut lack a mechanism for mechanical triturating ingested material (Clements 1997). Specialized fermentation chambers have been found in a few species, but high concentrations of SCFA in the gut of fish lacking these chambers suggests that material is retained in the intestine long enough for fermentation to take place. It appears that gastrointestinal microorganisms are transmitted in some species by the ingestion of infected faecal material, as occurs in herbivorous reptiles (Troyer 1984), and in

other species by the ingestion of infected food or water. Some species seem to have evolved specific mechanisms for the retention and transfer of endosymbionts. The parrotfishes, however, do not contain an obvious microbiota (Clements 1991), probably due to the slurry of calcium carbonate in the alimentary tract causing unfavourable conditions for the development of large populations of microorganisms (Clements 1997).

4.7   BIOLUMINESCENCE

4.7.1   *From oxygen defence to deep-sea communication*

Bioluminescence, the emission of ecologically functional light by living organisms, emerged independently during evolution on several occasions. The substrates of the luminous reactions, luciferins, are suggested to be the evolutionary core of most systems. The luciferases, the enzymes catalysing the photogenic oxidation of luciferin, thus serve to optimize the expression of the endogenous chemiluminescent properties of luciferin. It has been suggested that the primary function of coelenterazine, a luciferin with strong antioxidative properties that occurs in many marine bioluminescent groups, was originally the detoxification of deleterious oxygen derivatives such as the superoxide anion or peroxides (Rees et al. 1998). When marine organisms began colonizing deeper layers of the oceans, where exposure to oxidative stress is considerably lowered because of reduced light irradiance and lower oxygen levels, the strength of selection for antioxidative defence mechanisms decreased and their light-emitting function evolved. The endogenous production of reactive oxygen species would decrease in parallel with the decrease in metabolic activity at increasing depths, and mechanisms for harnessing the chemiluminescence of coelenterazine in specialized organs could have developed, while the beneficial antioxidative properties were maintained in other tissues.

Some species use lights as lures, such as barbells and fishing rods with luminous tips, whilst others have light organs in the mouth or even headlights

to illuminate their prey. For the great majority of these fish, photophores are used for signalling other members of the same species, or for camouflage. Most bioluminescent fish are self-luminescent, although a substantial minority of bioluminescent teleosts produce light that is due to symbiotic luminous bacteria housed in elaborate light organs.

4.7.2 Symbiotic luminescence

The majority of symbiotically bioluminescent fishes, in ten families in five orders, harbour common free-living species of marine luminous bacteria: *Photobacterium phosphoreum*, *P. leio gnathi* and *P. fischeri* (= *Vibrio fischeri*). Others, associated with the beryciform family Anomalopidae and nine families in the lophiiform suborder Ceratioidei, have apparently obligate symbionts that have recently been identified by small subunit (16S) rRNA analysis as new groups within the genus *Vibrio* (Haygood 1993). Fish with symbiotic luminescence have normally not more than one or two, or a maximum of four, light organs probably due to problems of infection and maintenance. The same organ may serve several purposes, such as illuminating prey, schooling and sexual communication.

4.7.3 Self-luminescence

Fish with self-luminescence often have many photophores, which allows them to use different ones for different purposes. Within the upper 1000 m of the ocean, down-welling light will silhouette the fish when looked at from below. Fish with photophores can make themselves invisible when viewed obliquely or directly from below by emitting light that matches the angular distribution and wavelength as well as the intensity of the ambient background light. The photophores, which are richly innervated by the autonomic nervous system, are arranged in ventrally directed tubes along the lower part of the fish. The light is produced in a dorsal chamber, lined with black pigment apart from a series of small ventral windows. After passing a colour filter transmitting at 485 nm, light then leaves the photophore in a particular pattern that differs in intensity at different angles (Bone et al. 1996).

4.8 CONCLUSIONS

In this chapter I have reviewed some of the most important physiological mechanisms that fish use to cope with the four major physical and chemical constraints imposed on life in the aquatic environment.

The high density of water reduces the effects of gravity and enables fish to remain suspended in the water column using a minimum amount of energy. Fish cope with buoyancy problems by applying either dynamic or static lift or a combination of both. Lift forces are generated by the caudal and pectoral fins acting as lifting foils at about the centre of gravity of the fish and depend on a minimum cruising speed to prevent the fish sinking. Static lift is obtained by the use of lipids and/or gas. Since the volume of gas is inversely proportional to the ambient pressure, which increases by 101 kPa for each 10 m of depth, the swimbladder must have mechanisms for efficient filling and emptying at different depths. Gas can be released either via the pneumatic duct into the gut whilst ascending/diving (physostomes), or into the circulation via the oval chamber (physostomes/physoclists).

The low compressibility of water influences the swimming performance of fish, which have to push water aside to move through it. For this purpose they have developed different motor systems, reduced the drag forces and the cost of locomotion, and increased the efficiency of respiratory and cardiovascular adaptations during swimming.

The most important characteristic of water is that it is an almost universal solvent, containing complex mixtures of salts, organic compounds and gases. Many of these are essential for life and are taken up by fish using specialized organs in complicated processes of ion regulation, osmoregulation, gas exchange and acid–base balance, or via digestion of food. The osmolality of fresh water is <10 mosmol, and sea water falls within the range 800–1300 mosmol. The freshwater teleosts have

blood osmolalities of about 260–330 mosmol kg^{-1}. Thus these fish will be subjected to a passive influx of water and efflux of ions. In marine fishes, which have blood osmolalities in the range 370–480 mosmol kg^{-1}, these fluxes will be reversed. At subzero temperatures, marine fish may produce macromolecular 'antifreeze' compounds in their blood serum. The antifreeze consists of glycoproteins or proteins, which coat and isolate ice crystals forming in the blood.

Water contains very little oxygen compared with air. Fish have therefore evolved a unidirectional flow of water over their gills to maximize oxygen uptake. Cutaneous respiration may be occasionally of some significance either when oxygen demand is very low, as in some Antarctic fishes, or when the diffusion distance is very short, as for fish larvae. The main tasks of the circulatory system are to transport respiratory gases, nutrients, metabolic waste products, endocrine factors and heat. To ensure an adequate supply of oxygen to all parts of the organism, oxygen is transported by haemoglobin. Different haemoglobins have evolved and have acquired special features to meet special needs. Both the number of these so-called isohaemoglobins and their functional heterogeneity is related to the constancy of physicochemical conditions in the environment.

Temperature is probably the most important environmental factor influencing the life of fish. Oxygen transport may be optimized to different temperatures by changing the concentrations of isohaemoglobins, as seen for the Atlantic cod. At high temperatures, the oxygen concentration in water will be markedly reduced, which makes it very difficult for fish to meet the extra oxygen demand. Fish thus have to make significant circulatory and respiratory adjustments in order to extract sufficient oxygen from the water.

The transparency of water is very poor. Since most food production is within the photic zone, most fish reside in this region, where prey capture depends on good visibility and well-developed eyes. In the dark zone of the oceans, however, fish that communicate and capture prey by producing their own light using photophores.

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5 Environmental Factors and Rates of Development and Growth

MALCOLM JOBLING

5.1 INTRODUCTION

Information about fish age, development and growth is a cornerstone in fishery research and management. Development describes the sequencing of life-history stages and growth is a measure of change in size of either the whole body or some body part; growth rate is a measure of size change as a function of time. Growth depends upon the quantity and quality of food ingested, with inadequate nutrition both retarding growth and delaying developmental transitions, such as the timing of onset of sexual maturation. When food is limited the onset of maturation may be delayed for months or years, until good feeding conditions arise. In other words, the timing of sexual maturation appears to be more closely associated with size than age, leading to the concept that maturation is initiated once a 'critical size' has been attained. Further, during adulthood, fecundity or gamete production may be related to body size, and alterations in nutrition can lead to either depression or enhancement of reproductive activity (see Hutchings, Chapter 7, this volume).

Perhaps the most intriguing issue involved in understanding development, growth and sexual maturation is determining how the brain 'knows' when the body has reached the appropriate size for initiation of the physiological cascade that culminates in the production of the first gametes. Over recent years, the concept of maturation at some 'critical size' has been extended to encompass both a 'critical weight' and a 'critical level of nutritional status, or fatness', and now incorporates notions about the way in which specific metabolic signals related to size and nutrition may be assessed and integrated within the brain and central nervous system (Robinson 1996; Kiess et al. 1999; Magni et al. 2000; Mystkowski and Schwartz 2000). Thus there are close interrelationships between the availability of food, increase in size and the accumulation of energy reserves, the timing of sexual maturation and reproduction. These, in turn, relate to production, which is determined by the rate of reproduction, the rate of growth of individuals within the population, and the rate of mortality. These functional rates determine population dynamics over time, as well as structural elements of the population, such as biomass, density and size–frequency distribution, at any point in time. As such, information about age and growth is extremely important in almost every aspect of fisheries. The purpose of this chapter is to examine ways in which age and growth data can be collected and analysed, and to provide a brief overview of the environmental factors that may have an impact upon rates of development, growth and reproduction of fish.

5.2 TERMINOLOGY OF LIFE-HISTORY STAGES

The problem of terminology and sequencing of the life-cycle intervals of fish is a long-standing one,

and particularly so for the earliest part of the life history. A good terminology should be simple and linked to form and function. Difficulties arise in producing a terminology that meets the needs of workers representing different disciplines (e.g. developmental biology, taxonomy, physiology, fisheries biology and management) and encompasses the myriad patterns of development seen in fish. For example, some species of fish hatch in a well-developed state, especially where there is viviparity, ovoviviparity or a protracted incubation period within the egg; other species have short egg incubation times and the fish hatch at a much earlier state of development (Blaxter 1988; Balon 1990; Jobling 1995; Hutchings, Chapter 7, this volume).

Balon (1975, 1984, 1990) proposed a saltatory model of development in which the entire life history, from the fertilization of the egg until death, can be divided into five periods: embryonic, larval, juvenile, adult and senescent. The model is termed 'saltatory' because the periods are separated by major thresholds involving a rapid transition to a new 'stabilized' state. Each period may be divided into phases, as a convenient means of identifying different levels of morphological or physiological development. Steps, which are the shortest intervals of ontogeny, are separated by less dramatic thresholds, and are found within a phase. Metamorphosis is a major threshold separating the larval period from the juvenile or adult period. Early in the life of the fish developmental events are reflected in rapid morphological and physiological changes, but in each successive period the developmental rate decreases until senescence and death.

The embryonic period, starting with fertilization of the egg, is characterized by endogenous nutrition. This may be from the yolk or, in the case of viviparous species, nutrition via special absorptive organs (Balon 1990). The embryonic period includes a cleavage phase, covering the time between fertilization and the commencement of organogenesis, and an embryonic phase within which there is intense organogenesis within the egg membrane. The embryonic phase continues until hatching, when the embryo enters the eleutheroembryonic phase (Greek *eleutheros*,
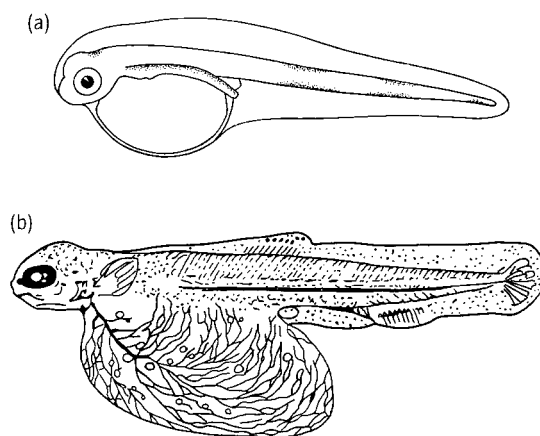
Fig. 5.1 Recently hatched, free embryos (eleutheroembryos) of two fish species that differ in developmental pattern. (a) The Atlantic cod, *Gadus morhua*, has small (1.1–1.9 mm diameter) pelagic eggs with a relatively short incubation time (9–25 days) and the fish are small (3.5–4.5 mm) at hatch. (b) Atlantic salmon, *Salmo salar*, produce large (5–6 mm diameter) demersal eggs which hatch to give large (15–25 mm) offspring after protracted incubation (50–160 days). (Source: from Jobling 1995.)

free)(Fig. 5.1) and this continues until most of the yolk has been utilized and the fish begins to take exogenous food.

The larval period starts when the transition to exogenous feeding has taken place. This period lasts until ossification of the axial skeleton. Some embryonic organs persist, and there may be development of organs which are later lost or replaced by others performing the same function. Examples are surface blood vessels on fins and filamentous appendages used in gas exchange. The larval period may be divided into two phases: the protopterygiolarval and the pterygiolarval phases. The first spans the interval between the first exogenous feeding and the start of fin differentiation. The pterygiolarval phase terminates when the median fin-fold is no longer visible. The larval period may be long, as in some species of eel (e.g. *Anguilla* spp.), whereas in salmonids it is difficult to distinguish a distinct larval period.

The juvenile period begins once the fins are

fully differentiated, and the temporary larval organs have regressed or been replaced. The transition from larva to young fish sometimes involves extensive changes from an unfish-like appearance to one resembling the adult, i.e. there is a metamorphosis. The juvenile period lasts until the fish mature and the first gametes are produced. Juveniles are characterized by their rapid growth, and there can be a distinct juvenile body colour or pigmentation pattern.

The adult period starts with gonad maturation, culminating in the production of the first gametes. The adult period usually incorporates spawning runs or migrations (see Metcalfe et al., Chapter 8, this volume), specialized reproductive behaviour (see Forsgren et al., Chapter 10, this volume), and changes in external morphology and colour. Spawning may be repeated for a number of years or seasons, as in iteroparous species, or may be performed only once, as is the case with the semelparous species, such as some eels and salmonids (see Hutchings, Chapter 7, this volume). During the adult period, available resources may be directed more towards the development of the gonads than towards somatic growth. Consequently, rates of growth are generally lower during this period than during the juvenile period.

The senescent period covers a period of extremely slow growth during which reproductive activity may also be reduced. The period of senescence can last for several years, during which there is a gradual decline in the numbers of fertile gametes produced (e.g. sturgeon, *Acipenser sturio*). Alternatively, the senescent period may last for no more than a few days or weeks, during which time the body undergoes rapid degenerative changes (e.g. Pacific salmon, *Oncorhynchus* spp.).

Balon's (1975, 1984) saltatory model and terminology of ontogeny are holistic, and there are compelling arguments for their adoption (Balon 1990, 1999). However, they have not been universally accepted due to a failure to highlight some transitional events that many workers consider important. For example, according to Balon's terminology, the larval period is defined as starting when the fish undergoes the transition from endogenous to exogenous feeding. Hatching is not deemed to be sufficiently significant to merit use as a criterion for demarcation of the transition between developmental periods. Many workers, however, consider the larval period to commence at the point at which the fish hatch, and will refer to the newly hatched fish as a yolk-sac larva. Blaxter (1988) recommends that the terms 'embryo' be used to cover the period from fertilization to the point of hatching, 'larva' to cover development from hatching to metamorphosis, and 'juvenile' for the period from metamorphosis to first spawning. As a supplement to this, Kamler (1992) provided a series of developmental divisions based upon the general sequence of growth patterns displayed during the early life of fish. An embryo grows slowly from fertilization to hatching, and growth accelerates following the transition to a yolk-sac larva. Larvae grow to reach the maximum size that their yolk reserves will support and then growth rate decreases, usually coincident with the start of exogenous feeding. Between the start of exogenous feeding and final yolk resorption there is often an energy deficit, involving negative growth; after final yolk absorption non-feeding larvae continue to show weight loss and die from starvation, whereas feeding larvae show rapid growth.

5.3 DEVELOPMENT AND GROWTH DURING EARLY LIFE HISTORY

Rates of development and the timing of transitional events from one life-history period to the next are, to a certain extent, genetically determined and can be considered as species-specific characteristics. For example, large eggs, such as those of salmonids, take longer to hatch than small eggs, and, in general, eggs from fish living at high latitudes take longer to hatch than those from the tropics (Fig. 5.2)(Kamler 1992; Jobling 1995; Rombough 1997). Environmental factors may, however, have a major modifying influence on rates of development. Ambient temperature, for example, is known to be one of the most potent factors influencing both rates of development and
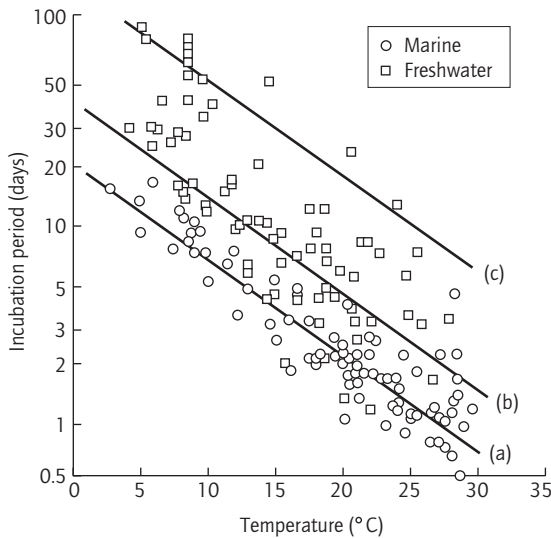
Fig. 5.2 Influence of incubation temperature on the time to hatch for eggs of a range of marine and freshwater fish species. Note that, in addition to temperature, egg size also has a major influence on incubation period. The lines indicate estimated incubation times for eggs of (a) 0.5 mm, (b) 2 mm and (c) 5 mm diameter, respectively. (Source: from Rombough 1997.)

the overall survival of the eggs and larvae (Blaxter 1988, 1992; Kamler 1992; Rombough 1997). Rates of development are generally found to increase with increasing temperatures. However, incubation of eggs at high temperature may result in increased incidence of malformations and abnormalities in the embryo, or the death of the eggs. Temperature can also influence size at hatching, efficiency of yolk utilization, time to metamorphosis, behaviour, rates of feeding and metabolic demands.

The simplest relationship used to describe the influence of incubation temperature on rates of development is a hyperbolic function, which encapsulates the concept of 'degree-days'. This states that the product of the incubation temperature (T in °C) and the time (D in days) required to reach any particular stage of development, e.g. from fertilization to hatch, is constant:

$$T \times D = \text{constant.} \tag{5.1}$$

A modification has been proposed in which temperature may be measured from a point other than 0 °C. When T_0 is defined as the new base temperature the expression becomes:

$$(T - T_0)D = \text{constant.} \tag{5.2}$$

In this expression T_0 is the so-called biological zero, i.e. the incubation temperature at which, in theory, the time to reach the given stage of development would be infinite. T_0 may be close to 0 °C for cold-water and temperate species, but will be higher in warm-water species. Thus, the introduction of T_0 would appear to make the hyperbolic relationship applicable to the description of developmental rates of a larger number of fish species, especially those which require warm water for egg incubation and embryo development (e.g. Weltzien et al. 1999). Nevertheless, when the degree-day formula is applied to experimental data involving a wide range of temperatures it may not be found to be satisfactory.

Numerous other mathematical expressions have been used to describe the curvilinear relationship between incubation time and temperature (Cossins and Bowler 1987; Kamler 1992), with both power law (i.e. $D = aT^b$) and exponential (i.e. $D = ae^{-bT}$) equations having been widely used to describe the relationship (Kamler 1992; Rombough 1997). However, both the power law and exponential functions have the weakness that they do not take into account the fact that there are temperature extremes outside of which egg incubation is impossible, and mortality will be complete. When data have been fitted to the power law function, the constant b, which describes the inverse relationship between incubation time and temperature, has usually been found to be within the range 1–1.5. With the exponential function the value of b will usually be 0.1–0.15. Since Q_{10} and the constant b in the exponential function relate to each other as in $Q_{10} = 10^b$, these constants translate to Q_{10} values of 3–4, meaning that the developmental rate roughly triples or quadruples with each 10 °C increase in temperature. Cold-water species appear to be particularly responsive. Developmental rate is also highly dependent upon egg size, with

the time to hatch at any given temperature being almost an order of magnitude longer for large eggs than small (Fig. 5.2). Rombough (1997) summarized data for various freshwater and marine species (n = 171) in a regression equation that accounted for 84.4% of interspecific variability in the time for eggs to hatch:

$$\log D = 1.20 - 0.0494T + 0.203d \qquad (5.3)$$

where D is incubation time (days), T is temperature (°C) and d is egg diameter (mm). This equation gave an overall Q_{10} of 3.1. Rates of posthatch larval development appear to be less temperature sensitive than rates of prehatch embryonic development, Q_{10} values of about 2 seeming to apply to rates of development of larvae following hatch (Rombough 1997). One should caution, however, that although it is possible to use Q_{10} to relate temperature to developmental and physiological processes, Q_{10} values do not remain constant over wide ranges of temperature. Thus, although Q_{10} values can be useful for predictive purposes over narrow temperature ranges, extrapolations to temperature extremes should not be attempted.

In addition to influencing rates of development of eggs, embryos and larvae, temperature may affect the interactions between growth and differentiation. The best-known effect is that on meristic characters. The number of serial structures such as vertebrae, scales and gill rakers is labile and susceptible to environmental influence (Blaxter 1988; Lindsey 1988). There is also some evidence of a prefertilization influence on meristic characters, i.e. the temperature experienced by the broodstock during gametogenesis may influence the meristic characters of the offspring.

The number of vertebrae tends to be higher in fish from polar and temperate waters than in their relatives from tropical waters. This phenomenon, termed Jordan's rule, is usually described in relation to latitude, but may be attributable to the fact that fish from different latitudes are usually subjected to different thermal environments during early development (Lindsey 1988). In addition, meristic counts of wild fish hatched in the same place often vary between years, and the differences

appear to be associated with year-to-year differences in temperature in the period during spawning and early development (e.g. Brander 1979; Løken et al. 1994). Further, within year-classes a protracted spawning season coupled to changes in water temperature over time may be associated with meristic differences between those individuals which hatch and develop at different times (Lindsey 1988). Thus, environmental influences on meristic counts may be superimposed upon genetically controlled responses (Lindsey 1988). For example, Løken and Pedersen (1996) reported an inverse relationship between incubation temperature and vertebral number in cod, *Gadus morhua*, although vertebral numbers differed between the offspring of coastal cod and northeastern Atlantic cod when they were reared at the same temperature. Meristic characters can be greatly modified by the environment experienced during early development. Later, but still quite early in ontogeny, these characters become fixed and remain unchanged thereafter.

Environmental factors, particularly temperature, probably influence meristic characters by differentially affecting the processes of growth through body elongation and differentiation expressed as segment formation; temperature may also have profound influences upon other developmental events such as muscle differentiation and the relative timing of organogenesis (Blaxter 1988, 1992; Johnston 1993; Brooks and Johnston 1994; Nathanailides et al. 1995; Johnston et al. 1996, 1997). Environmental factors may also influence sex determination in several animal groups, including fish (Baroiller et al. 1999; Baroiller and D'Cotta 2001). This phenomenon, known as environmental sex determination (ESD) (Janzen and Paukstis 1991; Crews 1996; Shine 1999; see also Forsgren et al., Chapter 10, this volume), means that the environment experienced by fish during early development can influence phenotypic sex (Conover et al. 1992; Baroiller et al. 1995, 1996, 1999; Craig et al. 1996; Patino et al. 1996; Römer and Beisenherz 1996; Strüssmann et al. 1996, 1997; Nomura et al. 1998). It is the effects of temperature on sex determination that have been most studied in fish, although both salinity and

xenobiotics are known to influence phenotypic sex in some fish species (Baroiller et al. 1999; Baroiller and D'Cotta 2001).

Sex ratios that deviate significantly from the theoretical 1:1 amongst groups of fish reared at different temperatures could arise from differential mortality of the sexes. Thus, deviations of the sex ratio from the expected 1:1 amongst fish reared under different temperature conditions cannot be taken as providing conclusive evidence of ESD (Strüssmann et al. 1997; Nomura et al. 1998). Conclusive evidence of ESD has, however, been obtained by progeny testing of fish that have been subjected to different temperature treatments, and by demonstration that temperature can induce a phenotypic sex change within gynogenetic monosex populations (Baroiller et al. 1995, 1996, 1999; Nomura et al. 1998; Kitano et al. 1999; D'Cotta et al. 2001a,b).

Whether or not temperature has any influence on the phenotypic sex of individuals within a given species will depend upon the strength of genetic sex determination, and when in development the temperature treatment is applied (Baroiller et al. 1995, 1996, 1999; Römer and Beisenherz 1996; Strüssmann et al. 1996, 1997). This is to be expected because determination of phenotypic sex in fish is also sensitive to sex steroid hormone treatments only at particular stages of development (reviewed by Purdom 1993 and Patino 1997). It is unlikely that the periods of sensitivity to temperature and sex steroids will differ, because the physiological effects of temperature treatment appear to be mediated via actions on genes coding for P450 steroidogenic enzymes, such as aromatase, and sex steroid hormone receptors (Crews 1996; Baroiller et al. 1999; Kitano et al. 1999; Baroiller and D'Cotta 2001; D'Cotta et al. 2001a,b).

5.4   GROWTH MODELS AND EQUATIONS

Growth equations are used to describe changes in the length or weight of a fish with respect to time, although the constants derived from such empirical equations may have no exact biological meaning. Numerical expressions of growth may be based on absolute changes in length or weight (absolute growth), or changes in length or weight relative to the size of the fish (relative growth). Length almost always increases with time, whereas weight can either increase or decrease over a given time interval depending upon the influences of the various factors that affect the deposition and mobilization of body materials. Measurements of growth in relation to time provide an expression of growth rate. Growth in length can usually be modelled using an asymptotic curve which tapers off with increasing age (Fig. 5.3). Growth in weight is usually sigmoidal, i.e. the weight increment increases gradually up to an inflection point from where it gradually decreases again. Thus, growth rates are constantly changing, and the absolute growth increments will be different for different sizes of fish.
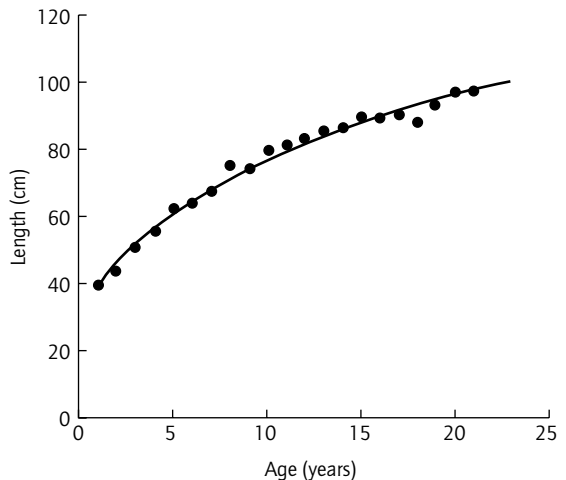
Fig. 5.3 Length at age plot for female spiny dogfish, *Squalus acanthias.* The parameters L_∞ and k of the von Bertalanffy growth function are about 104 cm and 0.106, respectively. Spiny dogfish are ovoviviparous, with prolonged intrauterine incubation of large eggs. Extrapolation of the regression line gives an intersection on the *y*-axis above the origin, providing an indication of intrauterine growth and an estimate of the length at 'birth' (*c.*25 cm), whereas the negative intersection on the *x*-axis gives an estimate of gestation time (*c.*2 years). (Source: data from Holden and Meadows 1962.)

A number of mathematical functions have been used to describe growth curves, including the Gompertz, the logistic, and a range of straight-line and exponential approximations (Beverton and Holt 1957; Ricker 1979; Weatherley and Gill 1987; Prein et al. 1993; Elliott 1994). Life-history patterns of fish vary in a consistent fashion, and growth and maturation parameters are closely interrelated (Adams 1980; Charnov and Berrigan 1991; Beverton 1992; Gunderson 1997; He and Stewart 2001; Hutchings, Chapter 7, this volume). As such, it may be possible to estimate both the age and size at first reproduction from the information encapsulated in a growth trajectory plot (Charnov and Berrigan 1991; He and Stewart 2001). Charnov and Berrigan (1991) and He and Stewart (2001) summarized the interrelationships and provided models, Beverton (1992) considered the relationships within the framework of the growth–maturity–longevity (GML) plot, and Gunderson (1997) reviewed the relationships for viviparous and oviparous fish species: viviparity seemed to be associated with reduced reproductive effort, increased age at maturity and low mortality relative to oviparous species of similar size.

The von Bertalanffy growth function (VBGF) fits many observations on the growth of fish and is widely used in fisheries research because the constants were readily incorporated into early stock assessment models (Beverton and Holt 1957). The simplest derivation of the VBGF is:

$$\delta L / \delta t = k(L_\infty - L) \tag{5.4}$$

where L is length, t is time, L_∞ is the asymptotic length, which is the length the fish would reach if it were to grow to an infinite age, and k is the growth constant expressing the rate at which length approaches the asymptote (Gulland 1969; Ricker 1979). Whereas L_∞ has a straightforward interpretation, that of k is less easy because it describes the instantaneous growth rate $(\delta L / \delta t)$ relative to the difference between L_∞ and the length of the fish at a given time. Integration of the VBGF gives:

$$L_t = L_\infty \left(1 - e^{-k(t - t_0)} \right) \tag{5.5}$$

where L_t is length at time t, and t_0 is the theoretical 'age' of the fish at zero size.

The two constants L_∞ and k can be estimated from measurements of fish length at known fish ages (Gulland 1969; Bagenal and Tesch 1978; Prein et al. 1993). Before personal computers became widely available it was difficult to fit the VBGF to length-at-age data, and several methods were developed for the estimation of L_∞ and k (Fig. 5.4). One method involves making a plot of the annual increment of length $(L_{t+1} - L_t)$ against length (L_t), where L_{t+1} is length at age $t + 1$ and L_t is length at age t. This gives a straight line with a slope of $-(1 - e^{-k})$, and an intercept on the abscissa (i.e. where $L_{t+1} - L_t = 0$) equal to L_∞. This equation is also known as the Brody equation, as mentioned by Schnute and Richards (Chapter 6, Volume 2). This expression not only establishes the constants in the VBGF but also provides an indication of the decline in the rate of growth with age. The constants can also be estimated from a plot of L_{t+1} on L_t, the Ford–Walford plot (Fig. 5.4). The rate of growth of the fish slows with age so the plotted line gradually approaches a 45° line passing through the origin. The two lines will intersect at L_∞, the point of intersection indicating when the lengths of the fish at the start (L_t) and end (L_{t+1}) of the growth period are identical, i.e. the fish has ceased to increase in length, and the annual growth increment is zero. The growth constant, k, can also be estimated from the plot of L_{t+1} on L_t because the slope of the line is equal to e^{-k}. Much work has been done on developing methods for fitting and testing VBGF data, and with the advent of the personal computer the handling of the data has become much easier (Gallucci and Quinn 1979; Misra 1986; Ratkowsky 1986; Cerrato 1990, 1991; Xiao 1994). For a generalization of the von Bertalanffy model see Schnute (1981).

Bayley (1977) pointed out that a weakness in several of the methods is a lack of independence between the variables plotted. In an attempt to overcome the problem, Bayley (1977) devised a method for the estimation of the VBGF constants $(L_\infty$ and $k)$ using measurements of instantaneous growth rates $(\delta(\ln W) / \delta t)$ and a description of the length–weight relationship $(W = cL^m)$. From

(a)

(b)
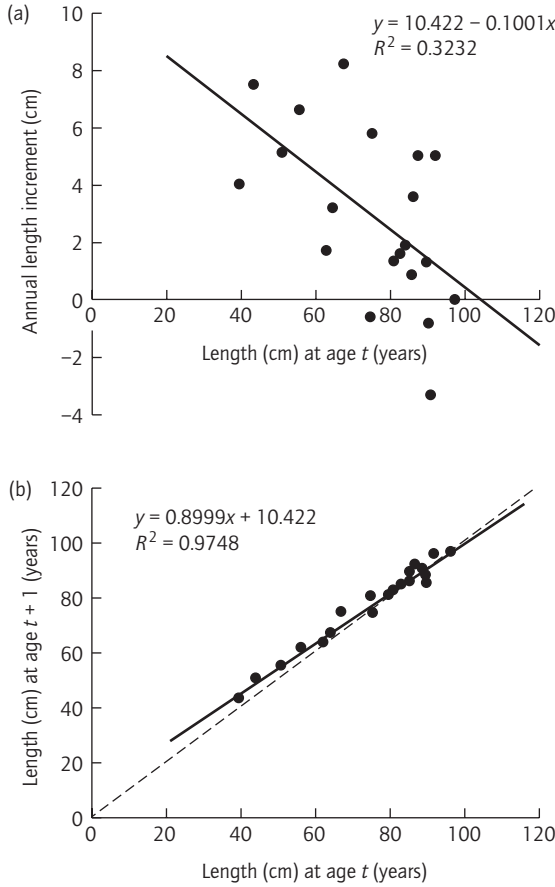
Fig. 5.4 Graphical methods for estimating the parameters L_∞ and k of the von Bertalanffy growth function using data for female spiny dogfish, *Squalus acanthias*, as an example (see Fig. 5.3 for length at age plot). (a) A plot of the annual length increment against length gives a straight line with a slope of $-(1 - e^{-k})$ and an intercept on the abscissa at L_∞. (b) A Ford–Walford plot gives a regression line (solid line) with a slope of e^{-k}. The point of intersection of the lines indicates L_∞.

these data Bayley (1977) derived an equation that led to a linear transformation of the non-linear VBGF:

$$\delta(\ln W)/\delta t = (m/L)[k(L_\infty - L)] = mk[(L_\infty/L) - 1]$$
(5.6)

or

$$(\ln W_2 - \ln W_1)/(t_2 - t_1) = -mk + mkL_\infty(1/L) \quad (5.7)$$

The latter has the form of a linear regression with a slope of mkL_∞, the intercept is $-mk$, and a plotted line will intersect with the abscissa at $1/L_\infty$, where, by definition, the instantaneous growth rate is zero. Thus, the constants of the VBGF can be estimated from successive measurements of length and weight, and calculation of m in the length–weight relationship; instantaneous growth rate is plotted against the reciprocal of fish length, the slope and intercept of the regression calculated, and the VBGF constants are then estimated from the values obtained. Bayley (1977) suggested that this method of analysis could be appropriate for the estimation of the VBGF constants for tropical fish species in which age determination may be extremely difficult. For these species growth is often estimated from data collected following the recapture of released marked fish, where it is not usually possible to control the time over which individual fish are at liberty. Analysis of growth data using this method does, however, require that there has been a marked change in fish weight and length over the growth period.

5.5 AGE DETERMINATION, BACK-CALCULATION AND VALIDATION TECHNIQUES

The ability to determine the age of fish is an important tool in fisheries research, and age data are vital for both growth modelling and the study of population dynamics. There are several approaches to ageing fish, including 'direct' observation of individuals, length–frequency analysis and the analysis of various hard structures (Bagenal and Tesch 1978; Weatherley and Gill 1987; Busacker et al. 1990; Devries and Frie 1996; Campana 2001).

The most accurate method for collecting age data is direct observation of individuals, but this is time-consuming and costly. However, under some circumstances it may be the only way in which reliable age and growth information can be obtained.

The method involves the release of marked fish into natural systems. Marked fish may be either hatchery-reared fish of known age or fish captured and marked *in situ*. The marked fish are later re-captured. The period of time between release and recapture is quantified and combined with data relating to changes in body size for use in growth models. Data collected using the mark-and-recapture method can also be used to gain insights into the size of the fish population, provided that certain assumptions are met (Youngs and Robson 1978; Guy et al. 1996). One prerequisite of the method is that the released fish can be easily recognized at the time of recapture. In other words, the mark applied must be distinct and, if not permanent, at least long-lasting. Further, if data from marked fish are to be of value in the estimation of growth rates and population sizes, the marks applied should not influence either growth or the vulnerablity of the fish to predators, i.e. mortality rates should not be affected.

Several marking and tagging techniques are available (Laird and Stott 1978; Guy et al. 1996; Campana 2001). Fish may be marked by fin mutilation, hot and cold branding or tattooing; marks may also be applied to the fish via subcutaneous injections of dyes, liquid latex or fluorescent materials. There are also many types of tags, some of which, such as the anchor tag and the plastic flag tag, are applied externally, whereas others, such as visible implant tags, coded wire tags and passive integrated transponders (PIT tags), are subcutaneous or internal. The advantage of tags over other marking techniques is that tags can be numbered serially, allowing for individual recognition. Chemical marks may be induced in the body tissues by feeding, injecting or immersing the fish in solutions of a chemical that is taken up and incorporated into the tissue in question. The hard calcified tissues, such as scales, otoliths and skeletal elements, are the most common tissues used because they incorporate certain chemicals permanently and in a form that can provide a 'time mark'. Examples of chemical markers include fluorescent compounds such as tetracycline and calcein, and metallic elements such as strontium and rare earth elements. Chemical marking techniques are par-

ticularly valuable in validation studies designed to cross-check fish ages as determined by other methods (Weatherley and Gill 1987; Brown and Gruber 1988; Casselman 1990; Rijnsdorp et al. 1990; Devries and Frie 1996; reviewed by Campana 2001).

Length–frequency analysis may be used to distinguish between different age groups of fish provided that the distribution of lengths is unimodal around a value that is distinct for the age group. Several graphical and statistical methods have been developed to enable age groups to be separated using an analysis of length–frequency data (reviewed by MacDonald 1987; Pitcher, Chapter 9, Volume 2). Although length–frequency analysis appears simple in principle, it may not be so in practice. Slower and disparate growth amongst older fish makes for less distinct peaks at older ages, and long spawning seasons lead to an increase in the spread of the distributions of length (Bagenal and Tesch 1978; Devries and Frie 1996).

Although direct observation and length–frequency analysis are used in age determination studies, the most frequently used method is the examination of hards parts such as scales, otoliths, spines, vertebrae and the opercular and dentary bones (Bagenal and Tesch 1978; Weatherley and Gill 1987; Brown and Gruber 1988; Casselman 1990; Rijnsdorp et al. 1990; Devries and Frie 1996; Campana 2001). This method is based on the fact that as a fish grows by increasing in length there will also be increases in the size of the hard body parts (Table 5.1). However, the use of hard parts for age determination also relies on the appearance of growth zones, rings or checks in these parts. These growth marks are referred to as annual marks, annual rings or annuli when they are taken to represent age in years, and daily rings or daily increments when they indicate daily growth.

For example, the number of scales of a bony fish remains nearly constant throughout life, so as the fish grows the scales must inevitably increase in size in more or less the same proportion. New material is added to the scale as it increases in size: in the elasmoid scales (cycloid or ctenoid) of teleost fishes this material appears as a series of bony ridges, or circuli. The arrangement of the circuli is

Table 5.1 Relationships between otolith length (OL) and fish standard length (FSL) (both in mm) for some common boreal marine fish species. (Source: from Jobling and Breiby 1986.)

Fish species	*n*	FSL size range (mm)	FSL = *a* + *b* OL	
			Intercept (*a*)	Slope (*b*)
Herring, *Clupea harengus*	76	51–279	−8.50	58.46
Pearl-side, *Maurolicus muelleri*	74	22–67	−12.80	35.31
Lanternfish, *Benthosema glaciale*	37	37–85	−3.31	31.79
Capelin, *Mallotus villosus*	96	49–159	24.02	44.31
Sandeel (sand-lance), *Ammodytes tobianus*	42	65–137	14.93	50.81
Atlantic cod, *Gadus morhua*	67	26–317	0.41	22.44
Haddock, *Melanogrammus aeglefinus*	65	20–283	11.06	17.24
Saithe (coal-fish), *Pollachius virens*	37	53–259	−4.24	23.50
Blue whiting, *Micromesistius poutassou*	27	56–318	−25.54	23.17
Norway pout, *Trisopterus esmarki*	75	72–252	−23.26	25.14
Silvery pout, *Gadiculus argenteus thori*	37	79–149	4.53	18.14
Red-fish (Norway haddock), *Sebastes* spp.	78	18–238	3.75	19.45

not regular because the fish does not grow at the same rate throughout the year. When food is plentiful, the fish grow rapidly and the scales increase in size by the addition of large numbers of circuli well separated from each other; when growth slows down or ceases the circuli are much closer together. Thus, periods of slow growth are denoted by a close clumping of circuli to form a distinct 'ring'. In temperate regions, the growth of fish is usually rapid during the spring and summer but is slow during the winter. These seasonal changes are reflected in the deposition of circuli in the scales. Thus, the winter growth check enables the age of the fish to be determined by counting the number of 'rings' formed by areas of close circuli on the scales. The greater the seasonal growth differences, the clearer the growth 'rings' on the scale: for this reason they are most easily seen on the scales of fish from high latitudes, where growth is distinctly seasonal. Thus, scales may be the hard part of choice for ageing fish from high latitudes, and they have the added advantage that their collection need not involve killing the fish. However, scales can be demineralized during prolonged periods of food deprivation and scales can be regenerated after damage; this can lead to errors in age determination unless sufficient care is taken with

sampling (Casselman 1990; Devries and Frie 1996; Campana 2001).

It may be difficult to determine the age of tropical and subtropical fish species by examination of the scales or other hard parts, because the growth 'rings' may not necessarily be annual. The formation of 'rings' may be associated with factors unrelated to specific seasonal changes, such as unpredictable changes in food supply, spawning events or density-related changes in growth (Bagenal and Tesch 1978; Weatherley and Gill 1987; Devries and Frie 1996). Thus, if age determination is attempted using readings of these growth 'rings' there must be some sort of validation by other methods (reviewed by Campana 2001). Unfortunately it may not be possible to use length–frequency analysis because the fish may spawn throughout much of the year and life cycles are short, so a 'direct' method using mark-and-recapture may be the method of choice.

Similarly, it is not possible to determine the age of elasmobranchs using scales because, unlike the scales of bony fishes, the placoid scales of sharks and rays do not increase in size as the fish grows. Instead, new scales are added in between the existing ones. This is a continuous process so that at any one time there will be a number of newly erupted

scales, as well as some in the process of disintegration. However, age determination of some elasmobranchs may be possible by examination of growth zones within vertebrae or spines (Holden and Meadows 1962; Holden 1974; Nammack et al. 1985; Brown and Gruber 1988).

When the scales and other hard parts increase in size in proportion to the size of the fish (e.g. Table 5.1), they may not only be used in age determination but can also be considered to represent a diary recording the growth history of the fish. Thus, using knowledge about the relationship between the size of the hard part and fish length, it may be possible to back-calculate the length of the fish at a given age by examination of the positioning of the various growth 'rings' (Bagenal and Tesch 1978; Weatherley and Gill 1987; Devries and Frie 1996). The data required for back-calculation are the length of the fish at capture, the radius of the hard part at capture (measured from the nucleus to the margin), and the radius of the hard part to the outer edge of each of the growth 'rings' (either annuli or daily increment rings). Back-calculation of length at any given age is then usually carried out by one of four methods: the direct proportion method, the Fraser–Lee method, various curve-fitting procedures or the Weisberg method (Bagenal and Tesch 1978; Devries and Frie 1996). The method to use depends upon the type of relationship between the length of the fish and the dimensions of the hard part used in the back-calculation procedure.

The direct proportion method can be used when the relationship between body length and hard-part radius is linear and has an intercept that does not differ from the origin: in this situation the growth of the hard part is directly proportional to the growth in length of the fish. The Fraser–Lee method is applicable when the intercept of the relationship between fish length and hard-part radius is not at the origin. Under these circumstances, length at time t (L_t) can be back-calculated using the formula:

$$L_t = [(L_c - a)/R_c]R_t + a \qquad (5.8)$$

where L_c is the length of the fish at the time of capture, R_c is the radius of the hard part at capture, R_t

is the radius of the hard part at time t, and a is the intercept of the regression line relating hard-part radius to fish length (Bagenal and Tesch 1978; Devries and Frie 1996). In some cases, the use of simple linear regression may be precluded due to a lack of linearity between the dimensions of the hard parts and the body, or because there are different body length to hard-part relations among age groups. Under such circumstances various curve-fitting procedures and covariance analysis may be used to address the problems (Bagenal and Tesch 1978; Bartlett et al. 1984). The Weisberg method is more complex than the others. It involves a modelling approach that enables age group and annual environmental effects to be distinguished. Thus there is a separation and identification of changes in growth from one time period to another, such as years of particularly good or poor growth, that may be superimposed upon age effects (Weisberg and Frie 1987; Weisberg 1993).

5.6 LENGTH–WEIGHT RELATIONSHIPS, AND INDICES OF CONDITION AND GROWTH

The length of a fish can be measured more easily and accurately than weight under field conditions, so length measurements are the most convenient method of growth expression. Frequently, information about fish weight may be required and this may be estimated from length if the length–weight relationship is known for the fish population under study. The length–weight relationship is generally expressed by the equation:

$$W = cL^m \qquad (5.9)$$

or

$$\log W = \log c + m \log L \qquad (5.10)$$

where W is weight, L is length, and c and m are constants. The numerical value of m is nearly always between 2.5 and 3.5, and is often close to 3 (Bagenal

and Tesch 1978; Weatherley and Gill 1987; Anderson and Neumann 1996; Sutton et al. 2000). When $m = 3$, the body is increasing in all dimensions in the same proportions as it grows. However, the relationships of the different body dimensions often change with respect to each other as the fish grows, so body shape changes as the fish increases in length. This means that m will be greater than 3 when a fish becomes more rotund as it increases in length, and less than 3 if the fish becomes 'slimmer' as it increases in body length.

As a fish grows, changes in weight are relatively greater than changes in length, due to the approximately cubic relationship between length and weight. Thus, measurement of change in weight may provide a more precise measure of growth over short periods of time. However, a change in weight may be a very transient indicator of growth, because weight can be both gained and lost. Thus, when fish are feeding and growing well, an individual may have a greater than usual weight at a particular length. On the other hand, when feeding conditions are poor, the fish may lose weight and be light for their length. Thus although length is the primary determinant of the weight of a fish, there can be wide variations in weight between fish of the same length both within and between populations. Thus, length–weight relationships can be used to assess the 'well-being' of individual fish. Since it is not particularly easy to interpret and directly compare the constants in the length–weight relationship, a series of indices of condition have been developed in an attempt to circumvent some of the problems.

The length–weight relationship given by equation 5.9 can be rearranged to give an index of condition, or condition factor (CF):

$$CF = [IW/IL^m] \times 100 \qquad (5.11)$$

where IW and IL are the weight and length of an individual fish respectively, and m is the exponent in the length–weight relationship. Alternatively, the condition of an individual fish can be calculated as IW/EW, where EW is the 'expected weight' of the fish calculated from the length–weight relationship. In practice, because m in the length–weight

relationship is close to 3, the condition index is usually calculated as Fulton's condition factor (K):

$$K = [IW/IL^3] \times 100 \qquad (5.12)$$

In most cases K will be satisfactory for analysing differences in condition related to sex or season when the fish used for comparison are of approximately the same length; however, if the length range is large, spurious results will be generated if m differs from 3.

Changes in growth rate and condition are accompanied by changes in the biochemical composition of the body tissues; the most marked changes occur in percentages of lipids and body moisture, whereas the relative proportion of protein tends to vary to a lesser extent (Weatherley and Gill 1987; Love 1988; Hislop et al. 1991; Shearer 1994; Brett 1995; Couture et al. 1998; Dutil et al. 1998; Sogard and Olla 2000; Sutton et al. 2000). As a consequence of this, there is a strong negative correlation between the percentages of body lipids and body moisture (Fig. 5.5), and this relationship seems to hold under different conditions of feeding, growth and gonad development (Weatherley and Gill 1987; Love 1988; Hislop et al. 1991; Sogard and Olla 2000; Sæther and Jobling 2001). Thus, temporal changes in the condition of the fish, related to the deposition and mobilization of energy reserves, will be reflected by movements up and down the lipid–moisture (or fat–water) regression line.

Attempts have been made to use a range of metabolic variables to obtain an assessment of the condition and recent growth history of wild fish (Busacker et al. 1990; Houlihan et al. 1993; Couture et al. 1998; Dutil et al. 1998). The metabolic indicators monitored include concentrations of nucleic acids, and enzymatic indicators of aerobic and glycolytic capacities of muscle, liver and intestine. Tissue RNA:DNA ratio has often been used both to assess fish condition and as an indirect measure of recent growth. It has been argued that because the DNA content of a cell is relatively constant, and RNA content varies with the rate of protein synthesis, the ratio of RNA to DNA provides an index of protein synthetic activity and
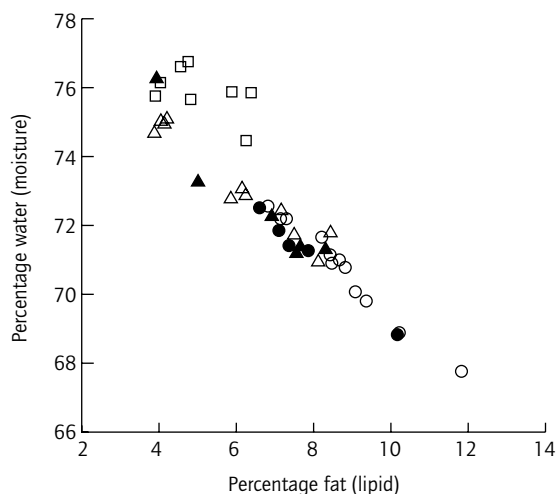
Fig. 5.5 The percentage of body fat (lipid) and water (moisture) in samples of turbot, *Scophthalmus maximus*, at the start of a growth trial ($\square$; weight *c.*200 g), after feeding for 12 weeks (weight *c.*450 g) on either a high-fat ($\bigcirc$, 25% lipid) or low-fat ($\triangle$, 17% lipid) diet, and then after 8 weeks (weight 550 g) of dietary reversal (i.e. $\bullet$, high-fat to low-fat diet; $\blacktriangle$, low-fat to high-fat diet). The 'fat–water' line is described by the following regression: %water = 80.11 – 1.08 %fat ($n = 44$; $R^2 = 0.866$). (Source: data from Sæther and Jobling 2001.)

hence growth (Bulow 1987). In addition to RNA : DNA ratio, tissue RNA content and concentration and RNA : protein ratio have been used as indirect indices of fish condition and growth. In studies with fish larvae it is usually the RNA : DNA ratio that has been used as the growth correlate, and results of a study on cod larvae provide evidence that the analysis of nucleic acids may provide valuable information about the recent growth and condition of individual larvae (McNamara et al. 1999).

Another biochemical component with the potential to correlate with recent growth history is ornithine decarboxylase activity (Benfey 1992; Benfey et al. 1994). Ornithine decarboxylase is the first, and rate-limiting, enzyme in the biosynthesis of polyamines, compounds essential for the biosynthesis of nucleic acids and proteins. Thus, it might be expected that changes in ornithine decarboxylase activity would precede changes in other

biochemical indices, such as protein synthesis, tissue amino acid incorporation and RNA : DNA ratios, used for the assessment of condition and short-term changes in fish growth. Intestinal mitochondrial enzyme activity also seems to correlate with rates of feeding and growth (Couture et al. 1998; Dutil et al. 1998). Nutrient absorption by the enterocytes of the gut involves active transport; this relates to $Na^+/K^+ATPase$ activity, and the enterocytes are mitochondria-rich cells in which ATP is produced aerobically (Ferraris and Diamond 1989; Hirst 1993). Consequently, links between intestinal mitochondrial enzyme activity, nutrient absorptive capacity and growth might be expected.

Prolonged fasting affects white glycolytic muscle more than oxidative muscle, and when food deprivation lasts a period of weeks there are often marked declines in muscle sarcoplasmic proteins and glycolytic enzyme activities (Love 1988; Couture et al. 1998; Dutil et al. 1998). Conversely, during periods of intense feeding the activity of white muscle glycolytic enzymes, such as phosphofructokinase, pyruvate kinase and lactate dehydrogenase, may be positively correlated with feeding and growth rates. Activities of mitochondrial enzymes, such as cytochrome *c* oxidase and citrate synthetase, in the oxidative red muscle appear to be poor predictors of growth. This is not surprising given the fact that during fasting it is the white muscle proteins that are mobilized, whereas the aerobic red muscle seems to be preferentially conserved (Love 1988). The high activities of glycolytic enzymes in the muscle and their sensitivity to food supply seem to make them useful indicators of condition and growth, with the monitoring of changes in lactate dehydrogenase activity appearing to be particularly useful (Couture et al. 1998; Dutil et al. 1998).

5.7 ENERGY BUDGET AND BIOENERGETICS: ENERGY PARTITIONING AND STORAGE

In simple terms, growth is the change that results

from the difference between the food that enters the body and the waste materials that leave it (Brett 1979, 1995; Cho et al. 1982; Weatherley and Gill 1987; Adams and Breck 1990; Elliott 1994; Jobling 1994, 1997). This can be represented by:

$$p\,C = M + G \qquad\qquad (5.13)$$

or

$$G = p\,C - M \qquad\qquad (5.14)$$

where C is the amount of food consumed, p is a coefficient indicating the availability of nutrients or food energy, M represents catabolic losses (metabolism) and G is the anabolic component, the nutrients or food energy retained as growth. Implicit in this energy budget equation is the dependency of growth on consumption, so the intake of food energy is the pacemaker of growth. However, the increase in growth with increased food intake may not be monotonic (Brett 1979; Weatherley and Gill 1987; Elliott 1994; Jobling 1994, 1997).

Temperature is the most all-pervasive environmental factor that influences aquatic organisms and, via its influences on feeding and metabolism, it affects growth. Increases in temperature initially lead to an increase in food consumption; feeding peaks at some intermediate temperature, and then declines precipitously as the temperature continues to rise (Fig. 5.6). It may be difficult to describe the influence of temperature on food intake in mathematical terms, but Hogendoorn et al. (1983) suggested that Hoerls function could be used to describe the effects of temperature on food intake of fish provided with unrestricted rations:

$$C = aT^{b}\mathrm{e}^{cT} \qquad\qquad (5.15)$$

where T is temperature and a, b and c are constants.

The proportion of the ingested energy lost as faecal and excretory wastes depends upon the nature of the diet (Cho et al. 1982; Jobling 1994), so the value of p differs between fish species that differ in trophic habits. For carnivorous species a value of p close to 0.8 may be appropriate, but for herbivores and detritivores values will be lower.

The proportion of the food energy lost in the faeces and nitrogenous excretory products may also be influenced to some degree by the amount consumed, fish size and temperature (Elliott 1994; Jobling 1994).

The metabolic term, M, encompasses fasting metabolism, activity metabolism and feeding metabolism. The latter is the metabolism linked to the processing of nutrients and the elaboration of tissues. Metabolic rates are usually assessed by an indirect method involving the measurement of oxygen consumption and the application of an oxycalorific coefficient (1 ml O_2 = 19.4 J) (Adams and Breck 1990; Cech 1990; Jobling 1994; Brett 1995). In an expanded model each metabolic component will be described using a separate mathematical function, which will include an allometric term to account for size effects and will also contain a temperature function:

$$M = aW^{b}\mathrm{e}^{cT}\mathrm{e}^{dS} + eC \qquad\qquad (5.16)$$

where W is body weight, S is swimming speed and a–e are constants. The weight exponent, b, for fish is about 0.8, and the temperature constant, c, will generally lie within the range 0.04–0.07, corresponding to a Q_{10} of 1.5–2.0. Metabolic costs associated with activity show an approximately exponential increase, whereas the metabolic costs associated with food processing, tissue synthesis and energy storage are proportional to the quantity of food consumed.

The difference between the rate–temperature curves for feeding and metabolism gives an indication of the resources available for growth under different temperature conditions, assuming that p represents a constant proportion of C across temperatures. The plotting of the growth rate–temperature relationship indicates that growth rate reaches a peak at an intermediate temperature (Fig. 5.6), with the optimum temperature for growth being slightly lower than that at which food consumption rate reaches its maximum. Relationships of this type have been obtained in a number of growth studies conducted on fish (e.g. Brett 1979; Hogendoorn et al. 1983; Woiwode and Adelman 1991; Xiao-Jun and Ruyung 1992; Elliott 1994; Liu et al. 1998; reviewed by Jobling 1997), but
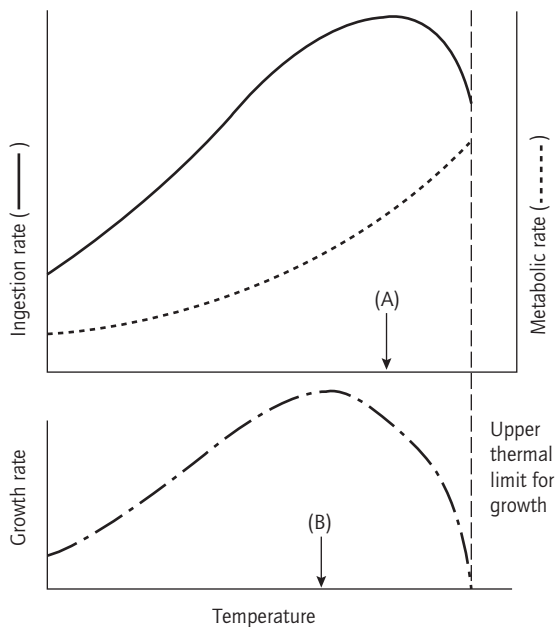
Fig. 5.6 Rate–temperature curves illustrating the effects of temperature on rates of ingestion, metabolism and growth. Note that the temperature at which ingestion rate reaches its maximum (A) is a few degrees higher than the optimum temperature for growth (B). (Source: from Jobling 1997.)

some authors have reported that the temperatures at which feed intake and growth peak are almost coincident (e.g. Larsson and Berglund 1998; Forseth et al. 2001)

The growth term, G, encompasses somatic growth related to tissue elaboration, the storage and mobilization of energy reserves, and reproductive growth; the latter may be difficult to assess accurately for wild fish. Thus, the changes relating to growth over time include the energy deposited as protein and lipid in the soma, the changes in the size of the energy storage depots and the energy directed towards the production of gametes. Protein growth may be positive throughout much of the year but quantities of lipids, and gonad sizes, may undergo marked fluctuations, including large net losses at certain times of the year. Seasonal changes in body composition will usually be most extreme in fish that inhabit temperate-zone or

high-latitude environments, and there may also be changes in composition that are directly related to body size (Weatherley and Gill 1987; Love 1988; Hislop et al. 1991; Shearer 1994; Jørgensen et al. 1997; Van Pelt et al. 1997; Sogard and Olla 2000; Sutton et al. 2000). In other words, fish tend to accumulate storage lipids during the summer growth season, and the reserves are then mobilized to provide metabolic fuel during the winter, when food consumption is low, and to support gonadal development (Brett 1979, 1995; Weatherley and Gill 1987; Love 1988; Elliott 1994; Jobling 1994; Jørgensen et al. 1997).

The feeding and growth responses seen in high-latitude fish during the summer months resemble those observed amongst fish that have been deprived of food under laboratory conditions: increased food intake, or hyperphagia, rapid growth and improvement in condition, and the repletion of energy reserves (Weatherley and Gill 1987; Broekhuizen et al. 1994; Jobling 1994; Jobling and Johansen 1999; Sæther and Jobling 1999). It is usually fish that are in poor condition that show the greatest response (Fig. 5.7)(Jobling et al. 1994). Thus, seasonal cycling may relate to a regulation of the balance between reserves held in the form of lipid depots and mobilizable parts of the musculature and structural components such as the skeleton and circulatory and nervous tissue. Shifts in the balance would be reflected in relative changes in major chemical components that constitute the tissues, for example in the relative proportions of body lipid and moisture (cf. Fig. 5.5). Large shifts would be expected to induce compensatory changes in feeding and energy accumulation. Following restoration of the balance between compartments, rates of feeding would be predicted to decrease and rates of growth and energy accumulation would slow (Broekhuizen et al. 1994; Jobling and Johansen 1999). This presupposes that specific metabolic signals arising from different tissues are integrated within the central nervous system, enabling continuous assessment of the status of the energy reserves (reviewed by Kiess et al. 1999; Magni et al. 2000).

In studies of fish growth the energy content of the tissues is usually determined by bomb calorimetry. Bomb calorimetry involves the rapid
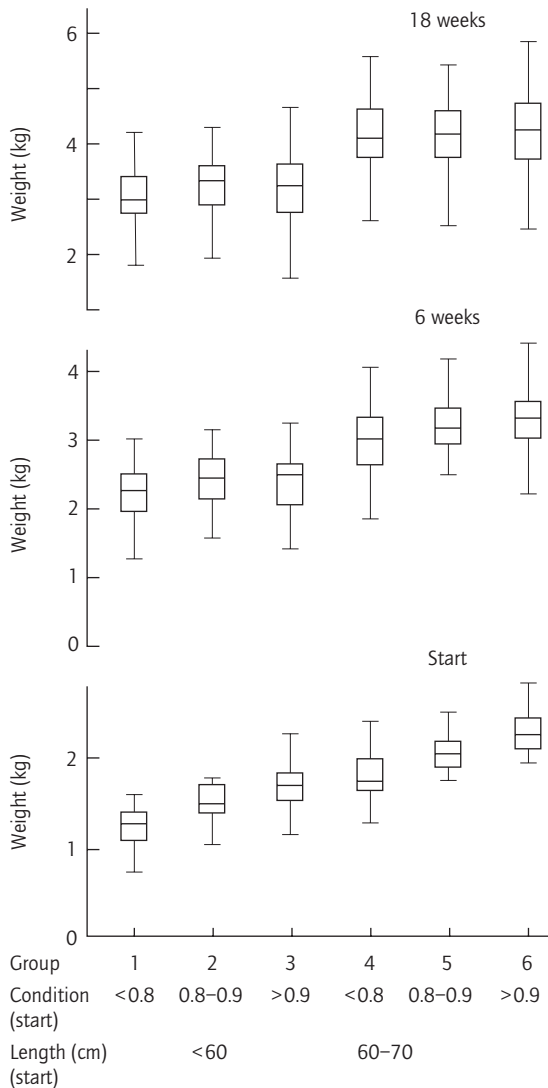
Fig. 5.7 The effects of initial length (L cm) and condition ($K = [W/L^3] \times 100$) on weight (W) change in groups of Atlantic cod, *Gadus morhua*, during 18 weeks of growth. Note that the cod that were in the poorest condition at the start displayed the highest rates of weight gain, and that at 18 weeks the body weights attained by cod within each initial length group were similar. The boxes indicate 50% of the 'population' and the bars the 95% confidence limits. (Source: from Jobling et al. 1994.)

combustion of the sample in oxygen at increased pressure, and heat production is measured. This provides a measure of the heat of combustion, or gross energy, of the sample. Alternatively, the chemical composition of the sample can be measured using a series of standard laboratory methods (Osborne and Voogt 1978; AOAC 1990; Busacker et al. 1990), and conversion factors for the complete oxidation of proteins, lipids and carbohydrates used to estimate gross energy content. Complete oxidation of proteins, lipids and carbohydrates yields approximately 24, 39 and 17 kJ g^{-1} respectively, although the energy yield from fish lipids may be slightly lower than that from lipids of terrestrial origin. The chemical analysis of the major components (moisture, protein, carbohydrates, lipids and ash) of animal tissues is usually termed a proximate analysis.

A characteristic of the growth of many fish species in nature is the marked seasonal variability. This seems to be almost universal outside of the tropics and is by no means rare within them; in the tropics and subtropics the variations in fish growth may be most closely related to seasonal changes in rainfall. It is those species that live at high latitudes that exhibit the greatest seasonal fluctuations in feeding and growth. These seasonal growth cycles are often attributed to the temporal changes in food availability that may occur in temperate and polar waters, but even in the absence of changes in food availability low water temperatures during the winter months would be expected to restrict growth (Fig. 5.6). However, the seasonal cycle of growth is not always, and perhaps never, wholly under temperature control; the growth of several high-latitude fish species seems to track the seasonal cycle of photoperiod (Brett 1979; Woiwode and Adelman 1991; Jobling 1994; Boeuf and Le Bail 1999). This comes particularly to the fore when the fish are exposed to constant temperature and unrestricted food supply. It is possible that photoperiod acts to synchronize an endogenous growth rhythm with prevailing environmental conditions. In this case photoperiod acts as a synchronizing timing signal, or *zeitgeber*. The response to photoperiod would be expected to be marked amongst high-latitude species, because it

is at these latitudes that photoperiodic signals are strongest and aquatic habitats are most variable on a seasonal basis. However, because the natural seasonal variations in food availability, temperature and daylength tend to follow similar cycles, it may not be easy to distinguish the effects of each variable on growth and energy partitioning.

5.8 GROWTH AT DIFFERENT LATITUDES: MODELS OF GROWTH COMPENSATION

Many species of fish have wide geographic distributions; populations of these species occur at different latitudes and inhabit environments that differ in both mean annual temperature and length of the growing season. For many of these species the annual growth increment is lower for fish from higher latitudes than for those living at low latitudes, but the differences appear to be less pronounced than expected from the differences in temperature and growth conditions experienced by the different populations (Conover 1990, 1992). For example, Conover (1990, 1992) provided evidence that there were minimal differences in size at the end of the first growing season for several species of fish that occur on the eastern seaboard of North America: Atlantic silverside (*Menidia menidia*), American shad (*Alosa sapidissima*), striped bass (*Morone saxatilis*) and mummichog (*Fundulus heteroclitus*). There are three ways in which such a situation could arise, which are not mutually exclusive. Firstly, size-selective mortality could be more pronounced in high-latitude populations leading to survival of only the largest fastest-growing individuals, whereas a greater proportion of the slower-growing fish might survive at lower latitudes: the net result would be little or no difference in mean size of the fish at the end of the growth season. Secondly, growth of fish in the populations at low latitude might be subject to greater constraint by food availability, so that fish in these populations grow at rates substantially below their full physiological

potential. Thirdly, there may be compensatory mechanisms that operate to counteract the negative effects of low temperature and a short growth season on the growth of fish that inhabit high-latitude environments.

There are two basic models of how compensatory mechanisms might be expressed. One model relates the compensatory mechanisms to local thermal adaptation, such that growth rates are maximized at temperatures commonly experienced by fish within their native environment. According to this model there would be differences in optimum temperatures for growth amongst populations inhabiting different thermal environments, and the compensation should be accompanied by a change in preferred temperatures (Fig. 5.8) (Jobling 1997). The second model focuses on latitudinal differences in seasonality rather than temperature *per se* (Conover 1990, 1992; Conover and Schultz 1995). In this model, high-latitude fish have a higher capacity for growth to compensate for short growing seasons: latitudinal compensation is observed as an elevation in the growth rate–temperature curve (Fig. 5.8). According to this model, genetic and environmental influences oppose one another along the gradient of decreasing length of the growing season, i.e. the fastest-growing genotypes are found in environments that have the most depressive effect on growth (Conover and Schultz 1995).

There are two ways in which these models could be tested. One method involves common-garden experiments in which fish from different populations are reared under the same temperature range, and growth rate–temperature curves are plotted for each test population (e.g. Jonassen et al. 2000). The second method involves reciprocal transplants, i.e. representatives from the different test populations are reared in each of the original habitats in order to examine the (phenotypic) responses of the different populations (prospectively different genotypes) to a combination of environmental influences.

The results of transplantation experiments have been equivocal, but when reared under the same conditions fish from high-latitude environments may grow faster than conspecifics from
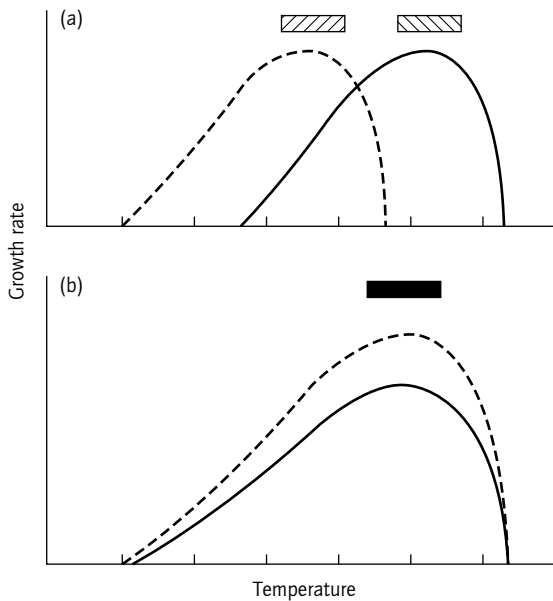
Fig. 5.8 Rate–temperature curves illustrating two ways in which compensatory adjustments could be made to counteract the effects of environmental differences on growth. (a) The rate–temperature curves are displaced in relation to each other; fish from low-temperature environments have a lower optimum temperature for growth, and grow faster at low temperatures, than do fish from warm-water populations (thermal adaptation). (b) Compensation is envisaged to occur by means of an elevation of the rate–temperature curve; fish with the highest growth capacity are found in environments that have the greatest inhibitory effects on growth (countergradient variation). Bars indicate the zones of thermal preferenda predicted for fish from different environments. (Source: from Jobling 1997.)

lower latitudes. This would tend to call into question the idea that there is a marked downward shift in the optimum temperature for growth in high-latitude populations (Fig. 5.8). Results from some common-garden experiments designed to test growth rate–temperature responses add support to this: optimum temperatures for growth of different populations have been found to be similar (McCormick and Wegner 1981; Conover and Present 1990). However, Jonassen et al. (2000) reported that juvenile halibut (*Hippoglossus hippoglossus*) from a high-latitude population had

both a higher growth capacity and a lower optimum temperature for growth than did halibut from lower-latitude populations. Additional evidence that there may be an elevation of the growth rate–temperature curve in fish from high-latitude populations has been obtained in studies conducted over more limited temperature ranges (Schultz et al. 1996; Conover et al. 1997; Brown et al. 1998; Imsland et al. 2001). Thus, growth compensation across the geographic range of a species may not be based simply on genotype–environmental temperature interactions, and it has been hypothesized that latitudinal growth compensations may have evolved to offset the disadvantages of being small at the end of the growing season (Conover 1990, 1992).

Although the ability to grow rapidly within a short growing season would clearly be advantageous for fish in high-latitude environments, there would also need to be forces operating in a negative direction to enable latitudinal variation in growth-rate capacity to be maintained (Conover and Schultz 1995). Such forces might, for example, relate to increased incidences of developmental deformities or to increased metabolic costs, or could encompass trade-offs involving negative correlations between growth capacity and disease resistance, or the ability to withstand prolonged periods of food shortage. Differences in metabolic rate related to latitude of occurrence have often been reported, and the metabolic compensations have usually been interpreted as being a response to temperature (Cossins and Bowler 1987). The potential benefits of metabolic compensation in relation to temperature are not immediately clear, but there are links between metabolic rate and the ability to maintain activity and growth (for discussion see Hochachka 1988; Clarke 1991, 1993, 1998). Consequently, an elevated metabolic rate may be a prerequisite for exploitation of food resources over a short growth season. Thus, the possibility arises that differential metabolic costs might represent a trade-off leading to the maintenance of latitudinal variation in growth-rate capacity. Interactions of this sort would have consequences for bioenergetic modelling, because it is usually assumed that such models can be con-

structed using a single set of species-specific physiological parameters. In other words, the type of trade-off described above invalidates the assumption of invariant species-specific parameters, and an accurate modelling of energy flow and nutrient partitioning would require population-specific knowledge to be available.

5.9 ESTIMATING FOOD CONSUMPTION

Estimation of food consumption by fish populations has widespread uses in ecological and fisheries research. Such estimations are required for the investigation of predator–prey interactions and predation mortality, for assessment of production dynamics of fish populations, and for the development of multispecies stock assessment models (Ney 1990; see also Shepherd and Pope, Chapter 7 and Pauly and Christensen, Chapter 10, both Volume 2). For accurate estimation of population food consumption many different types of data are required. These include information about population density and age structure, as well as quantitative assessments of food consumption rates of fish of different sizes under different environmental conditions, and information about dietary composition with respect to the relative proportions of the different prey types consumed.

Studies of the dietary composition of wild fish are almost invariably based on the analysis of stomach contents, unless one is interested in overall trophic structure, in which case stable isotopes provide a complementary method. Polunin and Pinnegar (Chapter 14, this volume) provide an extensive review of the use of stable isotopes. Here I review three approaches that are usually adopted when carrying out analyses of stomach contents: numerical analysis, volumetric analysis and gravimetric analysis (Windell and Bowen 1978; Bowen 1996). Each approach provides different types of information relating to prey selection and dietary composition, but none gives any quantitative assessment of the amount of food consumed. Of the numerical analyses the frequency of occurrence gives an estimate of the proportion of the popula-

tion that has fed on a particular prey type. This provides an indication of the uniformity with which fish within a population select their diet, but it does not give any information about the relative importance of the different prey types. The calculation of percentage composition by number gives the latter sort of information because it provides an estimate of the relative abundance of a particular food item in the diet. Percentage composition by number has its equivalents in percentage composition by volume and percentage composition by weight, obtained from the results of volumetric and gravimetric analyses respectively (Windell and Bowen 1978; Bowen 1996). There are weaknesses associated with all these forms of analysis, and in an attempt to overcome the problems there have been several attempts to develop indices that combine the information obtained using the different analyses (Bowen 1996).

In many cases it may be deemed desirable to have estimates of the size, or weight, of the different prey items at the time of ingestion. Sizes of partially digested prey can be estimated by measuring the dimensions of some digestion-resistant hard part such as an otolith, operculum, head capsule, carapace or chitinous element of a compound appendage. The initial size of the prey can then be estimated by reference to regression equations established for the relationships between prey size and the dimensions of the particular digestion-resistant hard part in question (e.g. Table 5.1). However, care must be exercised when interpreting the data obtained when using the method of reconstructed sizes or weights, because it is very easy to draw incorrect conclusions about dietary composition and the relative contributions of different prey organisms to the diet of the predator (for discussion see Jobling and Breiby 1986; Jobling 1987; Juanes et al., Chapter 12, this volume).

It is not usually practicable to quantify rates of food consumption of wild fish by direct observation, and two different indirect approaches have been adopted for the estimation of food intake by natural fish populations (Windell 1978; Adams and Breck 1990; Bromley 1994). The first approach is based on calculations of the energy budget and

bioenergetics modelling; the second relates to the combination of stomach contents data obtained in field surveys with information about gastric evacuation rates obtained from laboratory experiments.

Bioenergetics models can be used to estimate food consumption from growth, or vice versa, by incorporating information about fish body size, water temperature, diet composition and the energy densities of predators and prey. Model outputs are, however, subject to errors related to uncertainties about the accuracy of input variables, insufficient information about the metabolic costs of activity of wild fish, and possible problems with the extrapolation of physiological rate functions, developed in the laboratory, to the field situation. Models that vary in complexity have been developed for the estimation of food consumption or growth of natural fish populations, but all have their basis in the energy budget equation (Windell 1978; Weatherley and Gill 1987; Adams and Breck 1990; Hewett and Johnson 1992; Elliott 1994; Brett 1995; Forseth et al. 2001).

A bioenergetics model based on inputs derived from a series of laboratory experiments may provide good predictions of growth and/or food consumption of fish exposed to conditions towards the centre of their environmental tolerance range (Whitledge et al. 1998; Wright et al. 1999). However, such models may give erroneous estimations at environmental extremes or when fish are undergoing repeated cycles of food deprivation and refeeding. For example, Wright et al. (1999) reported that the models could overestimate the overwintering costs of largemouth bass (*Micropterus salmoides*) by 20% or more. Further, in tests made on fish undergoing cycles of deprivation and refeeding, model predictions were in error by 25–35% in some instances (Whitledge et al. 1998). Given that fish in the wild are unlikely to feed and grow at constant rates and that substantial variations are likely in both the short and long term, these test results may have important implications for field applications of bioenergetics models.

The alternative to the bioenergetics model for estimation of food consumption of natural fish populations involves examination of the rate at which food is digested and evacuated from the stomach. Several models are available for the estimation of food consumption of wild fish from gastric evacuation data, each model incorporating a set of assumptions about meal frequencies and the form of the curve that describes the evacuation of food from the stomach (Windell 1978; Adams and Breck 1990; Bromley 1994; Elliott 1994). Few of the models have, however, been rigorously tested under controlled conditions to check their predictive accuracy (Elliott and Persson 1978; dos Santos and Jobling 1995). In one approach it is assumed that stomach contents decline exponentially with time and that feeding is continuous between sampling times. At the opposite extreme the assumption is made that a constant amount of food is evacuated from the stomach per unit time (i.e. stomach contents decline linearly with time) and that digestion times are long relative to the timing of meals. Both approaches may have merit, since they may apply to fish that have different feeding habits. For example, fish which feed on small prey organisms or on food that is nutritionally poor (planktivores, herbivores, detritivores) may feed almost continuously, and the pattern of evacuation of these species is often found to be exponential. On the other hand, other species, such as many piscivores, consume large meals at infrequent intervals, and the evacuation of food from the stomachs of these fish can often be modelled using a simple linear relationship (Jobling 1986; Bromley 1994).

Irrespective of the model applied, gastric evacuation rate data must be accurate if food consumption estimates are to be reliable. Both the rate of evacuation and the form of the curve (e.g. exponential vs. linear) will be influenced by the type of prey, and, as with other physiological processes, gastric evacuation rates will be affected by water temperature (Jobling 1986; Adams and Breck 1990; Bromley 1994; dos Santos and Jobling 1995). A model that has been used extensively in field studies of food consumption by fish is the one developed by Elliott and Persson (1978):

$$C_t = \left(F_t - F_0 e^{-Et}\right) Et \big/ \left(1 - e^{-Et}\right) \qquad (5.17)$$

where C_t is the amount of food consumed during t hours, F_0 and F_t are the stomach content weights at the beginning and end of a sampling period of t hours, and E is the instantaneous rate of gastric evacuation (i.e. gastric evacuation is assumed to be exponential). Daily food consumption (C_{24}) is then calculated as the sum of the C_t values obtained for each of the periods within the 24 hours. This model seems to be applicable when feeding is more or less continuous within sampling periods, the amounts of food in the stomach at the start and end of a period are not the same, and when gastric evacuation is adequately described by an exponential function.

5.10   CONCLUSIONS

Fish, in common with other animals, convert part of the organic material they ingest into living biomass, but how effectively they are able to accomplish this is influenced both by the quantity and quality of the food they are able to obtain and by the environment to which they are exposed. Changes in environmental conditions may affect the growth of fish both via influences on the absolute and relative amounts of different food types available and via influences on behaviour and physiology. It is within this framework that fisheries biologists must attempt to match their estimates of fish population dynamics and productivity to the food base. Solutions to the problems are sought via a combination of observational studies and manipulative experiments. In the former, data are collected over time to monitor population-related processes, although considerable care must be taken at the planning stage to minimize problems associated with sampling error and bias (Bagenal 1978; Gunderson 1993; Murphy and Willis 1996). Most field studies of fish feeding and growth are observational; although data from such studies can give insights into population structure, age and growth, and diet, they do have shortcomings. For example, analysis of stomach contents may be used to obtain qualitative information about what fish eat, but the quantitative assessment of consumption remains a major prob-lem in fisheries research. Further, even though much effort has been expended in devising and validating techniques for age determination of fish (reviewed by Campana 2001), age determination of tropical and subtropical species remains problematic. The second approach to problems related to fish feeding and growth involves the manipulation of some variable that is suspected of having an influence on the growth response. This type of experiment will usually provide clearer data than observational studies, but it may prove extremely difficult to carry out adequately controlled manipulative experiments in the field. As a consequence, manipulative experiments are usually carried out on captive populations of fish held under artificial conditions, i.e. in hatcheries, large culture tanks or net pens, or in a laboratory setting. This, in itself, may create problems related to the extrapolation of measurements to field conditions. Thus, although there exists a large body of information about the various components of the energy balance equation, collected for many fish species subjected to different environmental conditions (for overviews see Brett 1979, 1995; Weatherley and Gill 1987; Adams and Breck 1990; Jobling 1994, 1997), there remain many unanswered questions as to how these data can be best used to provide information about feeding, growth and the dynamics of production of fish populations in the wild.

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6 Recruitment: Understanding Density-dependence in Fish Populations

RANSOM A. MYERS

6.1 INTRODUCTION

The process of recruitment is the conversion of eggs, through a series of density-dependent and density-independent processes, to the fish that reproduce in the next generation. Many simple questions concerning recruitment are quantitative questions that require estimates of quantities that are very difficult to determine. For example, the question 'When is the magnitude of recruitment determined?' requires a quantitative estimate of the density-dependent and density-independent components of mortality. This question has usually been addressed by correlating estimates of abundance at early ages with later ages, as reviewed by Cushing (1996). Although such studies are useful, they are very seldom carried out with estimates of measurement error variability that are crucial for the estimation of the truly important parameters. At the very least, a measure of the estimation error variance of all estimates should be used.

No standard definition of recruitment is accepted by all fish ecologists. While all agree that recruitment is the number of fish at some certain age or stage, the choice of the age and stage varies. Coral reef fish ecologists often define recruitment as the settlement of pelagic larvae or juveniles from the plankton (Hixon and Webster 2002; Jones et al., Chapter 16, this volume), marine fisheries biologists usually refer to recruitment as the first age where fishing occurs, while salmon biologists usually refer to recruitment as the return of adults to spawn. Here, I discuss population regulation and variability from the egg stage to first reproduction.

There are two principal sources of information on recruitment. First, there are time-series of data, containing spawner abundance and subsequent recruits. These come primarily from commercially exploited fish stocks (see Fig. 6.1). Fisheries biologists, with their access to long-term research surveys and extensive catch data, have concentrated on evidence from larger geographical scales that may contain data from more than one population. Many crucial questions can be addressed with such information but it can seldom be used to study mechanisms. Second, there are experimental and observational data on a much smaller scale. The best of this kind are from coral reef systems, where local populations are studied. Coral reef ecologists typically work on relatively common species, where zygote limitation (i.e. limitation by the number of eggs) is usually viewed as an unimportant source of variability in recruitment (Hixon and Webster 2002).

I proceed as follows: I first discuss the maximum reproductive rate, the carrying capacity and the life stages in which density-dependent and stochastic density-independent mortality occurs. This ends with a discussion of future directions for research. I then discuss generalizations that appear to be valid across many studies or populations, and on processes that have been shown to be of wide applicability from various published synthetic analyses. I only briefly review the large literature

on the influence of short- or long-term variation in the environment on recruitment, as it is well covered in a number of recent books, e.g. Cushing (1996).

Throughout this chapter, I use the empirical recruitment data that I have compiled and which is freely available from my website (http://fish.dal.ca/welcome.html).

6.2 THE LINK BETWEEN SPAWNER ABUNDANCE AND SUBSEQUENT RECRUITMENT

The spawner–recruit relationship is the basis for estimation of the key parameters needed to understand and manage fisheries, e.g. carrying capacity, maximum reproductive rate and the variability in recruitment. The wide scatter and the relatively 'flat' relationship often seen between spawners and subsequent recruitment misled the naive into dismissing such data without understanding what can be learned from it. Many fisheries biologists believed that the maximum reproductive rate is so high that recruitment would not decline at low spawner abundance. This belief was due to several factors. First, it had been observed for many fish populations that a reduction in spawner abundance was not accompanied by a corresponding reduction in the production of juvenile fish (Gilbert 1997). Furthermore, since many individual fish can produce a million eggs or more, this has been taken as proof that there can be no shortage of juvenile fish (McIntosh 1899). It was only through a very large meta-analysis of over 300 spawner–recruitment datasets that it has been widely accepted that the production of juvenile fish does in fact decline when spawner abundance is greatly reduced (Myers and Barrowman 1996; Myers 1997).

The maximum reproductive rate for the population, or equivalently the maximum slope of the spawner–recruit curve, which is realized as the origin is approached where stock size is zero, determines the limits to sustainable fishing and other sources of anthropogenic mortality that a population can sustain. The quantity, sometimes known as the compensatory reserve, is the most fundamental of all population parameters. Population biologists and national and international management agencies have come to a consensus that the maximum reproductive rate is the appropriate measure of the potential for a population to 'compensate' for fishing, and is used to construct management targets and limits (Sissenwine and Shepherd 1987; Clark 1991; Mace and Sissenwine 1993; Mace 1994; Myers and Mertz 1998). In this section, I examine examples of how this parameter is estimated. When spawners and recruits are expressed as absolute estimates of abundance, the maximum reproductive rate can be estimated directly from the fitted spawner–recruit relationship. This section explains the most common types of stock-recruitment models and provides examples of stock-recruitment data from a variety of fish populations.

The relationship between recruitment (R) and spawner abundance (S), perhaps expressed as numbers or biomass, both of which are proxies for egg production, would take the form

$$R = \alpha S f(S), \tag{6.1}$$

where α is the slope at the origin, and $f(S)$ is usually a monotonically decreasing function. As such $f(S)$ is the relationship between survival and spawner abundance.

The parameter α in equation 6.1 defines the scope a population has to compensate for any form of increased mortality. For this parameter to be calculated in equation 6.1, it is necessary that the units of spawners and recruitment be the same. For species that die after reproduction (e.g. Pacific salmon, *Oncorhynchus* spp.) this is simple: one can count the number of female recruits for each female spawner. For species that do not die after reproduction, this is more complex. The process is explained below.

The estimation of α requires an extrapolation because we seldom have abundance estimates at extremely low population sizes. For this estimation we require a functional form of the density-dependent mortality, $f(S)$, above:

$$\text{Ricker} \qquad E(R) = \alpha S e^{-\beta S} \tag{6.2}$$

Beverton–Holt $\qquad E(R) = \dfrac{\alpha S}{1 + (S/K)}$ (6.3)

Shepherd $\qquad E(R) = \dfrac{\alpha S}{1 + (S/K)^{\gamma}}$ (6.4)

where $E(R)$ is the expected recruitment and $-\beta$ is the density-dependent mortality. The parameter K has the same dimensions as the spawners, S, and may be interpreted as the 'threshold biomass' for the model. For values of biomass S greater than the threshold K, density-dependent effects dominate. The Ricker model shows overcompensation, i.e. at high spawner abundances recruitment declines. The parameter γ in the Shepherd model may be called the 'degree of compensation' of the model, since it controls the degree to which the (density-independent) numerator is compensated for by the (density-dependent) denominator (Shepherd 1982).

The Ricker and Beverton–Holt formulations are standards in fisheries science, but require some explanation for general ecologists. First, the units of R and S may be in biomass as opposed to numbers. The reason for this convention is that egg production in many species is more closely related to the biomass of spawners than to the number of spawners. The slope, α, determines the highest fishing mortality that can be sustained in a deterministic equilibrium. Note that in these models, all density-dependent mortality occurs during the egg, larval or juvenile stage. That is, density-dependent mortality occurs before the fish mature. This approximation is consistent with most analysis of data for marine fish (Myers and Cadigan 1993a).

The estimation of the slope at the origin requires an extrapolation to zero spawner abundance, and thus is an approximation. It is clearly necessary to have at least two individuals for successful reproduction, and in general almost always more for a population to be self-sustaining. Any management system will attempt to keep the population size above the point where such depensation occurs. Myers et al. (1995a) and Liermann and Hilborn (1997) examined a large number of commercially exploited fish stocks for depensa-

tory density-dependent mortality. There was no evidence for depensation in most spawner–recruitment time-series because compensatory mortality appeared to occur throughout the observed range of spawner abundances (Myers et al. 1995a). The clearest evidence for depensation occurred when population size was reduced to very low levels, e.g. below 100 spawners. Some species groups, such as the Clupeidae, contained some datasets that were consistent with depensation at a moderate abundance of around 20% of unfished spawner abundance, but it is unclear if this was due to long-term environmental change or to depensation (Myers et al. 1995a; Liermann and Hilborn 1997). We thus conclude that the assumption that survival, $f(S)$, is a monotonically decreasing function for the observed range of spawner abundances appears to be an adequate approximation for most commercial species except at very low spawner abundances. However, if populations are reduced to very low abundance, recovery may be very slow. For example, the spring-spawning herring (*Clupea harengus*) population in Iceland has not recovered since the 1960s, and the cod (*Gadus morhua*) populations in eastern Canada have increased at a slower rate than predicted by the data before the collapse.

I now examine several examples of spawner–recruit data in which absolute abundances are estimated. These examples are from a wide variety of habitats, include heavily exploited and non-exploited populations, and use a great variety of techniques in their assessment of the populations. We begin our examples with a sockeye salmon (*Oncorhynchus nerka*) population because its life history is simple to understand: almost all females mature at 4 years, spawn once, and die. We next consider brook trout (*Salvelinus fontinalis*), a slightly more complex example that was experimentally manipulated to investigate density-dependent mortality. The last two examples examine more complex life histories.

6.2.1 Sockeye salmon

For the population of sockeye salmon in the Adams River, British Columbia, females almost

always live for 4 years. Spawning females are counted in the river; this is the number of spawners on the *x*-axis (Fig. 6.1). The number of females produced from this group of spawning females is simply the number that return to spawn 4 years later in the river, plus the number which were harvested on their way to the spawning site. Plotting the number of returning females against the number of females that produced them yields a classic spawner–recruit plot.

Both the spawners and recruits are in the same
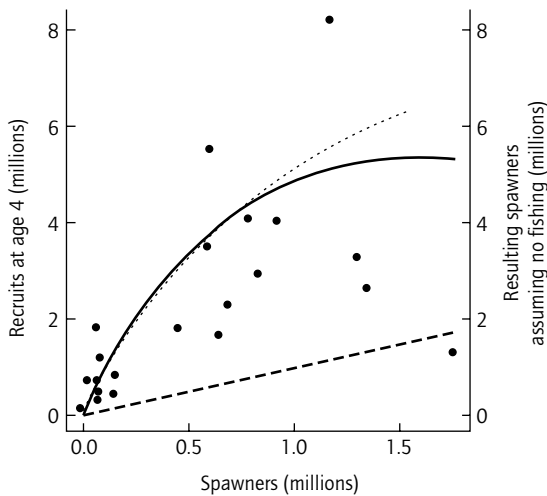
Fig. 6.1 Spawner–recruitment data for Adams River sockeye salmon (*Oncorhynchus nerka*), British Columbia, Canada. On the *x*-axis is the number of spawning females in the river for any one year. Each point represents the production of spawners produced for each batch of spawners in a given year. These 'recruits' are adults that return to spawn 4 years later. The solid and dotted lines are the maximum likelihood fit for the Ricker and Beverton–Holt models respectively. The straight dashed line is the replacement line. That is, if a point is above this line, the population should increase if no fishing occurs. If 1000 spawning females produced 5000 recruits 4 years later, the population would have increased by five times during the 4-year generation if no fishing had occurred. The solid curved line is the maximum likelihood estimate of the mean for Ricker spawner–recruitment functions under the assumption that the probability distribution for any SSB is given by a lognormal distribution. The curved dotted line is the equivalent line for the Beverton–Holt model.

units, in this case millions of females. If we plot the one-to-one line, or the replacement line, then it is a simple matter to see how much the population would increase if there was no fishing on the population. It can be seen that in most years the number of replacement females produced per female was approximately five or six. The average replacement rate at low abundance, where density-dependent mortality is not important, is given by the slope at the origin of the spawner–recruit curve; this quantity is usually termed, by ecologists, the maximum reproductive rate. Based on the fitted spawner–recruitment curves, at low abundance a female can produce approximately nine replacements. This allows the population to persist at very high fishing mortalities; typically around 80% of the returning fish from the population are harvested. However, this quantity also defines the limits of exploitation: the population will decline if much more than 80% of the population is harvested on average, and a lower harvest rate would be a much better management strategy.

For Pacific salmon, it is relatively easy to calculate the maximum reproductive rate because the fish are usually relatively easy to count, and because complications caused by multiple spawning and complex age structure are avoided.

6.2.2 *Experimentally manipulated brook trout populations*

Most good population dynamics data come from heavily exploited populations. We now examine seven populations that have experienced very little fishing pressure but which have been experimentally depleted to determine the nature of density-dependent mortality (DeGisi 1994). An experimental approach has clear advantages in that the experimenter can manipulate the populations at will.

The seven brook trout populations are from small lakes in the Sierra Nevada Mountains in California. Population sizes were estimated using maximum likelihood depletion methods from experimental gill-net surveys. These gave estimates of the number of mature fish present in the population at the time of spawning and an estimate of the number of fish produced from each

group of spawners that survived to age 1. In this example, the unit of spawner abundance is the number of mature fish present at the time of spawning, and the recruits are the resulting number of fish that survive to age 1.

In interpreting these data, one problem immediately becomes apparent: the units of spawners and recruits are not the same, and thus it is not possible to use these units to estimate the slope at the origin as in the sockeye salmon example. To overcome this problem, the standard procedure is to convert the units of recruits into the same units as spawners. That is, we estimate the number of spawners that would be produced from a given number of recruits, if no fishing has occurred. We use the same natural mortality as estimated by the analysis of these data (DeGisi 1994) and ask how many spawners would be produced from the observed level of recruitment. In this case, the age at maturity is 2 and the natural mortality was assumed to be close to 20% a year, although a slightly different value was estimated by DeGisi. We simplify slightly. Thus 80% of fish that reach age 1 would survive to spawn if 20% died each year. Once a fish reaches maturity, we need to estimate how many times it would spawn on average in the absence of anthropogenic mortality. For this calculation, we sum the probability that a fish will be alive in each year after it reaches the age of reproduction. This probability is 0.8 for the first year after spawning, $0.8 \times 0.8 = 0.64$ for the second year, and so on. This is known as a geometric series, and its sum is 5 in our case. That is, a fish that survived to 1 year of age would spawn an average of four times. This is calculated from the probability of surviving to spawn once, 0.8, multiplied by the average number of times the fish would spawn, five. To plot the spawners and recruits in the same units, we multiply the number of recruits from each age-class by the average number of times they would spawn over their lifetime. This is the scale on the right-hand axis of Fig. 6.2.

In each of the seven populations, the unexploited population persists around an equilibrium population size. For example, the Hell Diver 3 population appears to produce an equilibrium when the number of spawners is between 150 and 200 (Fig. 6.2). Above this level, the production of
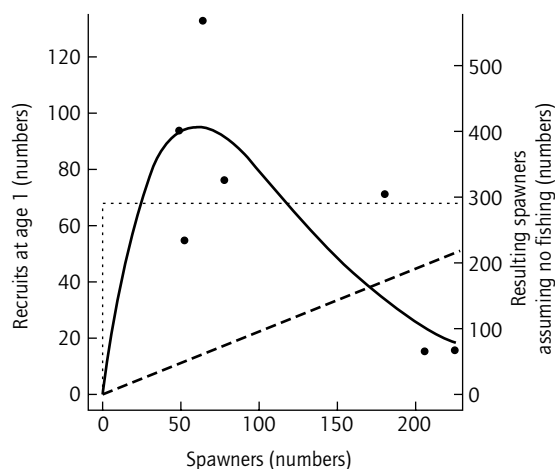
Fig. 6.2 Spawner–recruitment data for brook trout (*Salvelinus fontinalis*) in the Hell Diver 3 lake in the Sierra Nevada. On the *x*-axis is the number of spawning adults for any one year. Each point represents the production of 1-year-old recruits for each level of observed recruitment on two different scales: on the left-hand side is the estimated number of trout that survive to age 1, and on the right-hand side is the resulting number of spawners that would be produced if no fishing occurred on the cohort over the lifetime of the cohort. The scale on the right-hand side is the scale on the left-hand side multiplied by the average number of times a 1 year old would be expected to spawn if no fishing occurred (see text for explanation). The straight dashed line is the replacement line. The intersection of the Ricker spawner–recruitment curve (solid line) with the replacement line represents the approximate equilibrium for the population. The dotted line is the Beverton curve.

recruits decreases below the equilibrium level, while below this population size the production of recruits increases.

When the population was increased to high levels, average recruitment decreased in each of the seven experimental lakes. This form of density-dependent mortality, called overcompensation, has rarely been so clearly demonstrated. The maximum reproductive rate for these populations is estimated to be around 19 replacement spawners per spawner from the Ricker model, a value that is similar in all the seven experimental populations (Myers et al. 1999).

It is useful to examine Fig. 6.2 in detail to under-

stand the nature of the extrapolation to the origin. There are three data points where approximately 50 spawners were observed, and we calculate a production of replacement spawners of around 400 for this case, which results in a slope of around 8. The extrapolation to the origin increases a pattern that is typical for a curve with overcompensation. If there are observations at low spawner abundances, such as in Fig. 6.1, this is much less of a problem. Also note that the Beverton–Holt model does a very poor job of fitting these data, and results in an effectively infinite slope at the origin.

6.2.3   Iceland cod

The next example is the cod population from Iceland, based on data collected between 1928 and 1995 (Fig. 6.3). The history of this population has been reconstructed from detailed catch-at-age records over this time period and represents one of the best-documented fish populations in the world (Schopka 1994). This population has recently shown only a small decline in recruitment even though spawning biomass has been reduced to less than one-tenth of what it was 50 years ago.

More importantly, from the relatively low population level of 200 000 tonnes of mature fish, the stock can produce about 200 million 3-year-old recruits. Again, we can convert the production of these 200 million recruits to the same units as the spawners. To do this, we ask how much spawning biomass would be produced for each recruit, and then calculate the spawning stock biomass per recruit with no fishing, $SPR_{F=0}$, where the subscript F indicates dependence on fishing mortality, which is zero for this definition (Mace 1994). This is calculated as

$$SPR_{F=0} = \sum_{a=a_{rec}}^{\infty} w_a l_a p_a, \qquad (6.5)$$

where l_a is the natural survival from the age of recruitment to age a, p_a is the proportion of fish mature at age a, w_a is the weight at age a, and a_{rec} is the age of recruitment, which is 3 years old for Iceland cod. For explicitness, we must state that a_{rec} represents the first age at which abun-
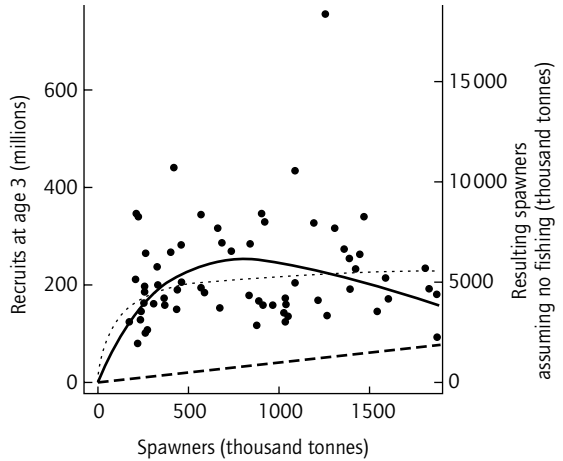
Fig. 6.3   Spawner–recruitment data for cod from Iceland. On the *x*-axis is the biomass of spawning adults for any one year. Each point represents the production of recruits for each level of observed spawner biomass on two different scales: on the left-hand side is the recruits in millions of 3-year-old cod, and on the right-hand side is the resulting spawning biomass if no fishing occurred on the cohort. To convert the scale on the left-hand axis to the one on the right-hand axis, multiply the number of 3-year-old fish by the average spawning lifetime biomass produced by one 3-year-old if no fishing occurred (see text for explanation). The straight dashed line is the replacement line. The intersection of the spawner–recruitment curves with the replacement line represents the approximate equilibrium for the population if no fishing occurred.

dance can be estimated, and it is also generally the first age at which it is feasible to harvest. This calculation results in the estimate that one 3-year-old cod is expected to produce around 24 kg of spawning biomass, if no fishing occurs. That is, the 200 million recruits would be expected to produce around 4.8 million tonnes of spawning biomass over their lifetime. The maximum reproductive rate can be calculated from the Ricker curve in Fig. 6.3: at low population sizes, a spawner should produce more than 20 replacements over its lifetime. This population has sustained a relatively high rate of exploitation, which has typically seen over 50% of the fish removed in any one year. Note that the slope at the origin for the Ricker model is much

less than that estimated for the Beverton–Holt model (the dotted line).

The cod population in Iceland and the brook trout population from lakes in the Sierra Nevada Mountains differ in almost every possible way; however, their maximum reproductive rate is approximately the same in both cases.

6.2.4 *Striped bass on the east coast of North America*

Recently, a detailed assessment of striped bass (*Morone saxatilis*) on the east coast of North America has been completed (National Marine Fisheries Service 1998). The NMFS assessment can be used to estimate spawner recruitment for the years 1982–95. The biomass of spawners increased by a factor greater than five during this period, primarily due to reduced fishing mortality. The reduction in fishing mortality allowed many more fish to reach maturity, which also produced a subsequent increase in recruitment (Fig. 6.4).

The maximum reproductive rate is given by the slope at the origin of the spawner–recruitment plot. In this case, both the Beverton–Holt and Ricker models give similar estimates of the slope at the origin of the curve. The recruitment was

converted to spawning biomass in the same way as for cod described in the last section. These data show that, at low levels, the replacement level is almost 20 spawners per spawner in the absence of anthropogenic mortality, similar to that for the Iceland cod.

The high levels of compensatory reserve estimated from the spawner–recruit data are also seen from research surveys of the Hudson River population of striped bass. Pace et al. (1993) showed that the young-of-the-year (YOY) index of striped bass in the Hudson River was unrelated to the number of larvae. This implies either density-dependent mortality between the early larval stage and the establishment of the YOY index, or inadequate sampling of the YOY when their abundances are high (see Persson, Chapter 15, this volume). Since the analysis of Pace et al. (1993), spawning stock has continued to increase in the Hudson River. Resulting YOY indices have also remained relatively constant despite this increase in stock size (National Marine Fisheries Service 1998).

6.3 GENERALITIES THROUGH META-ANALYSIS

The previous examples of spawner–recruitment relationships come from a wide variety of fish species with very different life histories and patterns of exploitation. For example, the cod population in Iceland and the brook trout population from lakes differ in almost every possible way; however, their maximum reproductive rates are very similar. Despite the wide variety in the species examined, one central biological point remains: the maximum reproductive rate was substantial (i.e. >1) for all the populations examined. However, the maximum reproductive rate is not so high that overfishing, particularly of pre-reproductive fish, will not cause stock collapse. Since time-series for individual populations are often short and noisy, we can use meta-analysis to estimate, for example, the rate of fishing that would lead to stock collapse.

Meta-analysis refers to the process of combin-
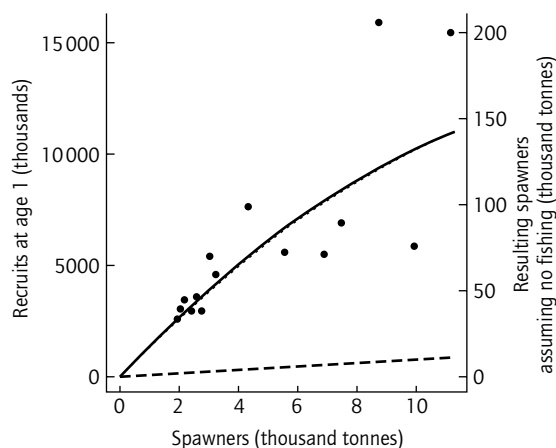
Fig. 6.4 Spawner–recruitment data for striped bass on the east coast of North America. The explanation of the scales is the same as for Fig. 6.3.

ing and assessing the findings from several separate research studies that bear upon a common scientific problem (Hedges and Olkin 1985; Cooper and Hedges 1994). The use of statistical methods of meta-analysis for research synthesis is now the standard accepted method for making crucial decisions in medical treatment, drug evaluations, and issues in public health and social policy. Recently, it has become a standard approach for evaluating the critical population parameters needed to understand fisheries dynamics (Mace and Sissenwine 1993; Myers and Barrowman 1996; Liermann and Hilborn 1997; Punt and Hilborn 1997; Myers and Mertz 1998; Myers et al. 1999). For its use in examining the effects of fishing on marine ecosystems, see Kaiser and Jennings, Chapter 16, Volume 2.

Until recently the formal implementation of meta-analytic methods was hampered by a lack of appropriate statistical methods and of compiled datasets. These two problems have been largely overcome. The compilations by Mace and coworkers (e.g. Mace and Sissenwine 1993) and by Myers and coworkers (e.g. Myers et al. 1995b) provide examples of the databases required for a thorough meta-analysis of compensatory reserve. Mace's data have been incorporated into the ongoing compilation by Myers. Recent advances in statistical software allow for the implementation of complex linear and non-linear mixed effects (variance components) models. These models have been used to great effect in meta-analysis (Myers et al. 1999).

Meta-analysis of compensatory reserve has received a great deal of attention because of its usefulness in estimating limits to fishing mortality, maximum sustainable yield and the shape of the spawner–recruit relationship. The broadest examination of compensatory reserve is an analysis of 246 fish populations by Myers et al. (1999). These analyses demonstrate that compensatory reserve appears to be relatively constant within a species and within groups of related species. The analyses employed variance components models that assume that the log of the standardized slope at the origin of the spawner–recruit curve is a normal random variable (Searle et al. 1992). This analysis suggested a new and unsuspected finding: the maximum annual reproductive rate, which is

the maximum reproductive rate divided by the average number of spawnings in an exploited population, for any of the species examined is usually between one and seven. This number may be less for some species and more for others, but the relative constancy of the annual reproductive rate is an unanticipated and very important finding.

The common belief that there is no relationship between spawner biomass and recruitment is founded on the notion that the maximum reproductive rate for fish is essentially infinite. This belief is based on the observations that fecundity of fish is often large and that no strong reduction of recruitment is observed at low spawner abundances over the range of the observations. The problem lies in that little information can be gleaned from individual datasets, particularly as data at low spawner abundance is sparse. Instead, we need to examine a variety of datasets simultaneously in order to make proper inferences about spawner–recruitment relationships (Myers and Barrowman 1996; Myers 1997).

6.4 CARRYING CAPACITY

A cursory examination of the spawner–recruit data for an Icelandic cod stock suggests that the carrying capacity is around 200 million 3-year-old recruits (Fig. 6.3). It would be extremely useful to have a theory to explain differences in carrying capacity, yet none exists. This is perhaps the greatest outstanding, and overlooked, problem in recruitment. One exception are students of salmon biology, who have studied this issue with some care (e.g. Bradford et al. 1997). Only recently have we begun to study marine species in the same way (Iles and Sinclair 1982; Rijnsdorp et al. 1992; Myers et al. 2001).

No serious ecologist believes that carrying capacity is constant for any population, as it is certain to change with the environment and the abundance of predators, parasites and competitors. It is crucial that fisheries ecologists begin developing a predictive understanding of the variability in carrying capacity as it is central to many ecological and management issues. It is clear that a meta-

analytic perspective will be required, so as to estimate the variability in carrying capacity both within and between populations. The first step to such an analysis is to standardize carrying capacity on a per unit area basis, so that it can be compared across populations. Then it will be possible to employ non-linear mixed effect models to carry out a meta-analysis of the carrying capacity for all regions simultaneously, and to analyse cofactors, such as primary productivity and species interactions, that could cause the carrying capacity to vary (Myers et al. 2001). I believe that such an analysis will greatly improve our understanding of the factors that limit carrying capacity, and thus recruitment.

6.5 VARIABILITY IN RECRUITMENT

Thus far, I have concentrated on the mean relationship between spawner abundance and subsequent recruitment; however, variability in recruitment is often the most notable feature of such data. I now look at recruitment variability using the spawner–recruitment database that I have assembled. I examine two estimates of the variability: the coefficient of variation (CV) of recruitment and the standard deviations of log residuals from a Ricker spawner–recruitment function (Fig. 6.5). Maximum likelihood was used to estimate the parameters of the spawner–recruitment function under the assumption that the variability in recruitment for any spawner abundance was lognormally distributed (see Myers et al. 1995b for details). Similar estimates of the variability were obtained if alternative spawner–recruitment functions were used. Unfortunately, it is very difficult to obtain unbiased estimates of recruitment variability. For example, ageing errors will reduce estimated variability in recruitment for catch-at-age analyses (Bradford 1991), while research surveys may overestimate the variability because estimation error may be an important source of variability. Thus, these results should serve only as a rough guide (see my website for more information).

There are very large differences among families in recruitment variability; however, most of the data shows recruitment variability with a CV of around 50% (Fig. 6.5). Surprisingly there exists no theory to explain this important observation. For example, why is the typical value not around 10% or 100%? We cannot pretend to have a quantitative theory of recruitment until we have explanations of this and similar observations.

There are other generalities that emerge about recruitment variability. The spectrum of the time-series of animal abundance typically contains significant low-frequency variation. Anyone familar with recruitment time-series will realize that this effect is almost always present; however, a few time-series, e.g. recruitment for Icelandic cod, do not show this effect. This may be because this species lies within the centre of its range (Myers 1991). Several empirical patterns have been proposed to help explain the patterns in recruitment variability; these are summarized in Table 6.1.

6.6 AT WHAT LIFE-HISTORY STAGE DOES DENSITY-DEPENDENT MORTALITY OCCUR?

In the spawner–recruit examples, we do not know at what stage density-dependent mortality and stochastic density-independent mortality occurs. This question was first addressed in terms of the critical period hypothesis that states 'the numerical value of a year class is apparently stated at a very early age, and continues in approximately the same relation to that of other year classes throughout the life of the individuals' (Hjort 1914). This is certainly true to some extent but with the following limitations: (i) some stochastic mortality after and (ii) density-dependent mortality changes the relative abundance, but good year-classes remain good. For some populations we can examine how interannual variability changes with age, and use models to examine when density-dependent and density-independent mortality occurs. Two contrasting situations can be seen in the data for
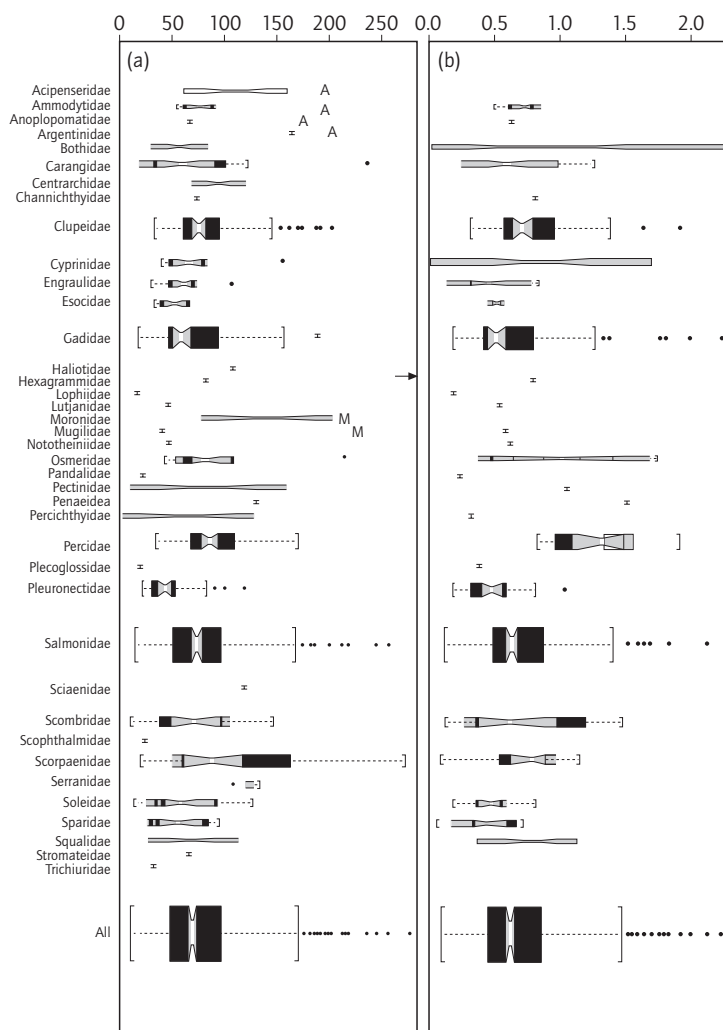
Fig. 6.5 Boxplots by family of (a) the coefficient of variation in recruitment ignoring the effect of spawner abundance and (b) the maximum likelihood estimate of the standard deviation of the natural log of the residuals from fits of the Ricker model σ assuming lognormal variability in recruitment (which is an estimate of the standard deviation of the density-independent mortality). Note that not all recruitment series have spawner estimates, so that (a) has more data than (b). The boxplots show the limits of the middle half of the data (the white line inside the box represents the median). The amount of data is shown as the width of the boxes, which are proportional to the square root of the number of data points. The notches are the approximate 95% confidence intervals of the median. If the notches on two boxes do not overlap, this indicates a difference in a location at a rough 5% significance level. The upper quartile and lower quartile provide the outline of the box. Whiskers are drawn to the nearest value not beyond 1.5*(interquartile range) from the quartiles; points beyond are drawn individually as outliers. Outliers are plotted as points, except for one that falls outside the range of the plot, which has been replaced by an arrow.

brown trout (*Salmo trutta*) from Black Brows Beck (Elliott 1994) and cod from the North Sea (Fig. 6.6). Very strong density-dependent mortality occurs in the first 6 months after eggs are deposited for brown trout, while mortality that varies among years, and is largely independent of density, occurs until maturity at age 3. For brown trout, recruitment variability increases with age (Fig. 6.7).

The pattern is quite different for cod in the North Sea where the variability in recruitment decreases with age. The decrease in recruitment

variability at age in cod is caused by strong density-dependent mortality during the demersal juvenile stage, and is seen in the 17 populations of demersal fish studied by Myers and Cadigan (1993a,b). Several observations from the cod data should be noted: (i) year-classes that are large soon after settlement remain relatively large for all subsequent surveys, (ii) the variability decreases with age and (iii) larger spawner abundances are slightly positively correlated with higher recruitment. The first two observations are clear from virtually all

Table 6.1 Patterns in recruitment variability.

Pattern	Species	Reference
CV(R) ~50%	Most species	This chapter
Var(R) ↑ with length of time-series	Most species	Myers et al. (1995a)
Var(R) ↑ at edge of species range	Cod, haddock, herring	Myers (1991)
Var(R) ↑ for greater fecundity (slight effect)	57 species	Mertz and Myers (1996), Rickman et al. (2000)
Var(R/S) ↑ at low spawner abundance	10 families	Myers (2001)
Var(R) ↑ with smaller duration of spawning	Cod	Mertz and Myers (1994)
Var(R) ↑ on offshore banks	Cod, haddock, American plaice	Myers and Pepin (1994)
Var(R) ↓ at older ages	Marine demersal fish	Myers and Cadigan (1993a)
Var(R) ↑ at older ages	Anadromous salmonids	Bradford (1995)
Var(R) is greater for anadromous than marine		Rothschild and DiNardo (1987)
Spatial scale of R ~500 km	11 marine species	Myers et al. (1997a)
Spatial scale of R ≤50 km	7 freshwater species	Myers et al. (1997a), Bradford (1999)

Var(R), variance of recruitment; CV(R), coefficient of variation in recruitment; Var(R/S), variance of survival for egg production to subsequent recruitment.

population dynamics data of demersal fish with a planktonic life stage (I return to this in a later section). The last observation is certainly weak for these data, but is a persistent feature of the vast bulk of spawner–recruit data (Myers and Barrowman 1996). Note that both of these very reliable datasets show similar levels of variation at age 3, with a CV of about 0.5, which we have previously seen to be commonly observed for fish (Fig. 6.5).

While the result for demersal fish appears to hold for many populations, the result for trout may not be true for salmonids in general, although there is sometimes increased variance in demersal fish due to density-dependent mortality in the juvenile stage (Myers and Cadigan, 1993b; Fromentin et al. 2001). For example, Bradford (1995) found that the variance in survival increased with age for many Pacific salmon species, and about half the variability in natural survival occurred after migration to the sea. It would be of great interest to apply the methods that I developed with Cadigan, which include estimation error, to examine the general question of the creation of variability in survival by density-independent mortality and the reduction in the variance by density-dependent mortality for salmonid data.

A complementary approach to this problem is to use otolith analysis to examine variation in survival within and among cohorts (Rice et al. 1987). If a cohort is sampled multiple times, it is possible to use otolith microstructure to measure patterns of daily growth, and hence greatly increase our understanding of recruitment processes. However, the amount of sampling required to test statistical models with such data can be overwhelming; careful modelling should precede such a project.

6.7 ESTIMATING DENSITY-DEPENDENT MORTALITY FROM LONG-TERM SURVEYS

Studies of recruitment have been hampered by the unwillingness of many biologists to use methods that account for the estimation error inherent in estimating the abundance of fish populations. With newer methods, it is possible to make better use of the many long-term research surveys of fish abundance. These surveys can be used to estimate the extent of density-dependent mortality and, if performed over multiple life-history stages, can be used to infer at which life-history stage compensation is occurring. Such an analysis is best carried out using an extension of key-factor analysis that includes estimation error. The original version of key-factor analysis assumed that measurements
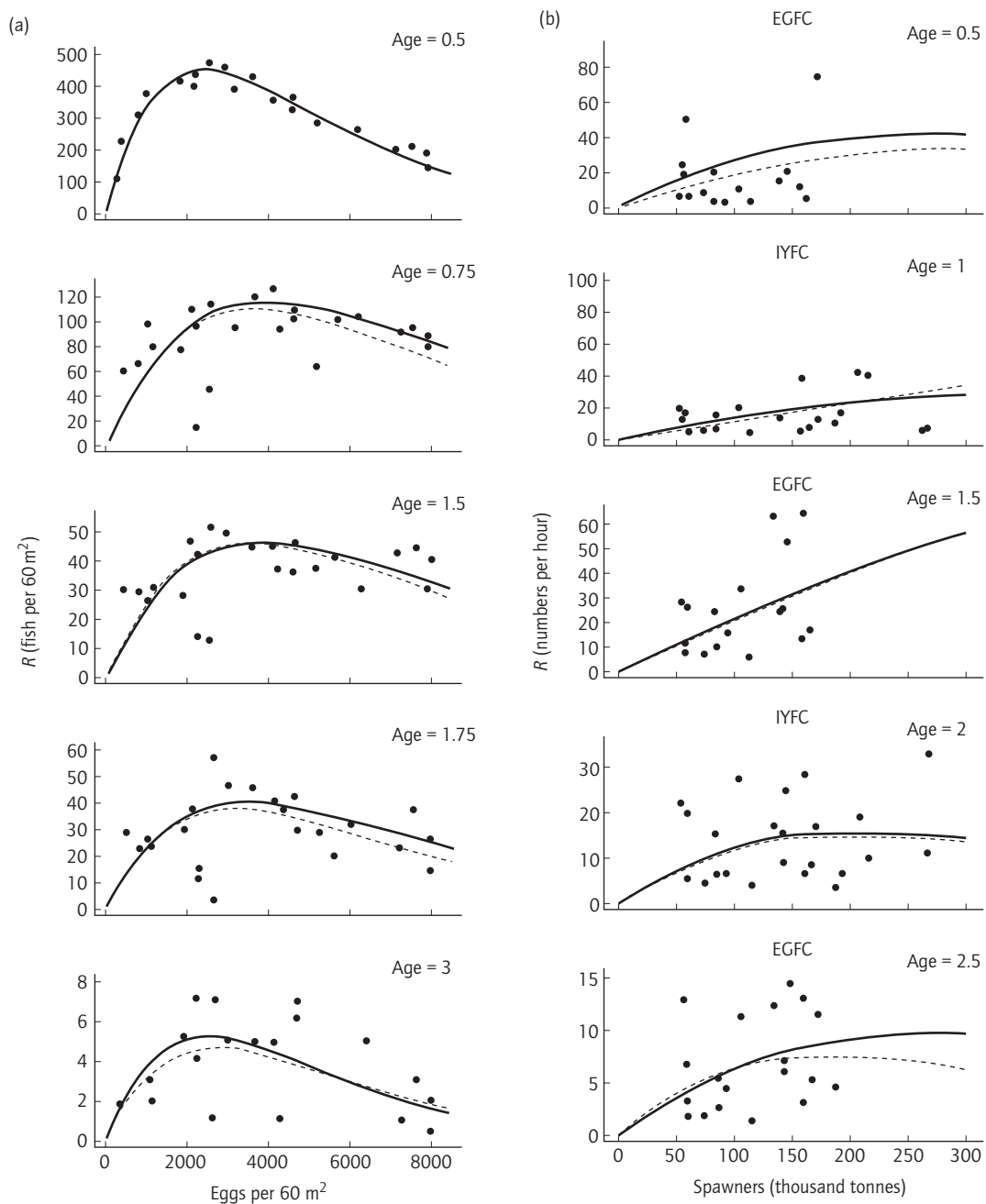
Fig. 6.6 Recruitment versus spawner abundance at five ages for (a) brown trout and (b) cod. Note that recruitment is estimated from two different surveys for North Sea cod: EGFS is the English Groundfish Survey and IYFS is the International Young Groundfish Survey, which covers a longer time period.
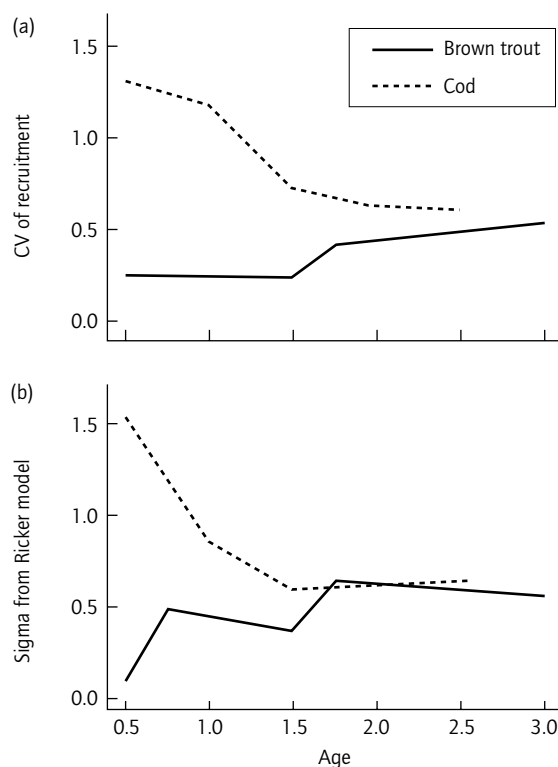
Fig. 6.7 Changes in (a) the coefficient of variation (CV) in recruitment and (b) the standard deviation of the log residuals of the recruitment from a Ricker model at five ages for brown trout and cod.

were made without error; this is not an adequate approximation for fish population data.

Myers and Cadigan (1993a,b) considered a population in which each generation is surveyed at several stages or ages. Let the number of individuals entering stage a be N_a. Consider the dynamics between two stages, a and $a + 1$, where the natural mortality is divided into three components: (i) the average mortality between the two stages that is independent of density, τ_a; (ii) the density-dependent component, δ_a, which is assumed to be proportional to the logarithm of the initial density; and (iii) the variable component unrelated to abundance, ε_a. The dynamics between two stages is described by:

$$N_{a+1} = N_a \exp(-\tau_a - \delta_a \log N_a + \varepsilon_a). \tag{6.6}$$

Note that the above formulation assumes that density-dependent mortality occurs before the stochastic component of density-independent mortality; this should be kept in mind when interpreting the results.

Myers and Cadigan showed that if estimates of the observation error variance are available from the sampling variability, or if multiple surveys of the same cohort occurred, it was possible to estimate the density-dependent mortality and the variance of the density-independent mortality. Furthermore, it is possible to estimate the delayed density-dependent mortality as well. They tested the hypothesis that population variability is created and regulated at the juvenile stage for 17 populations of groundfish. Density-dependent mortality was estimated using an extension of classical key-factor analysis (Varley and Gradwell 1960) that explicitly included estimation error. Myers and Cadigan concluded that the juvenile stage was crucial for density-dependent population regulation in these species, but that the source of interannual variability in year-class strength occurs during the larval stage or the very early juvenile stage. These quantitative estimates confirm previous analyses that show the strong influence of density on mortality in the juvenile demersal stage after settlement to the bottom (Rauck and Zijlstra 1978; Lockwood 1980; Van Der Veer et al. 1990).

One major disadvantage of Myers and Cadigan's method was that it was restricted to the assumption that density-dependent mortality is proportional to the logarithm of the initial density. This assumption was needed to obtain linearity of the model equations. However, it should be possible to consider much more general forms of density-dependent mortality using more modern methods, such as non-linear state space models estimated using the hierarchical Bayes methods (Gilks et al. 1994).

Much less is known about density-dependent mortality from research surveys of pelagic fish, probably because of the much greater difficulty of estimating abundance of pelagic fish compared

to demersal species. We know of no analysis for pelagic species similar to the work of Myers and Cadigan that have included the role of estimation error in the statistical models.

Long-term surveys of lakes have also generally shown strong density-dependent mortality during the preadult life stages. For example, long-term surveys using research traps for European perch in Windermere, UK (Mills and Hurley 1990), trawls for yellow perch in Oneida Lake, New York (Nielsen 1980) and mark–recapture studies of walleye in Escanaba Lake, Wisconsin (Serns 1982) have demonstrated the importance of density-dependent mortality during preadult life stages.

Density-dependent mortality has been observed in many long-term research surveys of stream fish. This was observed in those cases where cohorts were observed multiple times, for example brown trout (Elliot 1994), brook trout (McFadden et al. 1967), Atlantic salmon (Chadwick 1985) and several Pacific salmon species of the genus *Oncorhynchus* (Ricker 1954; Myers et al. 1997b). Strong density-dependent mortality and/or growth is expected in species that have territorial behaviour, which is typical of stream-dwelling species (Elliott 1994).

Extensive surveys of anadromous fish have been helpful for establishing the timing of density-dependent mortality. For example, the monitoring of the number of anadromous alewife (*Alosa pseudoharengus*) spawners into, and the number of seaward migrants out of, Damariscotta Lake, Maine showed that a five-fold change in egg production resulted in almost no change in recruits; strong compensation was occurring in the egg or larval stages (Walton 1987). These results are consistent with other studies of *Alosa* species (Lorda and Crecco 1987), and contrast with those of the demersal fish described above for which strong density-dependent mortality existed later in the post-larval stage.

In summary, long-term research surveys have provided valuable insights into the nature of population dynamics and compensation from fishery independent sources. If estimation error is explicitly included in the analysis of the results from such surveys, they allow quantitative estimates of the importance of density-dependent and density-independent mortality at various life stages. Fisheries ecologists have made very inefficient use of the excellent survey data available to them; the analysis is difficult and requires the use of subtle statistical methods. We should make better use of such data.

6.7.1   Density-dependent mortality within and between cohorts

Spawner–recruit data relies on a regression approach. Another source of evidence, the within-cohort data, is usually ignored. Although traditional methods of analysis of data within cohorts, such as key-factor analysis, are useless for fisheries work because of the assumption that abundance is measured without error, it is possible to extend this type of analysis using modern statistical methods (Myers and Cadigan 1993a,b). The basic idea of these methods is not to treat each cohort abundance as an unrelated number but to assume that the initial recruitment comes from a statistical distribution, usually lognormal, and to treat all variation in subsequent ages as also coming from a statistical distribution. This allows a much deeper understanding of the process.

Previous work has been limited by rather strict distributional assumptions, for example that recruitment is lognormal. The methods appear to be reasonably robust to this assumption; perhaps the more important assumption is the nature of the functional form of the density-dependent mortality. Recent state-space and non-linear time-series methods should allow this to be studied in the near future.

6.8   PELAGIC EGG, LARVAL AND JUVENILE STAGES

The population biology of the pelagic stages remains the most difficult of all problems related to understanding recruitment. The primary source of variability in recruitment is the enormous interannual variability in density-independent mortality during the pelagic egg and larval stages

of marine fish; however, it has been difficult to identify the source of this variability (Leggett and DeBlois 1994). Before discussing these issues in depth, I detail the most influential theory concerning interannual variability in larval survival.

6.8.1 *Match/mismatch hypothesis*

The match/mismatch hypothesis of Cushing (1969, 1990) has provided considerable insight about year-class success and its variability in marine fish populations. The central idea is that the closeness of the temporal match between the abundance peaks of larvae and their planktonic prey controls larval mortality. This may be a result either of the vulnerability of first-feeding larvae to starvation or to the fact that poorly fed larvae grow slowly and are more susceptible to predation. Since larval mortality is thought to be very high, the larval stage may be the principal determinant of year-class strength. This picture seems very plausible and it enjoys some empirical support (see Cushing 1990 for a review).

Figure 6.8, adapted from Cushing (1982), illustrates the match/mismatch hypothesis. The im-

portance of the match depends on (i) the length of time between peaks of the two distributions (t_0) and (ii) the width of the distributions, where δ and σ are measures of the width of the zooplankton and larval distributions respectively. For example, if the larval distribution has a width of 2 months, a mismatch of peaks equal to 2 weeks may be inconsequential. Cushing's idea can be put in a simple mathematical model (Mertz and Myers 1994), which results in powerful testable predictions. Namely, we can calculate how year-to-year changes in the food consumed by the entire cohort, F, are related to those changes in the delay between the peak of first-feeding larvae and the peak in their food supply, t_0. Since F is a maximum for $t_0 = 0$, we expect that the average value of t_0 is zero. The difference in food consumption, and hence survival from the assumption of the hypothesis, can now be simply calculated approximately as

$$-\frac{t_0^2}{\delta^2 + \sigma^2} \tag{6.7}$$

(see Mertz and Myers 1994 for details). That is, a difference in survival is now hypothesized to de-

Fig. 6.8 Illustration of a match and a mismatch of larval fish to their planktonic prey (time units are arbitrary). Production of larvae $P(t)$ follows egg release and in a match situation (top panel) the larval production peak closely coincides with the peak of palatable zooplankton (curve designated $Z(t)$). The match condition is characterized by $t_0 \sim 0$. The representative widths of the larval production and zooplankton peaks are σ and δ respectively.
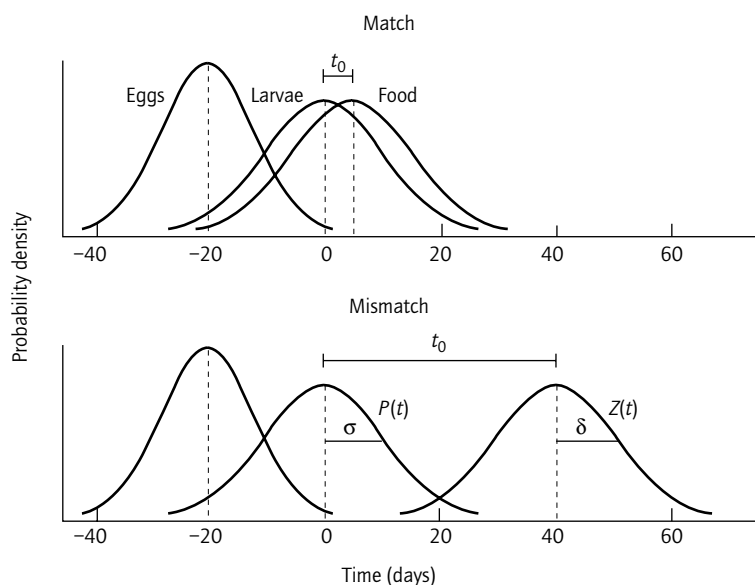
cline by the square of the difference in timings of the peaks, t_0 divided by the sum of the variances of the seasonal distribution of first-feeding larvae and zooplankton abundance. This formulation allows a priori quantitative testing of the match/mismatch hypothesis using data that is presently available from regions with regular plankton surveys.

There are other predictions from the above model that have been tested. Cushing (1990) noted that the effect of variable and unpredictable timing of the plankton peak will be mitigated if a fish stock spreads its spawning effort over a broad temporal window. This corollary of the match/mismatch hypothesis also suggests that there might exist a relationship between the width of the spawning window, measured by the standard deviation of the estimated egg production versus time curve, for a given stock and its recruitment variability. Mertz and Myers (1994) were able to confirm this hypothesis for cod stocks in the North Atlantic.

6.8.2   *Density-dependent mortality in the pelagic stage*

Density-dependent mortality has been often hypothesized as a key factor in population regulation in the pelagic larval stage; however, it has rarely, if ever, been convincingly demonstrated for any marine species (Cushing 1996). For example, attempts to demonstrate food limitation, which is the mechanism most often proposed for mortality, have generally yielded ambiguous results at best (Heath 1992; Leggett and DeBlois 1994; Lochmann et al. 1997). On the other hand, density-dependent mortality in the pelagic stage in freshwater species, or pelagic freshwater stages of anadromous species, has been clearly demonstrated in a number of cases (Walton 1987).

There are several reasons for the difference between our understanding of freshwater and marine systems (see Jones et al., Chapter 16, this volume). First, recruitment variability in fresh water may depend predominantly on biotic influences, particularly the predation by adults of one species on juveniles of another. Walleye (*Stizostedion vit-*

reum) predation has been shown to have a significant impact on year-class strength of yellow perch (*Perca flavescens*) in Oneida Lake (Mills et al. 1987). In contrast, these effects have not been convincingly demonstrated in marine systems (Leggett and DeBlois 1994). Verity and Smetacek (1996) have conjectured that predation is a less dominant influence in marine systems because fish densities appear to be 10–1000 times smaller than in freshwater systems (Horn 1972); however, Horn's estimate may not be relevant because he did not estimate densities that should actually occur in the ocean. The orders of magnitude difference in the density of larvae clearly suggests that density-dependent mortality may be more important during pelagic larval and juvenile stages in fresh water.

Second, there are fewer sampling difficulties in lakes than in the ocean, although some difficulties are similar, for example larvae avoid the sampling device and the avoidance behaviour changes with age or size. Many marine populations spawn over a wide geographical and temporal window, which may change among years (Hutchings and Myers 1994a), making sampling difficult. For example, the very well studied cod population off Lofoten (Pedersen 1984) actually also spawns outside the fjord. The strong advection that occurs for marine populations makes estimation very difficult (Helbig and Pepin 1998). The advected larvae may die, if they are advected into regions where they cannot survive (Myers and Drinkwater 1988), or they may survive and return to the spawning region at an older age (Polacheck et al. 1992).

Error in estimating abundance poses fundamental limitations to the kinds of questions that can be addressed. For demersal fish, it is possible to estimate the density-dependent and density-independent component of mortality between egg and demersal stage, or within the demersal stage. However, reliable estimates of the sources of variability within the egg and larval stage are almost impossible except for a very few species using enormous sampling effort, as illustrated by the California Cooperative Oceanic Fisheries Investigation.

Finally, an experimental approach is much

easier to undertake in freshwater systems than in the ocean. For example, out-planting artificially reared larvae or juveniles has been widely used in freshwater systems to study density-dependent growth and mortality. Whitefish (Corigonidae) has been experimentally stocked at controlled densities in lakes in Finland (Salojarvi 1991), gizzard shad has been experimentally stocked in reservoirs in Kentucky (Buynak et al. 1992), walleye in ponds in the midwestern USA (Fox and Flowers 1990) and steelhead (*Oncorhynchus mykiss*) fry into tributaries of Lake Superior (Close and Anderson 1992). Each of these studies demonstrated strong density-dependence in growth and/or mortality.

Research in this area has concentrated on the sources of stochastic density-independent mortality caused by lack of food, predation or advection. The first two are potentially density dependent, but we have little evidence for marine species that they are density-dependent in the pelagic stage. The most likely mechanism in the observed cases is food limitation. This has been clearly demonstrated for pelagic juvenile sockeye salmon, where large year-classes substantially reduce the zooplankton abundance (Hume et al. 1996). Food limitation during the freshwater phase of anadromous species that fluctuate greatly in abundance, such as the sockeye salmon, will be the most easy to demonstrate.

Although density-dependent mortality is probably important for many species in the pelagic stage, it cannot be quantified until a systematic approach is taken to estimation and meta-analysis.

6.8.3 Stochastic density-independent mortality in the pelagic stage

The most expensive research efforts in recruitment have been to understand the creation of variability in recruitment at pelagic stages of marine fish. Although progress has been made, the overall results are meagre; this ambitious research programme has not resulted in a fully predictive theory.

This research is usually justified because of the importance of predicting recruitment. Approaches to this task may involve finding environmental correlates of recruitment or the field sampling of pre-recruit life-history stages. Predictions of recruitment have been sought through the correlates of recruitment with environmental factors. Wind speed has been proposed as a determinant of recruitment in that storm-driven mixing can disperse larvae and their prey, reducing food availability (Lasker 1975, 1981; Peterman and Bradford 1987). Larval food supply may also be influenced by the lag between appearance of larvae and the peak of abundance of their prey (Cushing 1990). The intensity of turbulence may control the frequency of contact between larvae and their prey (Rothschild and Osborn 1988). Larvae may be exported to inhospitable waters by the action of wind-driven currents or the incursion of Gulf Stream rings (Myers and Drinkwater 1989). For thorough discussions of environmental influences on recruitment see Fogarty (1993), Wooster and Bailey (1989) and Cushing (1996).

The complexity of the mechanisms that have been proposed can be seen by examining one factor. Consider the effect of the wind, described by the vector w, on the survival of pelagic eggs and larvae in the Northern Hemisphere. The cross-shelf wind stress component, τ_x, will have little effect except on the neuston. The long-shelf wind stress component, τ_y, and the turbulence generated by the wind, which is proportional to $|w|^3$ and which will generally be non-linear, may have a plethora of important effects on survival (Cury and Roy 1989; MacKenzie et al. 1994; Dower et al. 1997). These factors may be critical for only short periods of the pelagic stage. For example, Ekman transport caused by the long-shelf wind stress component may decrease survival by transporting larvae offshore (Bailey 1981) or increase survival by increasing larval food supply (Bakun 1996). Recent theoretical models have shown that small-scale turbulence enhances encounter rates between larval fish and their prey (Rothschild and Osborn 1988), while earlier work suggested it would decrease survival by dispersing food (Peterman and Bradford 1987). Empirical laboratory and field observations have helped to clarify the issues

(MacKenzie and Kiorboe 1995); understanding the physics of the upper ocean allows the relative magnitude of the effects to be estimated, but the final link to resulting recruitment has not been established. Similarly, food limitation via Cushing's match/mismatch hypothesis has been investigated and some empirical links from field data demonstrated; again its overall importance is uncertain. It is difficult to produce quantitative estimates from any of these models but it is often possible to use data-driven physical oceanographic models of historic data to quantitatively estimate the effects (Myers and Drinkwater 1988).

One approach to understanding the sources of interannual variability in density-independent mortality is primarily empirical, by correlations with many environmental correlates. Much of this work has been marred by the extreme unwillingness to look at the statistical difficulties of the analyses (reviewed by Myers 1998) and the desire to blame all fisheries problems on the environment. For example, 5 years after there were claims that recruitment of 'northern' cod could be partially predicted from the presence of cold water that led to a greater probability of good survival of cod larvae, the collapse of the stock was being blamed primarily on cold water, a claim that did not stand up to scrutiny (Hutchings and Myers 1994b). The claim that poor recruitment of Northern cod was caused by warm water, and then by cold water, was based on the use of statistical methods that were at best unreliable. The resulting comedy of errors, which resulted in the loss of around 50 000 jobs, should cause any fisheries scientist to carry out such analyses with more care.

There are theoretical reasons to doubt that recruitment can be predicted with sufficient accuracy from environmental data to be useful for management (Bradford 1992; Mertz and Myers 1995). The basis of the simulations by Bradford (1992) and the analytical models of Mertz and Myers (1995) is the distribution of mortality across life-history stages that is typically observed (Bradford 1992; Bradford and Cabana 1997) and the strength of density-dependent mortality in the juvenile demersal stages (Myers and Cadigan 1993b). When these factors are combined, the ability to predict recruitment from environmental factors is very limited, even if the principal mechanism determining interannual survival during the egg and larval stage is well understood, which is seldom the case. The utility of spending large amounts of public research funding to establish predictions of recruitment based on environmental indices should thus be questioned (Walters and Collie 1988). Nevertheless there are broadly two main patterns that emerge from the empirical analysis of such data from a meta-analysis of over 50 studies where previously published environment–recruitment correlations had been retested with new data (Myers 1998). The two conclusions were, first, that correlations for populations at the limit of a species' geographical range have often remained statistically significant when re-examined and, second, that a dome-shaped relationship appears to exist between the recruitment success of small pelagic fish in eastern boundary current upwelling systems (Bakun 1996) and the upwelling intensity (optimal environmental window, OEW) (Cury and Roy 1989). Unfortunately, these environment–recruitment correlations do not appear to be very useful in practice. I recently examined the 47 environment–recruitment correlations reviewed by Shepherd et al. (1984) and found that only one was being used in the estimation of recruitment in routine assessments (Myers 1998).

6.8.4 Demersal stages

Density-dependent mortality probably occurs chiefly in the juvenile demersal stages for coral-reef fish, shelf demersal species and tidepools (Pfister 1996). We know much more about the mechanisms for density-dependent mortality in demersal stages of coral-reef fish than any other group. The mechanisms have largely been unravelled by field experiments that examine how food limitation interacts with predation. Predation mortality can be mediated through territorial behaviour or the 'growth mortality hypothesis' that proposes that greater competition for food increases the time required to grow to a size where they are less vulnerable to predation (Ricker and Forrester 1948). Forrester (1995a) experimentally demonstrated the second mechanism by artifi-

cially supplementing food for damselfish (*Dascyllus aruanus*). The link between predation and structural complexity was examined by Beukers and Jones (1998).

Hixon and Carr (1997) translocated 32 live coral-reef heads to a large sand flat so that they could manipulate orthogonally the density of prey and the presence of predators. They demonstrated that density-dependent mortality of juvenile coral-reef fish was dependent upon the presence of two suites of predators: transient piscivores attacking from above and resident piscivores attacking from below. If either predator was absent, mortality was entirely density-independent. Similarly, Steele (1997) has shown strong density-dependent mortality using manipulative experiments on temperate juvenile gobies; again, the density-dependent mortality was primarily due to predation. Forrester (1995b) also showed that juvenile and adult mortality of gobies was strongly density-dependent in a series of manipulative experiments. The experimental results that demonstrate that structural shelter for prey refuges is often limiting (Hixon 1991) strongly supports the importance of protecting the sea bottom from destructive fishing practices (Watling and Norse 1998).

The great success of manipulative field experiments for coral-reef fish should be emulated by researchers who study other systems. There have been some notable successes in other regions. DeGisi's (1994) whole-lake experiments on brook trout, discussed above, is one of the most ambitious. Another experimental approach is to supplement natural populations with artificially reared competitors. Such large-scale experiments have been undertaken on a marine species, cod, in Norway. These have revealed strong density-dependent mortality in the juvenile stage and shown that artificial enhancement of the species in the wild is generally not possible (Nordeide et al. 1994). Density-dependent mortality in this case appears to be caused by competition for limited food supply.

There are remarkably few experimental manipulations of abundance for stream populations. In one of the few such studies, LeCren (1965) used enclosures to demonstrate extremely strong density-

dependent mortality during the egg to fry stage in brown trout. I find this study particularly interesting because the pattern of density-dependent mortality was not observed in Elliott's study of interannual variability.

The most direct method of assessing compensation is by experimental manipulations of abundance in a carefully controlled manner. The advantage of this approach is obvious: powerful statistical methods of experimental design can be used to construct experiments that can resolve questions that are difficult to answer from observational data alone.

6.9   FUTURE RESEARCH

6.9.1   The need for quantitative theories

At present, our understanding of recruitment is limited to conceptual theories and empirical models, meaning spawner–recruitment functions. Although we can estimate biologically meaningful parameters such as carrying capacity and make quantitative predictions, we lack mechanistic models of basic biological and physical processes. Although we have physical models of some mechanisms (Rothschild and Osborn 1988), they are seldom capable of making predictions about recruitment. Thus, few recruitment studies are taken beyond the interpretive stage and can only claim that observations are consistent with a model or a concept. Ultimately, in order for 'recruitment science' to make progress, we need mechanistic models that make quantitative predictions about the functional form and mean of different processes. Such modelling is difficult, and unappreciated.

My late friend, Gordon Mertz, was a master of models that yielded testable quantitative predictions. For example, Mertz developed a model of Cushing's match/mismatch hypothesis which predicted that recruitment variability should increase as spawning duration decreases, a prediction supported by an analysis of Atlantic cod data (Mertz and Myers 1994). Similarly, he was able to transform very vague concepts of the relationship between fecundity and recruitment variability

into a quantitative predictive theory (Mertz and Myers 1996). I believe that it is this type of model that will yield a greater understanding of recruitment, not vague 'conceptual', non-parametric or black-box models.

It is useful for recruitment biologists to examine the role of the fit of a functional model to data. For example, Max Planck developed a quantitative model for black-body radiation that gave the world the beginnings of quantum theory 100 years ago (Pais 1982). If Max Planck, and the physicists of the day, had been satisfied with a non-mechanistic, non-parametric fit to the data or if the experimentalist at the University of Berlin had been satisfied with anything less than the most exacting measurements, we would not now have quantum mechanics. Thus, functional models are not the goal of science; rather they serve as intermediary steps between ever more refined mechanistic models. If progress is to be made towards understanding recruitment, we must take models and data more seriously.

6.9.2 The individual and recruitment

Modellers of fish populations traditionally assumed that all individuals of a given age are identical. However, we know that this is not the case since competition often takes place between individuals; this is the basis of recent work on individual-based models (Cowan et al. 1996; Letcher et al. 1996; Huse et al., Chapter 11, Volume 2).

Individual-based models that predict that the skewness and the coefficient of variation of weight distributions increase with population density assume density-dependent growth and unequal competition among individuals of a given age (Kimme 1986). Unequal competition assumes unequal resource partitioning, which can result from a combination of territorial control of resources, plastic growth, selective mortality and emigration. Since an animal's size is highly correlated to its competitive ability, relevant models predict a positive feedback cycle, whereby better competitors grow larger and become even better competitors (Latto 1992). Therefore, the weight distributions of such populations are expected to be positively skewed. Perhaps the reason why such predictions have not been considered to apply well to animal populations is the lack of effort to test these models under field conditions. Sampling throughout the range of a population under a large variety of densities is beyond the resources of most field biologists. However, such data are readily available for many fish populations from research surveys. For example, it is a simple matter to plot the length frequencies for Atlantic cod for a year of high abundance and low abundance (Fig. 6.9). For the year-class with high abundance, 1981, the mean size is reduced and the CV and skewness are greater compared with a year-class of relatively low abundance. This relationship holds over all years of the surveys. Atlantic cod shows clear territorial behaviour for the first year of life after the larval stage (Tupper and Boutilier 1995) and often shows strong density-dependent mortality (Myers and Cadigan 1993a) and growth. That is, cod may be more like coral-reef fish, at least during the demersal stage, than most people believe. Such analysis of data from surveys may be very useful in understanding recruitment.

6.9.3 Empirical analysis of multispecies interactions on recruitment

Perhaps the most exciting work in the near future will be the combination of the study of spawner–recruitment relationships with multispecies interactions. I predict that the synthesis of these two approaches will yield wonderful new discoveries. The massive analysis of many aquatic communities by Pauly, Christensen and many coworkers (Christensen and Pauly 1998; Pauly and Christensen, Chapter 10, Volume 2) and the recent extensions to dynamic models (Walters et al. 1997), allied to the approaches outlined here, could yield remarkable results.

It is crucial that the interspecific interaction coefficient be comparable over studies. This can be done by the same standardization as used in the delayed density-dependent analysis above or by a
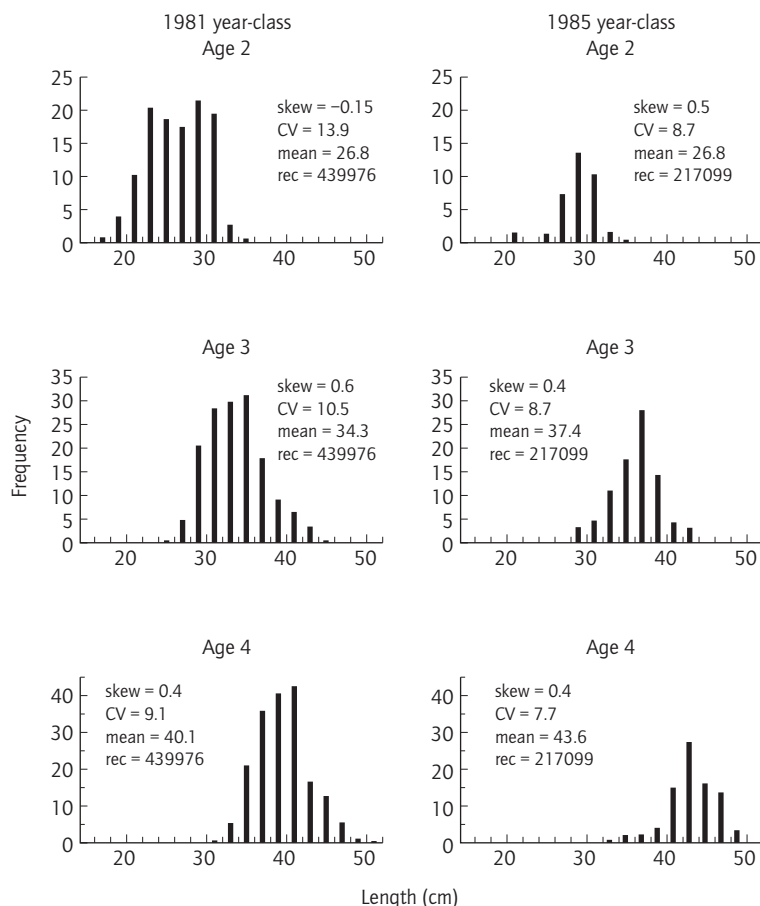
Fig. 6.9 Length frequencies of 2–4-year-old cod at low (1985) and high (1981) population levels for NAFO Subdivision 2J.

modification of the generalized key factor. All singles-species spawner–recruitment models are extreme approximations because they ignore species interactions. The complexity of multi-species interaction requires a meta-analytic approach. An excellent informal meta-analysis was carried out by Daan (1980) in a comparative study of species replacement.

6.9.4 Better use of data and the need for meta-analysis

When studies are being reviewed, effects are often examined to determine how frequently they are statistically significant. This can be a very mis-leading approach, even though it is intuitively appealing. For example, if the reviewer simply examines how often an outcome is statistically significant, then there will be a strong bias towards the conclusion that the process or treatment has no effect (Hedges and Olkin 1985). Furthermore, this bias is not reduced as the number of studies increases. If a large number of studies or populations are examined, the proportion of studies that yield statistically significant results is approximately the average power of the test used (Hedges and Olkin 1985). That is, reviewers of research studies may assume that they are examining the importance of an ecological process, but may only be examining the power of the tests used to exa-

mine it. Research synthesis without considering the statistical problems can lead to serious mistakes. I believe it is a mistake to expect 'definitive studies'.

Work should focus on obtaining quantitative estimates of the components of density-independent mortality that can be attributed to different causes, such as starvation, predation and advection, and quantitative estimates of density-dependent mortality at different stages. Results should be presented in such a way that they can be compared among populations and species. The components of the interannual variability in mortality can be compared among populations and species (Myers 1995). Similarly, if mortality is proportional to log density, then the coefficient of density dependence can be compared across populations (Myers and Cadigan 1993a). Virtually no systematic attempts have been made to carry out these studies.

6.10 CONCLUSIONS

Attempts to understand recruitment have dominated much of fisheries research in the last century. We have made good progress on some issues. The actual practice of managing fisheries is being changed into a quantified science, i.e. something closer to engineering instead of an art, because we discovered quantitative generalities and have developed the tools to apply them, e.g. Bayesian methods. For example, we now have estimates of the maximum reproductive rate, which allows the limits and exploitation to be well understood. Furthermore, we have a much greater theoretical and empirical understanding of the nature of recruitment variability (Table 6.1).

Further progress will require improved experiments, observations and analytical methods. Although experiments have elucidated many aspects of post-settlement recruitment processes for coral reef fish, experimental manipulations need to be extended to other systems. Recruitment studies have been limited to a few species that are either commercially important or easily studied. The most important outstanding questions concerning recruitment revolve around multispecies interactions; meta-analytic methods to infer these interactions from the present data are sorely needed.

ACKNOWLEDGEMENTS

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7 Life Histories of Fish

J.A. HUTCHINGS

7.1 INTRODUCTION

7.1.1 What is a life history?

All fish differ in the means by which they propagate genes to future generations. Some mature during their first year of life at a comparatively small size, while others delay initial reproduction for tens of years, by which time they can be extremely large. Some produce large numbers of small offspring while others produce few numbers of comparatively large offspring. Some spawn several times throughout their lives while others die after reproducing just once. It is differences such as these, usually most pronounced among families and orders, that predicated the seminal research on fish life histories by Svärdson (1949) on offspring size and number, Alm (1959) on the influence of growth rate on age and size at maturity, and Beverton and Holt (1959) on associations among growth rate, mortality and longevity. Life-history research thus addresses the tremendous variability that exists in reproductive strategies among species and, perhaps more importantly from an ecological and management perspective, among populations within species and among individuals within the same population.

Life histories can be defined as the means by which individuals, or more precisely genotypes, vary their age-specific expenditures of reproductive effort in response to physiologically, environmentally, ecologically and genetically induced changes to age-specific survival and age-specific fecundity. As such, life histories reflect the expres-sion of traits most closely related to fitness, such as age and size at maturity, number and size of offspring, and the timing of the expression of those traits throughout an individual's life. Life-history theory is perhaps most often used to predict the age and size at which an organism first reproduces and the effort it allocates to reproduction at that and subsequent ages, often measured as the numbers and size of offspring or proportional commitment of energy reserves.

In a practical sense, life-history theory can be used to predict how changes to abiotic and biotic environments, ultimately through their effects on age-specific survival and fecundity, influence selection on the fundamental 'decisions' that genotypes face concerning reproduction. For example, will a particular environmental perturbation, such as increased mortality among adults, favour genotypes that mature early or late in life? How might selection influence reproductive effort allocated to the behavioural, physiological and energetic components of reproduction, each of which will have possible consequences to future growth and survival? In addition, will genotypes that partition their reproductive effort among few large offspring be favoured over those that produce many small offspring?

Implicit within any prediction based on life-history theory is the assumption that natural selection favours those genotypes whose age-specific schedules of survival and fecundity generate the highest per-capita rate of increase, or fitness, relative to other genotypes in the same

population. This genotypic rate of increase is usually expressed by r, the intrinsic rate of natural increase. The analytical link between life history and fitness, or rate of increase, is often expressed by the discrete-time version of the Euler–Lotka equation, in which the fitness of genotype i, i.e. $r(i)$, can be calculated from

$$1 = \sum_{x=\alpha}^{x=\tau} l_x(i) m_x(i) \exp(-r(i)x) \qquad (7.1)$$

where l_x represents the probability of surviving from birth until age x, m_x represents fecundity at age x, and age ranges from maturity (α) until death (τ). The age-specific parameters l_x and m_x are commonly termed 'age-specific survival' and 'age-specific fecundity' respectively.

7.1.2   Why study life histories?

The study of life histories can be said to be at the heart of most research in ecology and evolution. This is because a life history is based on the two most fundamental components of life and the two most important metrics of fitness: survival and reproduction. If a genotype is to be successful evolutionarily, in that it is able to contribute its genes to succeeding generations at approximately the same rate as other genotypes in the same population, then it must survive to ages at which it can reproduce, and it must contribute to the production of offspring that will themselves survive to reproduce and produce viable offspring in the future.

Notwithstanding its relevance to ecology and evolution, life-history research has an integral role to play in the management and conservation of fish. This is because of the fundamental link that exists between individual life histories and population rate of increase. Among other things, rate of increase is inextricably linked to a population's ability to sustain different levels of exploitation, to increase after being reduced to low abundance and to withstand introductions of exotic species with which it might interact as competitor, predator or prey. Because the population rate of increase through recruitment is so important to understanding exploited populations, it is given special attention by fisheries biologists. The topic of

recruitment is discussed by Myers (Chapter 6, this volume).

A population's rate of increase, r_{pop}, is simply a function of the mean and variance of the fitness of the various genotypes that comprise that population, i.e. $\mu(r(i))$ and $\sigma^2(r(i))$, underscoring the necessity of understanding the factors that influence life-history variation among individuals within the same population. When estimates of r_{pop} are available over time for a single population, the influence of environmental stochasticity, i.e. unpredictable environmental perturbations that proportionately affect age-specific survival and fecundity of all individuals equally, can be incorporated into an estimate of intrinsic rate, such that the stochastic estimate of r, r_s, is

$$r_s = r_d - 1/2\left(\sigma_r^2\right) \qquad (7.2)$$

where r_d is the deterministic estimate of r and σ_r^2 is the variance in r through time (Lande 1993). The important point to note here is that increased environmental variability in demographic parameters will negatively influence a population's long-term growth rate, such that stochastic estimates of r will always be less than deterministic estimates.

Similarly, if fitness estimates of a single genotype, or more broadly a specific life-history strategy, are available over time, the fitness associated with that genotype or life history should be estimated as the geometric mean of the fitness estimates. Use of the geometric mean makes implicit the fact that fitness is determined by a multiplicative process: the total number of descendants left by an individual after n generations depends on the product of the number surviving to reproduce in each generation (Seger and Brockmann 1987). The geometric mean fitness of genotype i after n generations can be calculated as

$$\left[\left(r(i)_1\right) \times \left(r(i)_2\right) \times \left(r(i)_3\right) \times \left(r(i)_4\right) \times \ldots \times \left(r(i)_n\right)\right]^{(1/n)} \qquad (7.3)$$

Note that the geometric mean is strongly influenced by low values. Importantly, then, the more variable a set of values, the lower the geometric mean. Thus, selection should act to reduce the

variance in genotypic/individual fitness over generations, even if this entails a 'sacrifice' of the expected fitness within any one generation (Roff 1992). Such a 'bet-hedging' life-history strategy in fish, manifested as the spreading of reproductive risk across space and time, would include multiple spawning events within a single breeding season, breeding with multiple mates and multiple reproductive bouts throughout an individual's life. Myers (Chapter 6, this volume) deals specifically with the spatial and temporal variability of recruitment.

7.1.3 How variable are fish life histories?

When one thinks of life-history variability in fish, it is the extraordinary differences among species that initially come to mind. Age at maturity ranges from weeks in the tropical cyprinodont *Nothobranchius* sp. that inhabit temporary pools (Simpson 1979) to an average of 35 years for spiny dogfish, *Squalus acanthias*, off British Columbia (Saunders and McFarlane 1993). Size at maturity ranges from 8–10 mm and tenths of a gram in the smallest goby, *Trimmatom nanus* (Winterbottom and Emery 1981), to several metres and thousands of kilograms in the largest elasmobranch, the whale shark, *Rhincodon typus* (Helfman et al. 1997). The elliptical myxinid eggs are typically 2–3 cm in length (Martini et al. 1997; J.A. Hutchings, unpublished data) while oviparous chondrichthyan eggs are typically 6–7 cm in diameter in egg cases up to 30 cm in length (Bond 1996). Teleost egg sizes range widely. Among the smallest are those produced by the surfperch, *Cymatogaster aggregata* (0.3 mm diameter; Kamler 1992; Wootton 1998), and the lightfish *Vinciguerria* spp. (0.5 mm; Helfman et al. 1997); the largest among oviparous fishes are those produced by salmonids (2.5–10 mm; Tyler and Sumpter 1996) and by mouth-brooding marine catfishes (14–30 mm; Tyler and Sumpter 1996; Helfman et al. 1997). Number of offspring per female can vary from as few as two in viviparous sharks, such as the sand tiger, *Odontaspis taurus* (Helfman et al. 1997), to several millions in species belonging to the

Gadidae, Pleuronectidae and Molidae (Bond 1996; Helfman et al. 1997; Wootton 1998).

However, notwithstanding the considerable life-history variability that exists among species, there can be extraordinary variability in life histories within and among populations of the same species. The Atlantic salmon, *Salmo salar*, is among the most variable of vertebrates and provides an excellent example of the breadth in life-history variation that can exist within species (Hutchings and Jones 1998). Among populations, age at maturity differs ten-fold, ranging from 1 year for males in several North American and European populations (Hutchings and Jones 1998) to as much as 10 years for anadromous females in northern Québec (Power 1969). Similarly, size at maturity varies at least 14-fold, from less than 7 cm for males in Newfoundland (Gibson et al. 1996) to more than 1 m among females in Norway's River Vosso (Huitfeldt-Kaas 1946). Number of eggs per female varies from tens (Gibson et al. 1996) to tens of thousands (Fleming 1996), while mean egg diameter ranges from at least 4.5 mm in a non-anadromous Newfoundland population (Gibson et al. 1996) to 6.9 mm in Canada's Restigouche River (Canadian Department of Fisheries and Oceans, unpublished data).

Although the spatial scale of life-history variability among populations of many fish spans a broad geographical range, one does not require a broad geographical range to detect evolutionarily important variation in life history. This is an important point. One implication for studies of evolutionary ecology is that great distances, as much as several degrees of latitude, are not a prerequisite for selection to effect adaptive variation among populations. For fishery managers and conservation biologists, one implication is the possibility that sustainable harvest levels and minimum viable population sizes can differ significantly among populations across very small geographical scales.

Small-scale life-history variation among populations of brook trout, *Salvelinus fontinalis*, on Cape Race, Newfoundland, serves to illustrate this point (Ferguson et al. 1991; Hutchings 1991, 1993a,b, 1994, 1996, 1997). Selecting the most di-

vergent populations, Freshwater River and Cripple Cove River are separated by approximately 9 km. Brook trout inhabiting these rivers are unexploited, do not interbreed, do not differ in density and are not influenced by interspecific competition or predation (Ferguson et al. 1991; Hutchings 1993a). Despite these similarities, females in Freshwater River mature, on average, more than a full year earlier (3.1 years) than those in Cripple Cove River (4.2 years) at a five-fold smaller size (~11 g). Indeed, the minimum lengths at maturity, 62 mm for males and 70 mm for females among Freshwater River trout, may be the smallest recorded for this species. Regarding reproductive effort, relative to Cripple Cove River females, the smaller Freshwater River females allocate more than twice as much body tissue to gonads, produce significantly more eggs and produce 40% larger eggs, all the comparisons having been corrected for body size (Hutchings 1991, 1993a, 1996). The significant population differences in life history between these populations have been attributed to the consequences of environmental differences in food supply, and possibly habitat, to age-specific survival probabilities, fecundity and growth rate (Hutchings 1991, 1993a,b, 1994, 1996, 1997).

7.2   INFLUENCE OF SURVIVAL AND GROWTH RATE ON AGE, SIZE AND REPRODUCTIVE EFFORT AT MATURITY

7.2.1   *Age and size at maturity*

Age at maturity reflects an evolutionary compromise between the benefits and costs to fitness of reproducing comparatively early or late in life (Kozlowski and Uchmanski 1987; Roff 1992; Charlesworth 1994). Benefits associated with early maturity include increased probability of surviving to reproduce and an increased rate of gene input into the population, resulting in reduced generation time. However, early maturity can result in reduced fecundity and/or post-reproductive survival because of the smaller body size typically associated with earlier maturity within a population. By contrast, the primary cost of delaying initial spawning is the increased risk of death prior to reproduction. The primary fitness advantage to delaying maturity in fish is the larger initial body size attained by individuals when they first reproduce. Body size can be positively associated with survival (Hutchings 1994), fecundity (Wootton 1998), fertilization success (Hutchings and Myers 1988; Jones and Hutchings 2001, 2002), ability to provide parental care (Wiegmann and Baylis 1995), probability of attracting mates (Foote 1988) and ability to acquire and defend nest sites (van den Berghe and Gross 1989).

If one assumes that natural selection acts on age-specific expectations of producing future offspring (Fisher 1930), age at maturity can be predicted from the mean and the variance in juvenile and adult survival rates, that is, the survival preceding and following age at maturity respectively. Reductions in age at maturity are assumed to be favoured with decreases in the ratio of adult to juvenile survival and with increases in the variance in adult survival relative to the variance in juvenile survival (Cole 1954; Gadgil and Bossert 1970; Schaffer 1974a,b). Intuitively these predictions make sense. As external mortality (that unassociated with reproduction) at potentially reproductive ages increases, selection would be expected to favour those individuals (genotypes) that reproduce prior to those ages, thus increasing their probability of contributing genes to future generations. A similar argument can be made for environmental perturbations that increase the variance in survival at potentially reproductive ages, increased variance in survival being associated with increased uncertainty in an individual's persistence.

These predictions are generally presumed to hold true for fish. Leggett and Carscadden (1978) examined population differences in age at maturity among five populations of American shad, *Alosa sapidissima*, from Florida, USA north to New Brunswick, Canada. They found that males and females in the northern populations, for which they presumed juvenile mortality to be more variable than that in southern populations, matured as

much as 11 and 14% older, respectively, than their southernmost counterparts. Similarly, Hutchings and Jones (1998) reported a negative correlation between temporal variance in adult survival and age at maturity in anadromous Atlantic salmon. Reznick et al. (1990), documenting selection responses to predator-induced changes to mortality in guppies, *Poecilia reticulata*, found age at maturity among males and females to be 17 and 7% higher, respectively, in the environment characterized by high juvenile mortality relative to that in the environment characterized by comparatively low juvenile mortality. Fox and Keast (1991), comparing life histories of pumpkinseed sunfish, *Lepomis gibbosus*, populations subjected to either high or low overwinter mortality, documented 1–2 year reductions in age at maturity among males and females in the high-mortality environments. And age at maturity in bluegill sunfish, *Lepomis macrochirus*, populations exposed to high juvenile predation is reported greater than that in populations that experience comparatively low juvenile mortality (Belk 1995).

Notwithstanding widespread acceptance of the legitimacy of these tests, none included estimates of adult survival relative to juvenile survival nor attempted to exclude costs of reproduction from estimates of adult mortality. Nonetheless, in one study that attempted to fulfil these expectations, there is support for the aforementioned predictions of life-history theory. Among brook trout populations on Cape Race, Newfoundland, Canada, female age at maturity ranges from 3.1 to 4.2 years among populations whose adult : juvenile survival ratios range between 0.16 and 3.19 respectively (Hutchings 1993a,b). Evidence of a similar association between adult : juvenile survival ratio and age at maturity has recently been documented for brook trout populations elsewhere in Newfoundland (Adams 1999).

7.2.2 *Reproductive effort*

Following Hirshfield and Tinkle (1975), reproductive effort can be defined as the proportion of total energy devoted to the physiological and behavioural aspects of reproduction, measured across a biologically meaningful time period, such as gonad development, movement/migration to spawning grounds, reduction of feeding prior to and concomitant with reproduction, mate competition, nest construction, or parental care. In fish, a common surrogate of reproductive effort is the gonadosomatic index (GSI), i.e. the weight of an individual's gonads relative to that individual's total body weight. Among species, GSI ranges from as little as 0.2% in male *Tilapia* spp. (Helfman et al. 1997) and 0.5% in male white sticklebacks, *Gasterosteus* sp. (C.-A. Smith and J.A. Hutchings, unpublished data) to as much as 47% in female European eels, *Anguilla anguilla* (Kamler 1992). Additional metrics of reproductive effort have included direct estimates of energy or lipid losses associated with reproduction (e.g. Dutil 1986; Jonsson et al. 1991; Hutchings et al. 1999), magnitude and duration of parental care behaviours (e.g. Hinch and Collins 1991), size-specific fecundity (Leggett and Carscadden 1978; Koslow et al. 1995), migration distance to spawning grounds (Schaffer and Elson 1975) and changes to lean body mass (Giloolly and Baylis 1999).

Changes to reproductive effort in fish are thought to be associated with adaptive responses to age at maturity. For example, a decline in survival during potentially reproductive ages (i.e. adult survival) relative to that during pre-reproductive ages (i.e. juvenile survival) is predicted to favour genotypes that increase reproductive effort and, in addition, that mature earlier in life (Gadgil and Bossert 1970; Law 1979). Evidence of such a direct response to selection has been forthcoming from Reznick et al.'s (1990) work on Trinidad guppies: 30–60 generations after a shift in predator-induced mortality from adults to juveniles, guppies responded to the presumed increase in the ratio of adult to juvenile survival by reducing reproductive allotment and by increasing age at maturity. Life-history comparisons among populations have also supported these predictions concerning effort and maturity. Comparing pumpkinseed sunfish from five populations that experienced either high or low levels of overwinter mortality, Fox and Keast (1991) found males and females inhabiting high-mortality environments

to mature earlier and to have significantly higher GSIs than those inhabiting low-mortality environments. Among brook trout populations in Newfoundland, declines in the ratio of adult to juvenile survival are associated with earlier maturity and increase in reproductive effort, as approximated by GSI (Hutchings 1993a). A negative association between age at maturity and reproductive effort, measured as GSI and size-specific fecundity, has also been reported for yellow perch, *Perca flavescens*, populations in central Alberta, Canada (Jansen 1996).

Reproductive effort has been predicted to decline with increased variance in juvenile survival relative to that of adult survival. Murphy (1968) indirectly tested this hypothesis by correlating a proxy for recruitment variability with longevity in five clupeiforms, finding a positive association between the two, suggesting that increased variation in juvenile survival favours genotypes that reduce reproductive effort and, as a consequence, live longer lives. However, additional tests for positive associations between recruitment variability and longevity in fish have not yielded significant correlations (e.g. Roff 1991). Leggett and Carscadden (1978) compared North American shad populations and found that northern populations, which they suggested experienced highly variable juvenile mortality, produced fewer eggs per unit body size and had a higher incidence of repeat spawning than southern populations, presumed to experience comparatively low variation in juvenile mortality.

Reproductive effort has also been suggested to increase with age and size (Williams 1966; Gadgil and Bossert 1970). Based on his analysis of 31 fish stocks, Roff (1991) found support for Charlesworth and León's (1976) conditions under which reproductive effort would be expected to increase with age. Evidence of a positive association between some metric of reproductive effort and age has also been documented in brook trout (Hutchings 1993a, 1994) and smallmouth bass, *Micropterus dolomieui* (Gillooly and Baylis 1999).

7.2.3 Costs of reproduction

A central tenet of life-history theory is that the behavioural, physiological and energetic correlates of reproduction exact some sort of cost to future reproductive success in the form of reduced survival, fecundity and/or growth. Firstly, relative to a non-reproductive individual of age x, reproduction at age x can reduce the probability of survival to age $x + n$, where n might represent any unit of time from minutes to years. Secondly, reproduction can directly reduce an individual's future ability to produce offspring. High energetic costs expended at age x might leave a fish with insufficient energy reserves to produce the same number of offspring at age $x + n$. The third cost is a consequence of the energy allocated to the behavioural and physiological demands of reproduction at the expense of energy that would otherwise have been allocated to somatic growth. Reduced future size-at-age concomitant with a reduction in growth rate, coupled with the positive association typically observed between fecundity and body size in fish (Wootton 1998), results in a reduction in potential fecundity, such that an individual reproducing at age x will produce fewer eggs at age $x + n$ than an individual that did not reproduce at age x.

The seminal work in this area began with inductive arguments for why reproductive costs should exist and theoretical assessments of the life-history consequences thereof (e.g. Fisher 1930; Cole 1954; Williams 1966; Gadgil and Bossert 1970). The literature turned to a consideration of whether costs indeed existed and, if they did, what were the most appropriate means of measuring them (e.g. Reznick 1985). The primary challenge now lies in how to best estimate costs in natural populations, and to identify the primary physical and biological environmental factors that effect variability in the expression of costs between sexes, among individuals, among years, among generations and among populations.

To quantify reproductive costs precisely, one would manipulate reproductive effort for a specific genotype and then document the genotype-specific survival and/or fecundity consequences of those changes to effort. For most fish, excepting

parthenogenetic species, these are experimental criteria that cannot be met, notwithstanding the difficulty of assessing the degree to which a cost quantified under experimental conditions in the laboratory is likely to reflect costs experienced in the wild. Nonetheless, if we are to have any success in applying life-history theory to our understanding of the ecology, management and conservation biology of fish, some attempt must be made to quantify reproductive costs. Reznick (1985) discusses the strengths and weaknesses associated with various means of estimating costs in general, while Hutchings (1994) discusses these methods in relation to the study of fish.

One means of estimating costs, widely used in avian and *Drosophila* sp. life-history research (e.g. Pettifor et al. 1988; Chapman et al. 1993), is to experimentally manipulate some metric of present effort and then document the survival and/or fecundity consequences thereof. Examples of such manipulation in the fish literature are comparatively rare and are limited to species that exhibit parental care (Balshine-Earn 1995). Notwithstanding the attraction of such an experimental approach, it has its limitations. For example, costs estimated by manipulation of brood size will underestimate actual costs because they exclude the physiological and behavioural costs associated with producing the brood. Also, by artificially manipulating the size of brood to which a genotype was 'expecting' to provide care, one risks either underestimating or overestimating costs if some form of individual optimization (Pettifor et al. 1988) or adaptive phenotypic plasticity (Hutchings 1996; Jonsson et al. 1996) exists in the population under study.

One potentially informative method of estimating survival costs of reproduction is to quantify the difference in survival probabilities between ages x and $x + n$ for individuals that reproduced at age x and those that did not. To reduce the effects of individual differences in aspects of quality, such as body condition, on such an analysis (cf. Reznick 1985), one should control for both size and age. For example, Dufresne et al. (1990) found the survival among non-breeding 1- and 2-year-old threespine sticklebacks, *Gasterosteus aculeatus*, in the St

Lawrence River, Canada, to be more than twice that of their breeding counterparts. Using a similar comparison of survival probabilities, Hutchings (1994) documented evidence of survival costs of reproduction in three Newfoundland populations of brook trout that appeared to increase with age but to decline with body size. Indirect evidence of a negative association between reproductive cost and body size has also been recorded for the sand goby, *Pomatoschistus minutus* (Lindström 1998), and Atlantic silverside, *Menidia menidia* (Schultz and Conover 1999). As a practical tool for quantifying survival costs in the field, this method holds a great deal of promise and is critical if life-history theory is to be applied to specific management and conservation issues. Although one will inevitably be unable to control all the factors potentially influencing individual quality, costs estimated by such a technique should tend to underestimate rather than overestimate costs, if one assumes that the reproductive individuals are the highest quality individuals (Hutchings 1994).

Perhaps the most widely acknowledged cost in fish associated with reproduction at age x is the reduction in growth rate immediately prior to age x, and thence to ages $x + n$, that effects a concomitant decrease in fecundity, generated by the diversion of energy from somatic growth to the behavioural, energetic and physiological demands of reproduction (Bell 1980; Hutchings 1993a; Balshine-Earn 1995; Wootton 1998; Jobling, Chapter 5, this volume).

It has been argued that the most informative method for measuring a cost of reproduction would be to quantify correlated genetic responses estimated from a selection experiment (Reznick 1985). One such experimental protocol would be to select only those individuals having either low or high fecundity to breed at age x, to repeat this selection regime over several generations and then to determine whether there has been a correlated response to this selection regime in the form of a negative association between, for example, fecundity at age x and fecundity at age $x + n$. Despite their experimental limitations, intentional selection experiments in the field do have the potential to provide valuable insight into how reproductive

costs vary with changes to age-specific survival and fecundity. An example of intentional selection is a change to age-specific mortality effected by natural predators (Reznick et al. 1990); an example of unintentional selection is a change to age-specific mortality effected by fishing.

Many reproductive costs in fish can be attributed to the loss of lipids and proteins associated with various physiological and behavioural correlates of reproduction, such as gonad production (Wootton 1998), mate competition (Grantner and Taborsky 1998) and parental care (Lindström 1998; Mackereth et al. 1999). These energetic demands can be considerable, particularly when one compares the energetic losses of reproductive individuals relative to those of non-reproductive individuals during the same time interval. For example, post-reproductive Arctic char, *Salvelinus alpinus*, possess 35–46% less energy than non-reproductive char in spring (Dutil 1986). Rijnsdorp and Ibelings (1989) reported energy losses among reproductive North Sea plaice, *Pleuronectes platessa*, to be three to five times that of non-reproductive plaice. The source of energy losses differs between sexes, with non-gonadal reductions typically being greater among males than females (Jonsson et al. 1991; Hutchings et al. 1999), presumably as a consequence of the behaviours associated with mate competition. The magnitude of total energy losses attributed to reproduction also differs between sexes, but apparently not in a similar manner among, and potentially within, species. Energetic losses have been reported to be greater for females in Arctic char (Jørgensen et al. 1997) and plaice (Rijnsdorp and Ibelings 1989), equal in Atlantic salmon (Jonsson et al. 1991), yet greater among males in brook trout (Hutchings et al. 1999).

Energetic constraints associated with parental care alone have been reported to negatively influence future growth and fecundity (e.g. Balshine-Earn 1995; Wiegmann and Baylis 1995). Energetic losses might also effect survival and fecundity costs if reproduction is associated with immune system deficiencies, leading to an increased risk of infection or parasitism. Although direct links between reproduction and infection risk or para-sitism have not been unequivocally documented, if such links exist, increased parasitism could be implicated in acute and chronic reproductive costs, given observations that parasites have been shown to have a wide range of effects on fitness (Barber and Poulin, Chapter 17, this volume). These include reduced growth rate (Walkey and Meakins 1970), inhibited sperm development (Sinderman 1987), lower gonad weight as in the common goby, *Pomatoschistus microps* (Pampoulie et al. 1999), decreased fecundity as found in Pacific hake, *Merluccius productus* (Adlerstein and Dorn 1998), and reduced probability of attracting mates as observed for threespine stickleback (Milinski and Bakker 1990). The energetic demands of reproduction might also effect acute, short-term survival costs if individuals experience an increased risk of predation because of reduced locomotion, reduced vigilance and/or increased feeding rate.

Ecological constraints of reproduction in fish might result in reduced future survival probabilities, notably in the short term. Two primary means by which these might be effected are through increased risk of predation and increased risk of physical injury. The former can result from behaviours associated with attracting mates (Houde and Endler 1990) or caring for young (Pressley 1981). Physical injury, primarily as a result of mate competition, can also be expected to negatively influence short- and long-term survival probabilities (Hutchings and Myers 1987; Fleming 1996).

Reproductive costs in fish might also result from genetic trade-offs between correlated characters of fitness, although evidence of such antagonistic pleiotropy has not been reported for fish.

7.2.4   *Growth rate*

Growth rate is of major importance to life-history evolution, notably in organisms that continue to grow after attaining maturity, because of its determination of body size at age and because of the positive associations that can exist between body size and various metrics of fitness, such as fecundity (Wootton 1998), egg size (Kamler 1992), survival (Hutchings 1994), fertilization success

(Hutchings and Myers 1988; Thomaz et al. 1997; Jones and Hutchings 2001, 2002), parental care (Sargent et al. 1987; Wiegmann and Baylis 1995) and migration distance (Schaffer and Elson 1975). Once the physiological minimum reproductive size has been attained, an individual's maturation strategy is predicted to depend not only on the consequences to present and future survival of maturing at various ages but also on the consequences to present and future fecundity.

A trade-off between present and future fecundity, effected by declines in growth rate concomitant with maturity, formed the basis of initial predictions of how growth rate might influence life history (Gadgil and Bossert 1970; Schaffer 1974a,b; Bell 1980). Schaffer (1974b), for example, predicted that environments that allowed for increased growth during potentially reproductive ages should favour delayed maturity and increased reproductive effort. Although Schaffer and Elson's (1975) positive association between age at maturity and growth rate at sea in Atlantic salmon appeared to support this hypothesis, the correlation did not differ significantly from zero upon reanalysis (Myers and Hutchings 1987a).

Nonetheless, there is reason to believe that Schaffer's (1974b) predictions hold merit. Hutchings (1993a) suggested distinguishing the growth rate experienced during the juvenile stage from that experienced during the adult stage. He predicted that increases in juvenile growth rate relative to adult growth rate should favour increases in reproductive effort and reductions in age at maturity. These predictions were supported by empirical data on Newfoundland populations of brook trout (Hutchings 1993a). Fox (1994) tested this hypothesis and reported that pumpkinseed sunfish introduced into a previously fishless pond experienced a higher ratio of juvenile to adult growth rate, matured at an earlier age and had a significantly higher GSI relative to those in the original population. Positive associations between the ratio of adult to juvenile growth rate and age at maturity also exist for Newfoundland populations of ouananiche (*S. salar*; Leggett and Power 1969) and Swedish populations of brown trout (*S. trutta*; Näslund et al. 1998).

Reductions in age at maturity with increases in individual growth rate have been repeatedly documented in fish (e.g. Alm 1959; Hutchings 1993a; Fox 1994; Trippel et al. 1995; Godø and Haug 1999). The capacity of individuals to respond in such a manner, and the rapidity with which these changes can occur within populations, relative to generation time, suggests that this life-history response is phenotypically plastic, the magnitude of which would depend on the shape of the norm of reaction for age at maturity and on the magnitude of environmental change in growth rate. Two examples are gadids reported by Trippel et al. (1997) and yellowtail flounder, *Pleuronectes ferruginea*, by Walsh and Morgan (1999). Using empirical age-specific survival, fecundity and growth rate data for Newfoundland populations of brook trout, Hutchings (1996) explored the individual consequences to fitness of maturing at various ages in response to changes in growth rate. The resultant fitness functions supported the prediction that a reaction norm describing a negative association between growth rate and age at maturity can represent an adaptive response to environmental change. However, for one population, fitness was maximized by maturing as early in life as possible, regardless of growth rate. Selection for such a flat, non-plastic reaction norm can be expected when the probability of realizing the fitness benefits of delayed maturity (increased fecundity for females, increased access to mates for males) is relatively low (see Section 7.5).

7.2.5 *Life-history invariants*

The objective of most life-history research in fish is to test hypotheses of adaptive and non-adaptive variation to explain the extraordinary life-history variability expressed within and among species. An alternative approach has been to determine whether there is a constancy, or invariance, among life-history traits that may reflect adaptive life-history processes of a very broad and general nature. This search for constancy amidst diversity was very much evident when quantitative studies of patterns of growth, maturation and longevity in fish first appeared in the late 1950s. Alm (1959), for

example, sought patterns among growth rate, age and size at maturity from experiments he had conducted on Swedish populations of brown trout. Using data primarily from commercially important marine species, Beverton and Holt (1959) investigated general associations among growth pattern, as shown by the von Bertalanffy growth coefficient (K) and asymptotic length (L_∞), age (α) and length at maturity (L_α), natural mortality (M) and lifespan (proportional to M^{-1}). In addition to Beverton's (1992) excellent historical perspective of the search for invariants in fish, Charnov (1993) provides the most comprehensive treatment of life-history invariants to date.

The practical objective underlying much of the early search for life-history invariants in fish was to identify generalizations which could then be used to estimate natural mortality rate in commercially exploited fishes (Beverton 1992). For example, based on an analysis of 175 fish stocks (Pauly 1980; Charnov 1993), the invariant M/K for teleosts is approximately 1.7, although Charnov (1993) suggests a range of possible values extending from $1.6 < M/K < 2.1$. If one had an estimate of the von Bertalanffy growth coefficient, K, for a given stock, a comparatively easy metric to estimate (see Jobling, Chapter 5, this volume), one could then use the invariant $M/K = 1.7$ to estimate natural mortality for the same stock.

Life-history invariants are thus ratios of parameters and/or variables that have the same units of measure so that the ratios are dimensionless. Among the most commonly examined life-history invariants in fish are those between (i) mortality and growth rate, M/K, (ii) length at maturity and asymptotic length, L_α/L_∞, (iii) age at maturity and lifespan, $(\alpha M)^{-1}$, (iv) age and length at maturity, αL_α and (v) asymptotic length and growth rate, $L_\infty K$ (Beverton and Holt 1959; Pauly 1980; Roff 1984; Beverton 1992; Charnov 1993; Vøllestad and L'Abée-Lund 1994; Mangel 1996; Jensen 1997; Froese and Binohlan 2000; Reynolds et al. 2001).

In addition to their practical utility, invariants have the potential to provide insight into life-history evolution. For example, the invariant M/K implies that fast-growing fish experience higher natural mortality rates than slow-growing fish.

Another invariant that appears to have some consistency among taxa is L_α/L_∞, which Jensen (1997) suggests is 0.66 for fish, implying that all fish mature at a length that is approximately two-thirds of their maximum.

Despite its comparatively lengthy history, the application and understanding of life-history invariants is very much in its infancy. Most of the research to date has comprised a search for pattern among combinations of life-history metrics. Useful as this has been, the challenge now is to formulate and test hypotheses that would identify the processes responsible for the observed patterns. Mangel's (1996) study on life-history invariants in brown trout and Arctic char is an excellent example of an attempt to do just that.

7.3 OFFSPRING SIZE AND NUMBER STRATEGIES
7.3.1 *Theoretical context*

Why do some fish, ranging phylogenetically from the sea lamprey (*Petromyzon marinus*, Cephalaspidomorpha) through the Atlantic sturgeon (*Acipenser oxyrhynchus*, Acipenseriformes) and the Atlantic cod (*Gadus morhua*, Gadiformes) to the sunfish (*Mola mola*, Tetraodontiformes), produce hundreds of thousands, often millions, of very small eggs (<1.5 mm diameter), while other fish, including myxinids, chondrichthyans, many salmoniforms and mouth-brooding siluriforms produce comparatively few, relatively large eggs (>4 mm diameter)?

The evolutionary implications of the trade-off between offspring number and offspring size in fish were first considered by the Swedish fish biologist Gunnar Svärdson (1949). He suggested that there must be an upper limit to fecundity and that this upper limit depends on the influence of egg size on offspring survival and parental reproductive success. Otherwise, he argued, directional selection – or, as he put it, a tendency to increase egg number every generation – would favour continually increased numbers of eggs per female. Svärdson (1949) remarked that, 'From a theoretical point of view it is rather easy to conclude that there

must be a selection pressure for decreasing egg numbers, but it is not so extremely evident how this selection works.′

The theoretical underpinning of most research investigating the adaptive significance of offspring size and number variability is a graphical model proposed by Smith and Fretwell (1974), who asked how a parent should distribute a fixed amount of energy or resources to an indeterminate number of young. Optimal egg size is defined graphically by the point on the fitness function at which a straight line drawn from the origin (the dashed lines in Fig. 7.1a) is tangential to the offspring sur-

vival curve (the solid curves in Fig. 7.1a). In other words, the optimum corresponds to the egg size at which the instantaneous rate of gain in fitness per unit increase in offspring size is at its maximum. As this instantaneous rate of gain increases, along with the slope of the line drawn from the origin, optimal egg size decreases (Winkler and Wallin 1987). Smith and Fretwell's (1974) model has formed the basis of many theoretical treatments of the evolution of egg size, including those examining the effects of parental care (Sargent et al. 1987), food abundance (Hutchings 1991, 1997) and lifetime reproductive effort (Winkler and Wallin 1987).
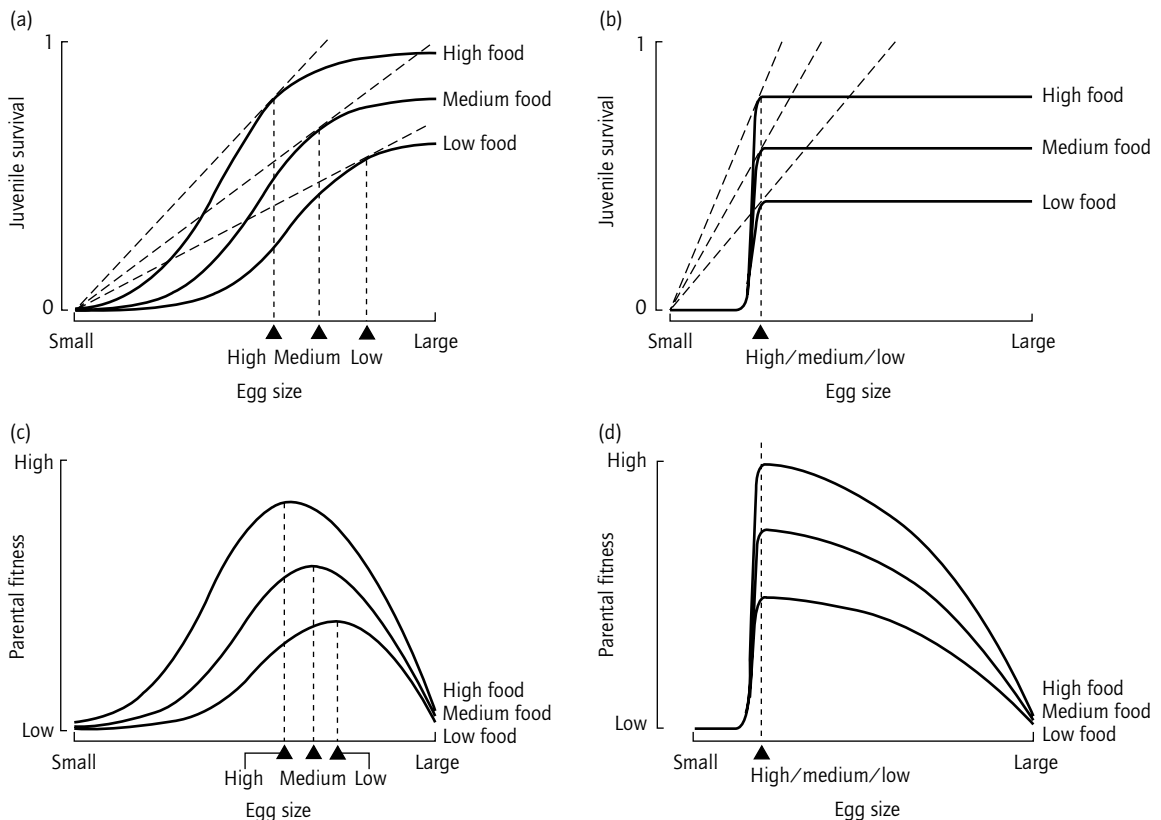
Fig. 7.1 Functions relating juvenile survival (a and b) and parental fitness (fecundity × egg-size-specific survival probabilities, the latter for c and d taken from panels a and b, respectively) to egg size in environments differing in food abundance. Solid triangles below the abscissas indicate egg-size optima. (Source: from Hutchings 1997, with kind permission of Kluwer Academic Publishers.)

Strong empirical support for Smith and Fretwell's (1974) model was recently obtained from a study of Atlantic salmon egg size and maternal fitness (Einum and Fleming 2000).

7.3.2   *How does egg size influence offspring survival?*

At first glance, it might seem reasonable to assume that the larger the egg, the greater an offspring's survival probability. Indeed there is considerable experimental evidence (Houde 1989; Pepin 1991, 1993; Chambers 1997; Wootton 1998) that larger offspring are produced from larger eggs, have increased survival during short periods of low food supply, can be more competitive than smaller offspring and, by virtue of their faster swimming speeds, may have a lower risk of predation. Field-based data have provided indirect evidence that survival in early life may be positively associated with size and individual growth rate at hatching, both of which are presumed positive correlates of egg size (Elliott 1994; Wootton 1998). Gronkjaer and Schytte (1999) reported that otolith hatch-checks of Baltic cod larvae that survived 20 days post-hatch were similar to or larger than the overall mean, suggesting an association between size at hatch and larval survival. Meekan and Fortier (1996) documented both positive and equivocal evidence that high individual growth rate enhances larval cod survival. Despite these potential benefits to fitness, larger egg sizes may impose constraints that negatively influence survival. For example, larger eggs can have longer development times (Kamler 1992) that prolong a potentially vulnerable period of life, greater oxygen demands (Kamler 1992; Quinn et al. 1995) and may, in addition to the young that emerge from them, be more visible to predators (Litvak and Leggett 1992; Pepin et al. 1992). Thus, the costs and benefits to offspring of emerging from large and small eggs can be expected to vary with a variety of factors, including the habitat into which eggs are released, such as being buried in substrate, attached to plants/rocks or dispersed freely into the water column, parental care, food supply and risk of detection by visual predators.

7.3.3   *Hypotheses to explain variability in strategies of the size and number of offspring*

Various hypotheses have been proposed to explain variation in egg size and fecundity within and among species of fish. Many adaptive explanations centre upon proposed selection responses to species- and age-specific differences in the quality of parental care (Sargent et al. 1987) and to seasonal (Rijnsdorp and Vingerhoed 1994; Trippel 1998), population (Kaplan and Cooper 1984; Hutchings 1991, 1997) and individual (Jonsson et al. 1996) differences in access to food resources. Quinn et al. (1995) suggested that among-population variation in sockeye salmon, *Oncorhynchus nerka*, egg size can be explained as adaptive responses to differences in the size composition of incubation gravel, arguing that the positive association between egg size and substrate size may be related to the latter's influence on dissolved oxygen supplies relative to the surface-to-volume ratio constraints of eggs.

The reduction in egg mortality achieved by various forms of parental care, expressed in the form of burying of eggs, predator defence, mouthbrooding and egg fanning, is considered a primary selective factor responsible for the positive association between egg size and amount of parental care among species (Sargent et al. 1987; Forsgren et al., Chapter 10, this volume). Parental care may also offset the mortality costs associated with the longer developmental times of larger eggs. By extension, the positive association between egg size and maternal size documented within many fish species has been attributed to a greater ability of larger females to provide parental care to their young (Sargent et al. 1987). Larger females may be able to provide greater protection to eggs. However, the generality of this hypothesis must be tempered by the observation that egg size also increases with female size in fish that provide no parental care. This is shown by Atlantic cod (Chambers and Waiwood 1996; Kjesbu et al. 1996), Atlantic herring, *Clupea harengus* (Hempel and Blaxter 1967), caplin, *Mallotus villosus* (Chambers et al. 1989), and striped bass, *Morone saxatilis* (Zastrow et al. 1989).

Population differences in average egg size are often considered a proxy for adaptive variation. But, as previously noted elsewhere (Hutchings 1991; Reznick and Yang 1993), the relationship between offspring size and offspring survival must differ among environments, or among populations, for environment- or population-specific egg-size optima to exist (Fig. 7.1). Hutchings (1991) reported the first such phenotype × environment interaction on offspring survival in fish. Brook trout survival in the laboratory during the first 50 days following yolk-sac resorption was found to increase with egg size, but the effects of egg size and food abundance on juvenile survival were not additive: decreased food abundance increased mortality among juveniles from the smallest eggs but had no effect on the survival of juveniles produced from the largest eggs, a finding similar to that observed for brown trout (Einum and Fleming 1999). Based on these experimental data, and supported by field data on egg size and food abundance (Hutchings 1997), fitness functions described therefrom suggested that low food supply would favour the production of comparatively few, large offspring while high food abundance would favour females that produced many, comparatively small offspring (Hutchings 1991).

The dependence of environment-specific egg-size optima on the shape of the function relating offspring survival to egg size is illustrated in Fig. 7.1, where parental fitness (Fig. 7.1c,d) is approximated by the product of egg survival and egg number, holding gonad volume constant. Two basic functions are considered: the size-dependent case, for which offspring survival varies continuously with egg size (Fig. 7.1a), and the size-independent case, for which survival above and below a very narrow range of egg sizes is constant (Fig. 7.1b). For the former, any factor such as food supply that is expected to increase offspring survival across all egg sizes is predicted to effect a reduction in optimal egg size (Fig. 7.1a), thus favouring females that produce relatively numerous, smaller offspring (Fig. 7.1c). By contrast, if offspring survival is independent of offspring size, optimal egg size is predicted to remain unchanged with changes in a factor that increases offspring

survival (Fig. 7.1d). Under such circumstances, the evolutionarily stable strategy of investment per offspring would appear to be one of maximizing the number of offspring, each approaching the physiologically minimum size, within a brood.

Given the within-individual trade-off that must exist between egg size and egg number for a specific gonadal volume, it is evident that for selection to favour an increase in egg size, the survival benefits to offspring produced from larger eggs must exceed the parental fitness cost of producing fewer eggs (Wootton 1994; Hutchings 1997). Unfortunately, explicit recognition of this necessity is notably rare in many discussions of egg-size optima, particularly in the marine fish literature. The fecundity cost associated with the production of large eggs must be acknowledged if natural variation in egg size in fish is to be interpreted within an ecological or evolutionary framework. Demonstration that larger eggs have lower predation or starvation mortality than smaller eggs need not in itself reveal anything about the selective advantage of producing large eggs or of the strength of a year-class composed of large eggs.

While the search for adaptive explanations for egg-size variability is perhaps more appealing intellectually, researchers need always be cognizant of the possibility that the observed variation has no adaptive basis. For example, egg size in many fish is negatively influenced by water temperature (Pepin 1991; Kamler 1992; Chambers 1997). Trippel (1998) also cautions that seasonal declines in egg size in batch-spawning marine fish, such as Atlantic cod, might reflect a decline in the physiological condition of the female and a reduced ability to allocate sufficient resources to each egg. It is also worth considering the high probability that a considerable amount of the variation in egg size, notably within females, is purely a function of developmental noise or instability (Markow 1994). For example, among brook trout in Freshwater River, Newfoundland, for which the diameters of ten randomly chosen eggs were measured for each of 114 females (J.A. Hutchings, unpublished data), egg volume *within* females differed by an average 23%! Although one could argue that variable egg sizes within females in this case represents an

adaptive response to unpredictable environmental heterogeneity (Kaplan and Cooper 1984), the hypothesis that this rather considerable amount of egg-size variability within females is a function of developmental noise cannot be discounted.

7.4 ALTERNATIVE LIFE-HISTORY STRATEGIES

Within populations, significant life-history variation can exist among individuals of the same sex. A common observation is to find some males maturing relatively early in life, often at a comparatively small size, attempting to obtain secondary access to females by 'sneaking' fertilizations in competition with later-maturing larger males who often have primary access to a female through territorial or mate-defence behaviours. Taborsky's (1994) review identifies 25 families (130 species) in which alternative reproductive strategies have been documented, the most common being the labrids (e.g. Warner 1991), cichlids (e.g. Martin and Taborsky 1997) and salmonids (e.g. Jones 1959; Gross 1984; Thorpe 1986). A considerable literature exists on the terminology used to describe reproductive strategies and tactics (e.g. Taborsky 1994; Gross 1996), much of which centres on the degree to which the alternative life histories are of genetic or environmental origin. For simplicity, and given that the relative contribution of genetic and environmental factors to the expression of alternative life histories is generally not known, I use the term 'alternative reproductive strategy' to refer to the combination of life history and behavioural correlates of distinctive reproductive alternatives evident within a sex, within a single population, at one point in time (cf. Henson and Warner 1997).

What precisely constitutes an 'alternative reproductive strategy'? The phrase is often used somewhat loosely to describe usually two, occasionally three, sets of reproductive or mating behaviours exhibited by members of the same sex within a single population. However, by focusing solely on behaviour, one risks downplaying the observation that significant life-history differences, and thus significant influences on fitness, often exist *within* as well as between alternative strategies.

Atlantic salmon males, a case in point, are typically described as exhibiting alternative strategies (Myers 1986; Thorpe 1986; Hutchings and Myers 1988, 1994; Metcalfe 1998). Following a seaward migration as smolts, anadromous males return to their natal river and mature comparatively late in life (4–7 years) at a large size (45–90 cm). By contrast, mature male parr do not migrate to sea prior to reproduction, spawning relatively early in life (1–3 years) at a comparatively small size (<7–15 cm), whereafter they may or may not migrate to sea. Prior to spawning, dominant anadromous males defend access to an anadromous female while mature male parr establish what appears to be a size-based dominance hierarchy immediately downstream of the courting anadromous fish (Jones 1959; Myers and Hutchings 1987b). Mature male parr compete with one another and with anadromous males for the opportunity to fertilize eggs (Hutchings and Myers 1988; Thomaz et al. 1997; Jones and Hutchings 2001, 2002).

However, it is not simply the gross differences in body size and mating behaviour between anadromous males and mature male parr that require explanation; age at maturity, body size and survival to maturity can differ significantly among individuals adopting either the parr or anadromous male strategy (Myers et al. 1986; Hutchings and Myers 1994). Thus, any evaluation of the fitness associated with the mature parr and anadromous male phenotypes will be incomplete without explicit consideration of the influence on fitness arising from life-history differences within each of these two strategies. Hutchings and Myers (1994) proposed a model to incorporate the existence of multiple age-specific sets of fitness functions within populations of Atlantic salmon. They suggested that the fitness of parr and anadromous males might best be represented as two multidimensional fitness surfaces, and that the points of intersection of these surfaces specified an evolutionarily stable continuum of strategy frequencies along which the fitness associated with each strategy would be equal. Approaching the same question from a developmental perspective and from considerations of proximate, rather than ulti-

mate, influences on fitness, Thorpe et al. (1998) have developed a model that also incorporates fitness surfaces to explain life-history variation within salmonids.

7.4.1 Maintenance of alternative reproductive strategies

There are several means by which alternative maturation phenotypes can be maintained within populations. As with many characters, the origins of alternative phenotypes may be purely genetic, purely environmental, or some combination thereof. If alternative strategies have any genetic basis, then the fitness associated with each maturation *genotype* must, on average, be approximately equal, otherwise the less fit genotype would be continually selected against and eventually disappear from the population. Under such circumstances, the frequencies of the strategy-specific genotypes within populations are said to be evolutionarily stable if such populations cannot be invaded by genotypes adopting other strategies (Maynard Smith 1982).

Negative frequency-dependent selection has been hypothesized to be the primary means by which alternative mating genotypes are maintained within populations (e.g. Gross 1984; Myers 1986; Partridge 1988). As the frequency of a given strategy increases within a population, increased competition among individuals adopting that strategy would lead to reduced average fitness among those individuals (see the dashed curve in Fig. 7.2). In contrast, the average fitness of individuals adopting the alternative strategy would increase because of reduced competition (solid curve in Fig. 7.2), resulting in a shift in the incidence of strategies towards the rarer of the two. In theory, then, the frequency of alternative strategies within a population eventually achieves an equilibrium at which the average fitness of individuals adopting each strategy is equal (Fig. 7.2).

Despite its prevalence in theory, evidence of a genetic basis for alternative mating phenotypes is limited, although it is not clear if this is due to very low or negligible levels of heritability or to the rarity of research devoted to this question. Evidence that alternative reproductive strategies in
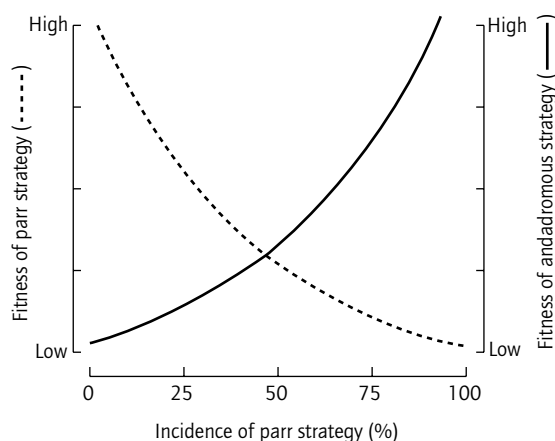
Fig. 7.2 Graphical representation of negative frequency-dependent selection in male Atlantic salmon life histories. As the incidence of either the mature male parr or anadromous male strategy increases within a population, the average fitness of individuals adopting that strategy declines. The equilibrium frequencies of the two strategies, at which individual fitnesses are equal, is identified by the point of intersection of the two fitness functions.

some species may be under complete genetic control exists for the pygmy swordtail, *Xiphophorus nigrensis*. Zimmerer and Kallman (1989) found that the four mating phenotypes in this species, distinguishable by body size and behaviour, appear to be controlled by genetic variation at a Y-linked locus. Breeding experiments suggest that the male parr and anadromous male phenotypes in Atlantic salmon have a heritable basis (Naevdal et al. 1976; Thorpe et al. 1983; Glebe and Saunders 1986; Herbinger 1987). Also, the relatively larger testis size in the subordinate of two strategies also provides compelling evidence of a genetic basis to alternative maturation phenotypes in corkwing wrasse, *Symphodus melops* (Uglem et al. 2000), Atlantic salmon (Gage et al. 1995) and plainfin midshipman, *Porichthys notatus* (Brantley and Bass 1994).

Within-population variation in reproductive strategies may not be under direct genetic control, reflecting instead a breadth of mating behaviours and ages at maturity that are purely a consequence of stochastic variability in the environment. Thus,

individuals attempting to sneak fertilizations in competition with behaviourally dominant individuals may be engaging in this behaviour because of environmentally predicated influences on phenotypic attributes that have reduced the probability of obtaining a mate. Examples would be comparatively smaller body size or poorer body condition. Under such circumstances, one would predict that the fitness of individuals adopting such suboptimal maturation phenotypes, which may be fixed for a breeding season or for life, would be less than that of males adopting alternative behaviours.

On the other hand, individuals might adopt different maturation phenotypes as they age or as environmental circumstances change within a single breeding season, possibly reflecting a condition- or status-dependent behavioural or life-history response. For example, bluehead wrasse, *Thalassoma bifasciatum*, adopt non-territorial behaviours when they are young, becoming territorial as they grow older and larger (Hoffman et al. 1985). Another reef fish, the peacock wrasse, *Symphodus tinca*, will facultatively switch between spawning in its own territory and within those of other males (van den Berghe 1990). Thorpe et al.'s (1998) stochastic dynamic modelling of male Atlantic salmon life histories explores how proximate changes to body condition might influence the adoption of the parr or anadromous male strategy in Atlantic salmon. Forsgren et al. (Chapter 10, this volume) deal further with the behavioural aspects of alternative reproductive strategies.

A third, and not necessarily mutually exclusive, means by which alternative reproductive strategies can be maintained within populations is through some form of adaptive phenotypic plasticity (Warner 1991). One means of incorporating both environmental and genetic influences on the expression of alternative reproductive strategies was proposed by Hutchings and Myers (1994) for Atlantic salmon. For example, the expression of the mature male parr strategy in Atlantic salmon appears to be influenced by both genetic and environmental factors; the fastest growing males in a population are those most likely to mature as parr

(Myers et al. 1986; Thorpe 1986; Metcalfe 1998) and there is evidence that male parr maturity has a genetic basis (Naevdal et al. 1976; Thorpe et al. 1983; Glebe and Saunders 1986; Herbinger 1987). To incorporate both the environmental and genetic determinants of alternative reproductive strategies in this species, parr maturation can be modelled as a threshold trait (Myers and Hutchings 1986; Falconer 1989) such that adoption of either the parr or the anadromous strategy depends on whether an individual's growth rate in early life exceeds that specified by a genetically determined growth-rate threshold (Myers and Hutchings 1986; Thorpe 1986; Hazel et al. 1990; Hutchings and Myers 1994; Thorpe et al. 1998).

Theoretical representations of such growth-rate thresholds for male parr maturity are presented in Fig. 7.3. Sigmoid curves describe how the probability of parr maturity might increase with parr growth rate, approximated here by size-at-age, among four populations. The lengths-at-age at which 50% of the males are expected to adopt the parr strategy can be identified as parr maturation thresholds, which would be averaged among all male parr within a population.

Population differences in demography would be expected to generate population differences in parr
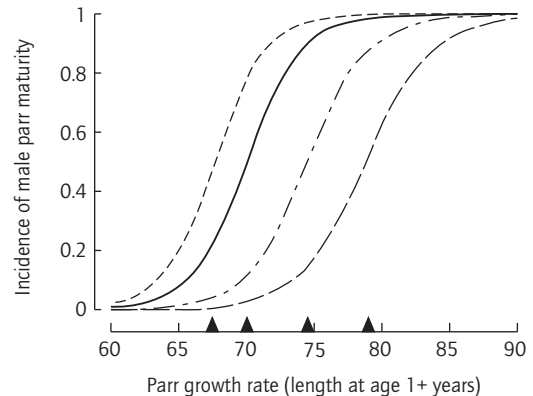
Fig. 7.3 Growth-rate thresholds for male parr maturity among four hypothetical populations of Atlantic salmon. The solid triangles represent the lengths-at-age at which 50% of the male parr in each population would be expected to adopt the parr reproductive strategy.

growth-rate thresholds. Evidence of such sigmoid relationships exists for male parr in Newfoundland's Little Codroy River (Myers et al. 1986; Hutchings and Myers 1994), the only natural population for which individual parr maturity and growth-rate data have been published. Here it is the maturation response to environmental stimuli, be they behavioural or environmental, that would be under selection. Note that the actual strategies adopted *need not have equal fitness*, but selection for the reaction norm underlying the environmental-, condition- or status-mediated response might result in negative frequency-dependent selection for alternative growth-rate thresholds within populations (Hutchings and Myers 1994).

7.4.2 Management implications

From a management perspective, the incidence of male parr maturity has at least three implications. Firstly, the higher the incidence of male parr maturity, the lower the production of anadromous male salmon. This can be attributed to the higher mortality experienced by mature male parr in fresh water relative to their immature counterparts (Myers 1984; Hutchings and Jones 1998). For example, the increased mortality and delayed age at smolting experienced by mature male parr may be responsible for the loss of 60% of the anadromous male salmon production in some populations (Myers 1984). A second consideration is that spawning contributions by mature male parr are not explicitly incorporated into stock assessments of Atlantic salmon populations. This exclusion may affect the interpretation of the spawning escapement of males required to maintain a viable population, perhaps most notably for populations in which the incidence of male parr maturity is quite high. Thirdly, from a conservation perspective, it is not clear how the incidence of parr maturity influences effective population size, or N_e (Jones and Hutchings 2001, 2002). Populations with low escapement of anadromous males may have a comparably high N_e because of the genetic contributions of mature male parr. Alternatively, increased incidence of male parr maturity may be

associated with increased variation in reproductive success which would reduce N_e. Indeed, genetic differences among small Atlantic salmon populations may be primarily attributable to mature male parr (M.W. Jones, unpublished data). These hypotheses merit study.

7.5 EFFECTS OF FISHING ON LIFE HISTORY

Phenotypic and genetic life-history responses to fishing can be categorized as follows.

1 A comparatively rapid (<1 generation) phenotypic response effected by increased individual growth rates concomitant with reductions in fish density (Policansky 1993).

2 A comparatively rapid (<1 generation) phenotypic change effected by plastic responses along reaction norms for life-history traits such as age at maturity and reproductive effort (McKenzie et al. 1983; Hutchings 1993b, 1997; Nelson 1993).

3 A comparatively rapid (<1 generation) genetic change at the population level caused by extremely high mortality rates that differentially and rapidly reduce the frequency of some life-history genotypes, e.g. late-maturing genotypes, relative to others, e.g. early-maturing genotypes (Hutchings 1999).

4 A comparatively slow (10–30 generations) genetic response effected by selection against life-history genotypes, or against norms of reaction, whose fitness in the presence of fishing is less than that of other genotypes, or other norms of reaction, in the population (Law and Grey 1989; Hutchings 1997; Hendry and Kinnison 1999).

Although categories 1 and 2 are both phenotypic responses, their distinction is a useful one because the latter makes explicit the hypothesis that reaction norms for life-history characters exist and that the pattern of phenotypic responses to environmental change can therefore have an adaptive basis (Haugen 2000; Haugen and Vøllestad 2000). The primary distinction between the two categories of genetic response is that short-term genetic changes in gene frequencies (category 3)

do not depend on the level of heritability of a life-history trait, although they are assumed to be heritable. By contrast, long-term genetic responses by a trait to selection, R, are influenced both by that trait's heritability, h^2, and by the difference in the average value of that trait among reproductive individuals relative to the average in the population as a whole, or in other words the selection differential, S (Falconer 1989), such that $R = h^2 S$.

The predominant changes to life history associated with fishing are reduced age and size at maturity, the latter often being a simple consequence of the former, although increases in both characters might occur under certain circumstances (Heino 1998; Rochet 1998). The rapidity with which many of these changes has occurred is consistent with the hypothesis of a phenotypically plastic response to exploitation. In theory, reductions in density effected by fishing should lead to reduced competition for resources, resulting in an increase in individual growth rate and possibly body condition. Given the widely documented negative association between individual growth rate and age at maturity in fish (e.g. Alm 1959; Roff 1992; Hutchings 1993a), a comparatively rapid decline in age at maturity can be explained as a plastic response to increases in individual growth. Such associations have been documented in exploited populations of marine fish such as Atlantic cod (Chen and Mello 1999), yellowtail flounder (Walsh and Morgan 1999) and North Sea plaice (Rijnsdorp 1993).

Increases to individual growth rate and reductions in adult survival are also predicted to increase reproductive effort. Although there has been considerably less attention directed to such changes, there is evidence that temporal changes in size-specific fecundity in the orange roughy, *Hoplostethus atlanticus*, may reflect a life-history response in reproductive effort to fishing. Between 1987 and 1992, when the commercially exploited orange roughy stock off east Tasmania was reduced by 50%, individual fecundity increased 20% on average (Koslow et al. 1995). Law (1979) reported a 60% increase in the fecundity of 3-year-old northern pike, *Esox lucius*, 12 years after an experimental harvest in Windermere, UK. The

questions remain, of course, whether such plastic changes in age at maturity are adaptive and whether the affected population's growth rate, and its associated risk of overfishing following a reduced age at maturity, will be negatively affected by such changes. Beverton et al. (1994), for example, estimated that early-maturing (6 and 7 years old) northeast Arctic cod experience considerably higher natural mortality rates (0.25 and 0.17 respectively) than those that delay maturity to age 8 and later ($M = 0.15$). Thus, a reduction in age at maturity, unaccompanied by any fitness advantage associated with such a response (see category 2 above), can have serious consequences to a population's growth rate and persistence.

Based upon age-specific survival, fecundity and growth-rate data for several unexploited brook trout populations, Hutchings (1993b, 1997) predicted how optimal norms of reaction for age at maturity and reproductive effort might change under increasing levels of exploitation (Fig. 7.4). The magnitude of change will depend on the shape of the reaction norm, on the magnitude of change in individual growth rate and on the heritability for the shape of the reaction norm. Although these changes would be reversible in the short term, over perhaps less than ten generations, persistently strong selection effected by fishing might select against the shape of plastic reaction norms under zero or low fishing mortality, as shown by the dashed reaction norms in Fig. 7.4, favouring other, possibly non-plastic, reaction norms that are optimal under high fishing pressure. These are shown by the solid reaction norms in Fig. 7.4. Thus, although initial changes to life history effected by exploitation may be plastic and therefore reversible, persistently high selection intensities may effect genetic changes in the shapes of reaction norms and the loss of plasticity for the trait(s) in question within the exploited population (see Haugen 2000 for a potential example in grayling, *Thymallus thymallus*).

While some short-term changes in age at maturity appear to be linked to increases in individual growth rate, and can potentially be explained as phenotypically plastic responses to fishing, others are not. One example is that of the northern stock

Fig. 7.4 Hypothetical norms of reaction for age at maturity (a) and reproductive effort (b) for a fish population in an unfished state and at low and high levels of exploitation. The abscissa reflects an environmental gradient that may have influences on individual growth rate, body condition and density.

Concern that selection induced by fishing gear might effect genetic responses in fish populations has been discussed at least since the 1950s (Miller 1957). Long-term changes in size at maturity, for example, have been interpreted as selective responses to the size-selectivity of fishing gear, notably gill-nets, as seen in lake whitefish (Handford et al. 1977), pink salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*; Ricker 1981), and Atlantic salmon (Bielak and Power 1986). Evidence that long-term changes in age at maturity may represent evolutionary responses to exploitation has also been forthcoming in studies of cod (Rowell 1993; Law 2000) and plaice (Rijnsdorp 1993) in the North Sea.

As expressed succinctly by Rijnsdorp (1993), fisheries are large-scale experiments on life-history evolution. The potential for fishing to effect significant evolutionary change within a population is no different from that of any other form of predator-induced mortality that differentially affects the survival of individuals of different ages and sizes. The question is not whether fishing represents a primary selective pressure effecting evolutionary change in exploited fish populations – clearly it must. The important questions surely concern the type of life-history responses (see categories 1–4 above), the reversibility of the responses and the consequences of the responses to population growth rate and likelihood of population recovery (Hutchings 2000; Law 2000, 2001).

7.6 CONCLUSIONS

Life histories ultimately determine an individual's fitness, a population's persistence and growth rate at low abundance, and a commercially exploited stock's ability to sustain exploitation. The study of life histories is at the heart of research addressing the evolutionary ecology, conservation and exploitation of fish. There is a need for studies that focus on the underlying basis for life-history change in fish. Are life-history responses to environmental change generally effected by changes in gene frequencies or by phenotypic modification

of Atlantic cod extending from southeastern Labrador to the northern half of Newfoundland's Grand Bank. Between the mid-1980s and the mid-1990s, female median age at maturity declined by more than 1 year, a reduction of approximately 17% (Lilly et al. 1998). However, these changes were not associated with either increases in individual growth rate or increases in body condition (Lilly et al. 1998). Hutchings (1999) suggested that the most parsimonious explanation for these changes in age at maturity was an extremely rapid differential reduction of late-maturing genotypes by severe overfishing, relative to that experienced by early-maturing genotypes.

along norms of reaction? Compared with theoretical interest in the former, there has been a lack of research addressing genotype-by-environment interactions in fish life-history responses. Such work might attempt, for example, to describe norms of reaction for life-history traits, to quantify the heritability of reaction norms (Haugen & Vøllestad 2000), to assess the degree to which the shapes of reaction norms can be modified by selection, and to provide empirical tests for the existence of genetically determined, environmentally triggered threshold characters.

Tests of life-history theory are hampered by a lack of empirical data on survival and reproductive costs in wild populations. Despite the difficulty of quantifying these parameters, their absence leaves purported demonstrations of adaptive life-history responses to selection severely wanting. Even when data on natural mortality (M) are presented, there is rarely any attempt on the part of the researcher(s) to distinguish that part of the mortality attributable to external factors from the mortality consequences of a particular genotype's reproductive decisions regarding its age and effort at maturity. In other words, the use of M as a metric of the degree to which mortality favours a particular life-history decision, such as age at maturity, results in a circular argument given that the life-history consequences of that genotype's decision as to when to mature are already embedded in M. The same is true when using K, the von Bertalanffy growth coefficient, as a metric of the degree to which growth rate favours a particular life-history decision: K already incorporates the growth costs of reproduction effected by a genotype's age and effort at maturity.

Perhaps the ultimate value in studying fish life histories lies in the hope of eventually being able to predict how short- and long-term anthropogenic, biological and physical environmental perturbations influence age-specific rates of survival and fecundity, rates of increase, population persistence and community composition. Based on the theoretical and empirical strengths of fish life-history research over the past 50 years, there is room for considerable optimism that such an objective can be achieved.

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8 Migration

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8.1 INTRODUCTION

Migration is a common feature of the life histories
of many of the world's economically important
species of fish. For many, these movements are
extensive, and the regular seasonal changes in
population distribution that result often have
significant implications for commercial fisheries.
Consequently, understanding migration is impor-
tant to the cost-effective and sustainable exploita-
tion of fish stocks.

'Understanding' in this context may simply in-
volve an appreciation of the seasonal arrival and
disappearance of a stock, allowing fishermen to
target their activities effectively. Alternatively, it
may involve a more detailed knowledge that al-
lows the development of realistic models of popu-
lation dynamics that can be used to assess the
likely effects of different management strategies.
However, fish migration is a very broad subject. At
one end it involves the behavioural ecology of
whole populations, at the other it focuses on the
neurobiology of sensory systems that form the
basis of the orientation and navigation abilities of
individuals.

While the different aspects of migration fasci-
nate the biologist, not all are directly relevant in a
fisheries context, and some are beyond the limited
scope of this chapter. Further, it is not our aim to
give exhaustive accounts of the life-history strate-
gies, or migration circuits, of all economically
important migratory fish. For this the reader is
directed to other, more extensive texts relating to
migration (e.g. Harden Jones 1968; Baker 1978;
McKeown 1984; McDowall 1988) or to individual
species (e.g. Pickett and Pawson 1994). Our aim is
to review the occurrence of migration in the life
histories of commercial fish species and the eco-
logical principles that drive migratory behaviour.
We describe a number of different migratory strate-
gies and attempt to explain how understanding mi-
gration is of value to fisheries management and
conservation. Many species of fish live in environ-
ments that are hostile, at least to human observers,
and their migrations are therefore particularly dif-
ficult to study, so finally we review the field tech-
niques used to study fish migration and consider
how these are likely to develop and improve our
understanding in the future.

8.1.1 Definitions

'Migration' is a word in common parlance and
most of us, lay person or scientist, have a sense of
what it means. Nonetheless, it is difficult to find a
generally agreed definition and there are almost as
many interpretations as there are books on the sub-
ject. Those who work on different animal groups
tend to use the term in different ways. Ornitholo-
gists usually regard migration as some form of
regular, long-range movement between wintering
and breeding areas, and expect an element of
seasonal 'to and fro-ness' of both individuals
and populations. This is quite different from the
entomologist, who has little expectation that
populations, let alone individuals, of migratory

aphids or locusts will return to the place from which they departed.

While there is endless debate over the details of various definitions, there is general agreement that 'migration' involves the movement of individuals and populations from one, usually well-defined, area or habitat to another. Furthermore, migration is usually understood to imply that there is some cyclical element to the movement, on either an annual or life-cycle scale, which distinguishes it from 'dispersal'. Though possibly rather broad, such a definition is quite adequate for the purposes of this chapter, and there is little value in debating what is, and what is not, 'true' migration. For fuller discourse on this subject, the reader can refer to a variety of books (e.g. Harden Jones 1968; Baker 1978; McKeown 1984; Dingle 1996).

It should be noted that many species of fish also make regular *vertical* movements, usually linked to the day–night cycle, that are referred to as 'migration'. Such movements certainly have implications for fisheries, particularly with respect to the availability of fish to fishing or survey gear. However in this chapter we restrict our definition to horizontal migrations. First, however, it is necessary to consider scales of migratory movement.

8.1.2   Scales of movement

Some littoral species, like blennies (family Blenniidae), make seasonal inshore and offshore movements that extend no more than a few kilometres. In temperate waters, species like herring (*Clupea harengus*), mackerel (*Scomber scombrus*), cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*) make more extensive movements over several hundreds of kilometres. Finally, some species migrate over distances of several thousands of kilometres. Examples include diadromous species like Atlantic salmon (genus *Salmo*), Pacific salmon (genus *Oncorhynchus*) and eels (*Anguilla* spp.), which move between fresh water and the open sea, and the various species of tuna, billfishes and large sharks that make extensive transoceanic migrations. Clearly, if the distance moved is small (say a few kilometres) and does not

impact on the activities of fishermen, then such migrations may not be very important in a fisheries context. Alternatively, migrations that cover large distances will be a crucial factor determining the seasonal changes in the distribution of fish stocks and therefore of the fisheries which exploit them.

8.1.3   Terminology

In addition to defining migration, there is a need to understand some of the terms used to describe fish migrations, particularly with respect to the movements of individuals within and between freshwater and marine habitats. Fortunately, there is much less debate about these definitions. The terms proposed by Myers (1949) and used widely since (e.g. Harden Jones 1968; McDowall 1988) are used here (Fig. 8.1).

Oceanodromous: 'Truly migratory fishes whose migrations occur wholly within the sea.'

Potamodromous: 'Truly migratory fishes whose migrations occur wholly within fresh water.'

Diadromous: 'Truly migratory fishes which migrate between the sea and fresh water.'

When Myers (1949) first introduced the term 'diadromy', he also defined three subcategories: 'anadromy' and 'catadromy', which had been in long usage in the fish literature (Meek 1916), and 'amphidromy', which was a new term. These subcategories refer to various forms of diadromy, in which the directions of movement and the life-history stages that undertake them vary. Recently, these categories of diadromy have been expanded and refined (McDowall 1998a).

1 Anadromy refers to diadromous fishes in which most feeding and growth take place at sea, prior to the migration of fully grown adult fish into fresh water to reproduce; there is either no subsequent feeding in fresh water or any feeding is accompanied by little somatic growth; the principal feeding and growing biome (the sea) differs from the reproductive biome (fresh water). Examples are salmon, shad and sea-lamprey.

2 Catadromy refers to diadromous fishes in which most feeding and growth occurs in fresh water prior to the migration of fully grown adult fish to
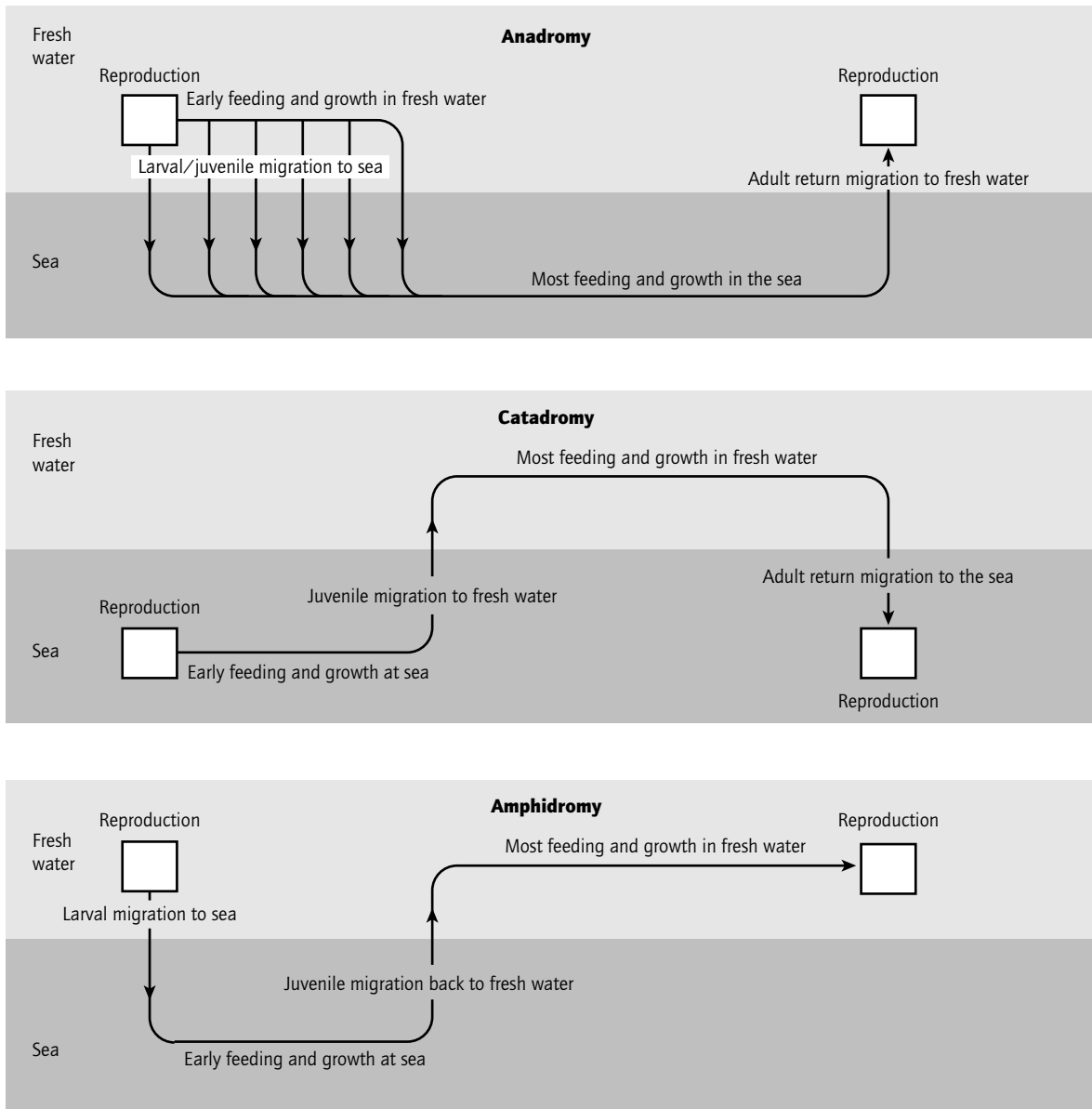
Fig. 8.1 Different forms of diadromy.

sea to reproduce; there is either no subsequent feeding at sea or any feeding is accompanied by little somatic growth; the principal feeding and growing biome (fresh water) differs from the reproductive biome (the sea). Examples are American and European eels.

3 Amphidromy refers to diadromous fishes in which there is a migration of larval fish to sea soon after hatching, followed by early feeding and growth at sea, and then a migration of small post-larval or juvenile fish from the sea back into fresh water; there is further prolonged feeding in fresh water, during which most somatic growth from juvenile to adult stages occurs, as well as maturation and reproduction; there is usually no migration related to reproduction, and the principal feeding biome is the same as the reproductive biome (fresh water). An example is the ayu (*Plecoglossus altivelis*) from Japan.

8.2   EXPLOITATION AND ECOLOGY

8.2.1   *Migration among commercial species*

Worldwide, there are approximately 25 000 species of fish (Eschmeyer 1998), of which probably only 200–300 make extensive migrations (Harden Jones 1980). Yet, while migration is not a common feature for most fish species, it nonetheless seems to be widespread in the life histories of most economically important species. For example, in 1997, which is the most recent year for which FAO data are available, the average world catch of finfish, excluding shellfish, was about 79.5 million tonnes from over 740 species. Of this total, the top 40% (32.1 million tonnes) comprises only 15 species, all of which are considered to be migratory (Table 8.1). So why is migration such a common feature of economically important species?

8.2.2   *Why do fish migrate?*

One bit of sea often appears very much like any other, but below the surface there is tremendous diversity. Marine habitats are a complex of physi-

cal variables, such as depth, water currents, topography, sediment type, temperature, salinity, oxygen, illumination and biotic variables, such as food availability and predator abundance. In freshwater lakes and rivers, there are similar, but probably more apparent, differences in habitat type.

Such features can vary widely spatially and temporally, particularly between seasons. With such diversity, it is very unlikely that any one habitat will be equally suitable for all life-cycle stages, and many fish species do indeed show some ontogenetic and/or seasonal changes in habitat use. A habitat with plenty of small prey and few large predators may be ideal for small juvenile fish, but is less likely to be suitable for larger adults of the same species that need larger prey and may be less vulnerable to predation. To make optimum use of such environmental diversity, many fish species have evolved migratory life histories and move between different areas, each of which is best for the activities of feeding, growing and spawning. As a result, the size of a population is not limited to the number of individuals that can be supported by a single habitat. Improved survival and reproductive success is the ultimate selective advantage of migratory behaviour.

8.2.3   *Migration and exploitation*

Migrating fish tend to move along known pathways at known times, and so are more concentrated both spatially and temporally and hence easier to catch. This latter aspect applies particularly to diadromous fish, which are targeted by fisheries as they migrate through narrow bottlenecks at the mouths of rivers. When it comes to the fisheries exploitation of the very small amphidromous fishes, which tend to return to fresh water from the sea at lengths as small as 20–25 mm, it is only their spatiotemporal concentration at the time of migration that makes fishing economic. Thus there are significant fisheries for the tiny migratory larvae of diverse goby species in many different places, such as the Philippines, Tahiti, the Caribbean, Sri Lanka and Réunion. There are also fisheries for galaxiids in Australia, New Zealand and Chile (reviewed in McDowall 1988). The same

Table 8.1 FAO finish catch data for 1997 for the top 15 most important species with evidence for migratory behaviour.

Species	Catch (million tonnes)	Catch as proportion of total worldwide catch of all finfish (%)	Cumulative catch (%)	Evidence for migration
Anchoveta (Peruvian anchovy), *Engraulis ringens*	7 685 098	9.66	9.66	Ben-Tuvia (1995)
Alaska (walleye) pollock, *Theragra chalcogramma*	4 368 108	5.49	15.16	Hamatsu and Yabuki (1995)
Chilean jack mackerel, *Trachurus murphyi*	3 597 117	4.52	19.68	Serra (1991)
Atlantic herring, *Clupea harengus*	2 532 525	3.18	22.86	Harden Jones (1968), McGladdery and Burt (1985), Creaser et al. (1984)
Chub mackerel, *Scomber japonicus*	2 423 235	3.05	25.91	Belyaev (1984), Novikov (1986)
Japanese anchovy, *Engraulis japonicus*	1 666 503	2.10	28.00	Novikov (1986), Wu (1989)
Capelin, *Mallotus villosus*	1 604 555	2.02	30.02	Carscadden (1984)
Skipjack tuna, *Katsuwonus pelamis*	1 425 638	1.79	31.82	Gauldie and Sharp (1996), Watanabe et al. (1995)
Atlantic cod, *Gadus morhua*	1 362 174	1.71	33.53	Harden Jones (1968), Malmberg (1980), Rose (1993)
Largehead hairtail, *Trichiurus lepturus*	1 201 491	1.51	35.04	Lin (1987)
Yellowfin tuna, *Thunnus albacares*	1 128 377	1.42	36.36	Suzuki et al. (1978), Bard et al. (1987)
European pilchard (sardine), *Sardina pilchardus*	1 031 467	1.30	37.75	Tosello Bancal (1989)
South American pilchard, *Sardinops sagax*	721 711	0.91	38.66	Novikov (1986), Wu (1989)
European sprat, *Sprattus sprattus*	701 202	0.88	39.54	Heincke (1992), Hoziosky et al. (1989)
Blue whiting, *Micromesistius poutassou*	697 597	0.88	40.42	Carre and Geistdoerfer (1981)
Total worldwide catch of the top 15 finfish species	32 146 798			
Total worldwide catch of all finfish species	79 530 900			

principle applies to the exploitation of the juvenile life stages of catadromous fishes as they enter fresh water. Glass-eels can be harvested most efficiently and economically when they are concentrated, usually at the mouths of rivers or in estuaries. An example is the elver fishery in the River Severn in England (Templeton and Churchward 1990).

8.3   FISH MIGRATIONS

The range of migratory life-history strategies is extensive. In this section we describe the migrations of a selection of migratory species to illustrate different factors driving their migrations.

8.3.1   *Oceanodromous fish*

Fish movements and water currents

Although the adults of many open-ocean species are large or powerful swimmers, individuals of most species are, either as eggs and/or free-swimming larvae, at the mercy of prevailing water currents, which therefore play an important part in the life cycle of most species. The idea that the

distribution and migrations of a fish stock could be linked by a particular water-current system gave rise to the concept of 'hydrographic containment' (Cushing 1990) and it appears that stocks of a number of important commercial species such as plaice, herring and some species of tuna could be contained in this way.

In the open sea, as distinct from estuaries, two distinct current regimes can be recognized. Ocean currents dominate on the high seas, whereas tidal currents are more important on the continental shelves. In the main ocean basins the effects of the tides are slight and the surface circulation is driven largely by the prevailing planetary wind system (Fig. 8.2a). This generates subtropical gyrals that circulate clockwise in the Northern Hemisphere and anticlockwise in the Southern Hemisphere (Fig. 8.2b). These gyrals are bounded on their northern and southern edges by zonal currents, which flow broadly east or west. While open-ocean currents are generally rather slow ($3-7\,\mathrm{cm\,s^{-1}}$) and extend to depths of $100-200\,\mathrm{m}$, western boundary currents such as the Gulf Stream in the North Atlantic and the Kuroshio in the North Pacific (Fig.

8.3) are very much stronger ($50-100\,\mathrm{cm\,s^{-1}}$ or more) and extend to depths of $1000\,\mathrm{m}$. In many places, there are substantial countercurrents below the surface circulation (Harden Jones 1968; Arnold 1981).

There is compelling evidence to indicate that ocean currents play a major role in the movements of larvae of several species of eel from their spawning areas in the open ocean to the freshwater habitats where the juveniles feed, grow and develop into adults. Schmidt (1922, 1923) was the first to publish an account of the migrations of the European eel *Anguilla anguilla* from its spawning grounds in the Sargasso Sea. Subsequent analysis of the hydrography of the North Atlantic has shown that the eel's leptocephalus larva is transported by the Gulf Stream and North Atlantic Drift (Fig. 8.3) to the European continental shelf over a period of nearly 3 years (Harden Jones 1968). More recently, the location of the spawning area of the Japanese eel *Anguilla japonica* has been identified in the northwestern Pacific Ocean in an area between the Philippines and the Mariana Islands (Tsukamoto 1992). This discovery suggests a simi-
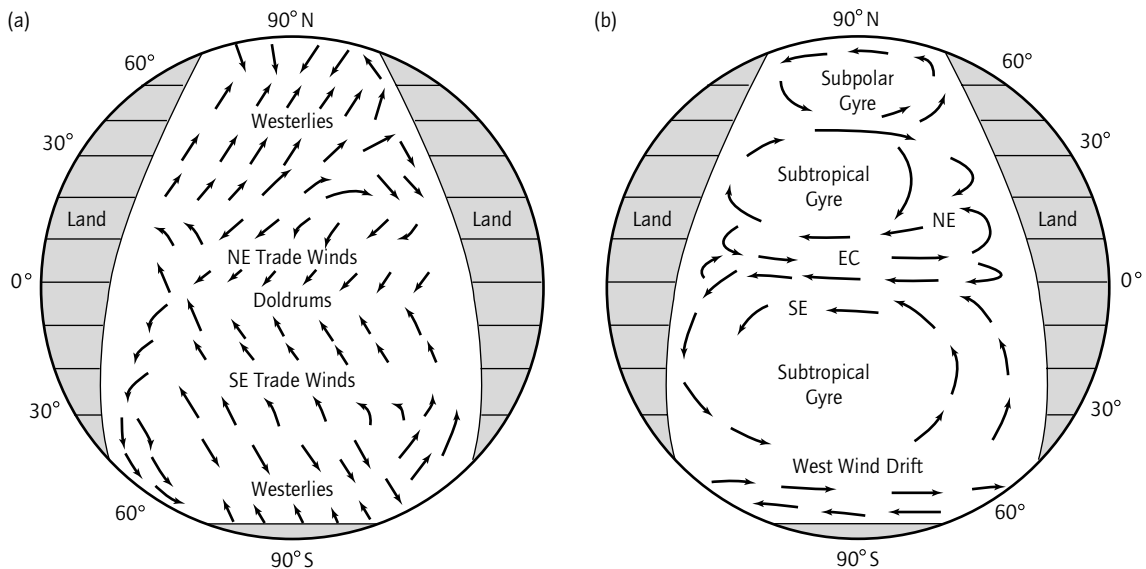
Fig. 8.2 Generalized atmospheric (a) and oceanic (b) circulations. NE, North Equatorial Current; EC, Equatorial Counter Current; SE, South Equatorial Current. (Source: redrawn from Gross 1972. Reproduced by permission of Prentice-Hall.)
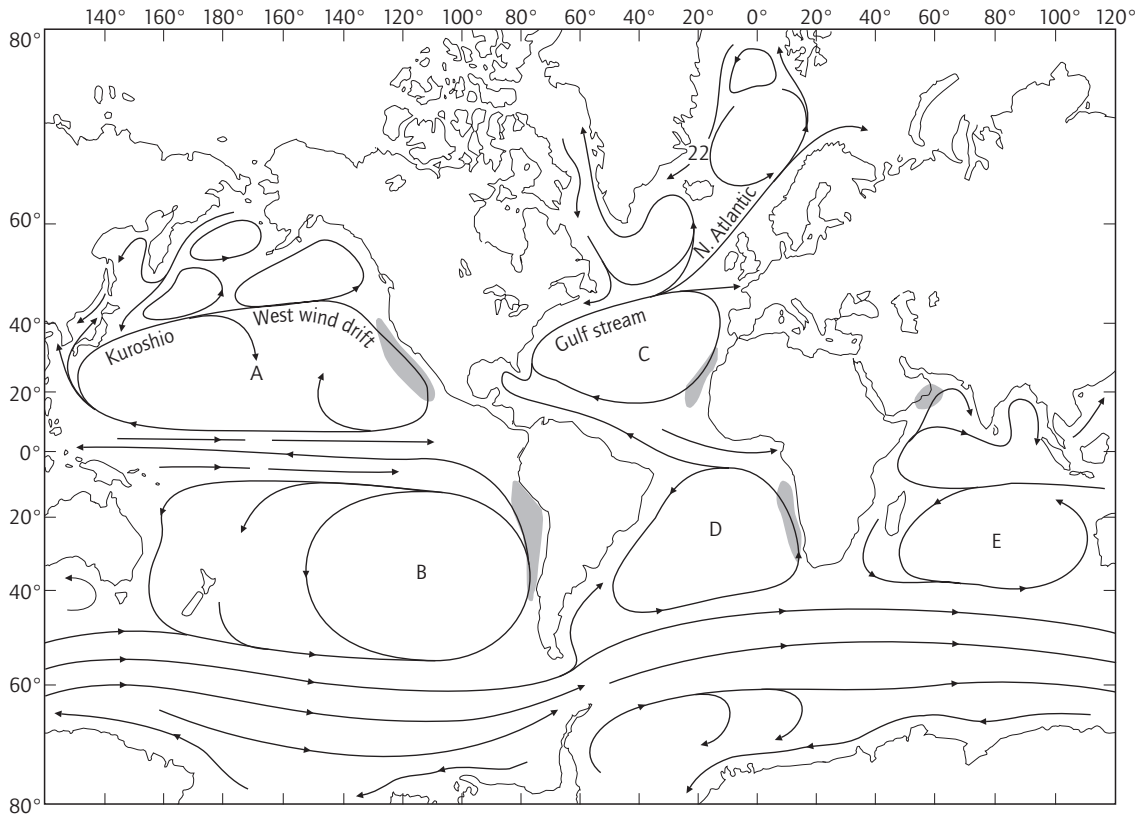
Fig. 8.3 Simplified chart of the surface ocean currents of the world oceans. The main subtropical gyrals are A, North Pacific; B, South Pacific; C, North Atlantic; D, South Atlantic; E, South Indian. Selected main ocean currents are also indicated. Important areas of upwelling in the eastern boundary currents are shown as stippled areas. (Source: redrawn from Bramwell 1977.)

lar role for the North Equatorial and Kuroshio currents (Fig. 8.3) as a means of transporting leptocephali of this species to the coastal waters of eastern Asia, where the adults originate.

In shallow seas on continental shelves, water movements are dominated by tidal currents. In shelf seas, the constraining effects of ocean basin geometry and the influence of the Coriolis force result in development of amphidromic systems in which tidal waves rotate around amphidromic points at which there is no rise and fall in water level. On the European continental shelf, for example, the tidal wave rotates approximately once every 12.5 h, giving rise to a system of tidal streams

(Fig. 8.4) in which the water flows in opposite directions for successive periods of about 6.25 h. During neap tides, peak tidal stream speeds can range from as little as a few centimetres per second in the central North Sea to about $1\,\mathrm{m\,s^{-1}}$ in the Dover Strait. During spring tides, peak tidal stream speeds increase to between 0.1 and $2.0\,\mathrm{m\,s^{-1}}$ respectively.

Whether in the open ocean or in shelf seas, most teleost fish spawn in midwater and their pelagic eggs and larvae usually drift downstream with the residual current. At some later stage in their life history, the adults must make some compensatory movement if the population is to remain within
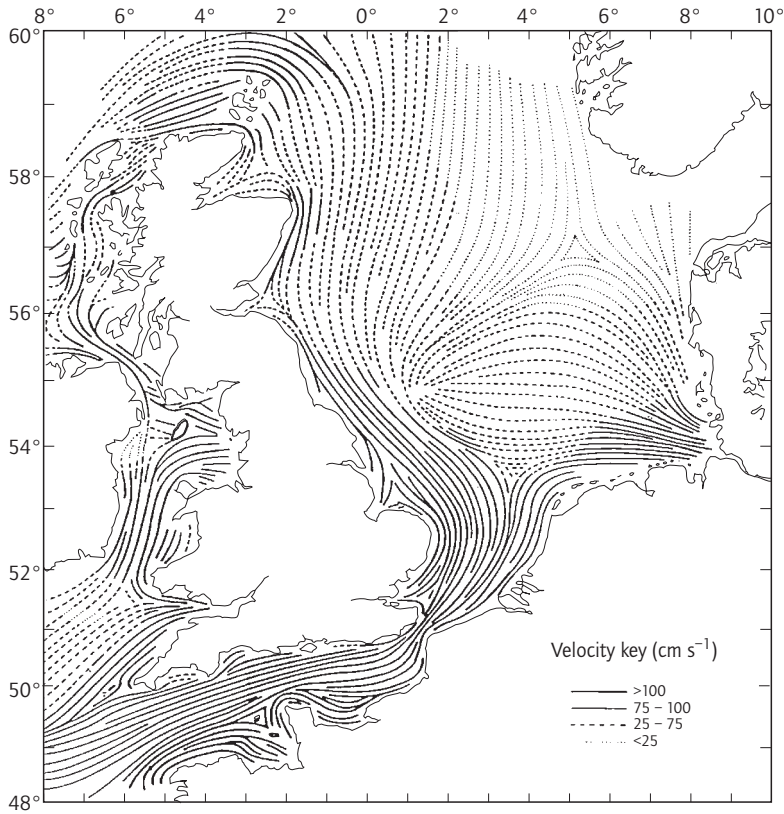
Fig. 8.4 A tidal stream chart for the North Sea and adjacent areas. (Source: from Harden Jones et al. 1978.)

the same hydrographic system (Harden Jones 1968). While such movements may involve adults having to swim actively against the current, this may not necessarily be required. In the open ocean, fish may exploit deepwater countercurrents (e.g. bluefin tuna, see below); on continental shelves fish may make selective use of the oscillating tidal streams (e.g. plaice, see below).

Marine fish make up over 90% of the total world commercial finfish catch. Here we describe the migrations of three very different species. The first is a highly migratory open-ocean species, the Atlantic bluefin tuna (*Thunnus thynnus*). The second is the European sea bass (*Dicentrarchus labrax*), a shelf-sea species whose seasonal migrations in UK waters appear to be a thermoregulatory mechanism that allows the females successfully to develop their ovaries. The third species is the

plaice (*Pleuronectes platessa*) that, in some areas of the North Sea, takes advantage of the tidal currents to minimize the metabolic cost of migration.

An open-ocean species: the bluefin tuna

Tuna and billfishes support major commercial and sport fisheries in temperate and tropical oceans throughout the world and are one of the classic groups of migratory fish of the open ocean. However, their migration routes, areas of abundance and availability can vary significantly from year to year, and our lack of understanding of their migrations is a significant source of problems in the management of tuna fisheries.

North Atlantic bluefin tuna are assessed and managed on the basis that there are two distinct stocks: one in the west and one in the east. In the

east, the stock is thought to have its major spawning area in the Mediterranean Sea, with highest concentrations around the Balearic Islands, Tyrrhenian Sea and the central Mediterranean. Females in the east mature earlier (4–5 years) and achieve a smaller maximum size than their conspecifics in the west. Spawning occurs in May and June. Having spawned, some fish begin a migration circuit entirely within the Mediterranean but the majority migrate out through the Gibraltar Strait, often in shoals of up to 10 000 fish. Subsequently, these fish migrate north, possibly aided by the North Atlantic Drift (Fig. 8.3), the northeastern limb of the North Atlantic gyre (Baker 1978). Until the 1920s this northerly movement seemed to extend no further than the English Channel. However, it now appears that the migration circuit extends as far north as Norway, with some individuals travelling as far as 5000 km in a few months. Subsequently, between November and February, the tuna return south in deeper water and this leg of the migration may be aided some of the time by deepwater countercurrents. In the spring, bluefin tuna return to the surface off the west coast of Spain and Portugal, where they gather and exploit the small gyral currents of the area for feeding before re-entering the Mediterranean in the current that flows continuously eastward in the middle of the Gibraltar Strait (Rey 1983).

The western stock is thought to have its major spawning area in the Gulf of Mexico and in the Florida Straits, where spawning occurs from mid-April into June. Females, which are thought to spawn first at an age of about 8 years, can live for 20 years or more, grow up to 3 m in length and exceed 600 kg in weight. Depending on her size, a single female can spawn between 1 million and 30 million eggs in a single season. Juveniles are thought to occur in the summer over the continental shelf, primarily in the area from 34°N to 41°W and offshore of that area in the winter. Although we know very little about movements between the western and eastern stocks of North Atlantic bluefin tuna, present assessment models assume constant proportional annual migration rates both west to east (about 4%) and east to west (1–6%) (Punt and Butterworth 1994). However, results from recent experiments in the Gulf of Maine with giant bluefin tuna tagged and released with pop-up satellite tags show that all 12 fish that were successfully located during the known May–July spawning period were in a region of the mid-Atlantic bounded by Bermuda and the Azores (Lutcavage et al. 1999). While it is not known if these fish were actually spawning, the results suggest that the migratory behaviour is complex and argue for reconsideration of existing assumptions about North Atlantic bluefin tuna migration patterns, spawning areas and stock structure. Even minor mixing could, in principle, have a marked effect on stock assessment owing to the difference in population size between the two stocks. While it is possible to model the effects of different levels of mixing resulting from different migratory behaviours, there are insufficient data to indicate which model is correct. Such models are therefore inadequate to provide reliable predictions about how the condition of one stock may affect that of the other (ICCAT 1999).

A shelf-sea species: the European sea bass

The European bass is found from the Mediterranean Sea, along the Atlantic coast north from Morocco to Ireland in the northwest and to Norway in the northeast. The species is exploited by commercial fishermen and sports fisheries, with most fish caught in the southern part of its range (Pickett and Pawson 1994).

Spawning occurs between February and June, and temperature appears to play an important part in its timing and location. Bass eggs are rarely found in water below about 8.5–9 °C (Thompson and Harrop 1987). Bass spawn in midwater and their eggs take 4–9 days to hatch, depending on temperature (Jennings and Pawson 1991). Over the following 2–3 months the growing larvae drift inshore on the prevailing current into sheltered creeks and estuaries where they feed and grow over the next 4–5 years.

Conventional tagging studies show that juvenile bass probably stray no further than 80 km from their release site (Pawson et al. 1987), but as they approach maturity there is a marked increase in

the scale of their seasonal movements. Broadly speaking, the pattern is for fish at the northern limits of their geographical range to move south and/or west in autumn, with a return migration in spring (Fig. 8.5). Fish from summer feeding grounds on the west coast of the UK move south to the Celtic Sea, while fish living in the southern North Sea and eastern English Channel move south and/or west to winter in pre-spawning areas in the western English Channel.

Conventional tag returns of adults caught on summer feeding grounds indicate that individuals usually return to specific feeding areas. However, the distances moved appear to depend on where fish spent the summer (Pawson et al. 1987). Those living around Cornwall and South Devon may move less than 100 km, while others living around Cumbria or in the southern North Sea may move distances of 400–500 km to the western English Channel. Some bass have been shown to move 800 km from their summer feeding area around the south coast of the UK to winter in the Bay of Biscay.

The seasonal movements of adult bass appear to be strongly linked to environmental temperature and gonad development (Pawson and Pickett 1996). Adolescent bass, classed as those that are maturing but have yet to spawn for the first time, will overwinter in water that falls below 9 °C, but females do not develop fully mature gonads. Successful gonad maturation appears to depend on fish remaining in water above 10 °C through the winter and, to achieve this, fish in the more northerly part of their range need to migrate south and/or west in autumn and winter (Pawson et al. 2000).

Such distinct seasonal movements have a pronounced effect on the temporal and geographic distribution of the bass fishery. Bass above 36 cm, which is the legal minimum landing size, are
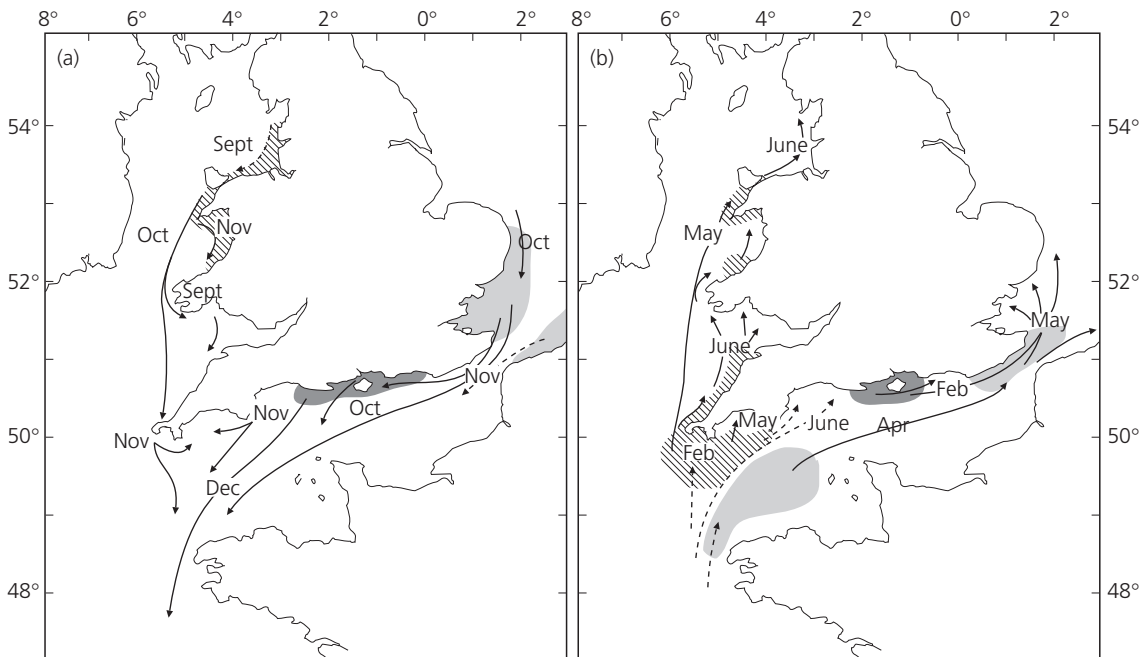
Fig. 8.5 Typical migration patterns of adult sea bass populations around England and Wales as shown by conventional tagging experiments (solid arrows) and postulated movements (broken arrows) in (a) autumn and (b) spring. The three different forms of shading indicate different adult populations. (Source: from Pawson et al. 1987.)

caught throughout the year in the English Channel, whereas at the northern limits of their range in the Solway Firth the main fishing season is restricted to July and August (Pawson and Pickett 1996). In the summer, bass tend to move into shallow warmer water and much of the fishing is concentrated in inshore areas. In winter, adult fish move offshore into deeper water, and large catches of pre-spawning bass are taken, particularly by French pair-trawlers, in the western English Channel in late winter and spring. In spring and early summer fish move north, and fisheries in the Solent, South Wales and the Thames Estuary peak through May and June, and again in September and October when the fish return south.

The knowledge that the seasonal movements of bass are tightly linked to environmental temperature makes it possible to predict how climatic changes may affect distribution and stock structure. For instance, if winter temperatures become warmer, bass that currently spend summer in the southern North Sea, but migrate to the western English Channel in winter, might remain in the southern North Sea for the whole year. If this situation persisted, these fish would experience a different pattern of exploitation than previously and thus constitute a separate stock for management purposes. Meanwhile, the stock of bass that continues to overwinter in the western English Channel would no longer receive an influx of recruiting adolescent or adult fish from the southern North Sea. Bass stocks in the English Channel as a whole might thus become depleted by the existing level of fishing effort.

A shelf-sea species: the North Sea plaice

The plaice is an important commercial species in the North Sea, being the fifth most valuable finfish to be landed by the UK fishing fleet in 1998 (most recent data). As plaice have been studied since the early 1900s, we probably now understand the biology and migratory behaviour of North Sea plaice better than those of any other commercial species in European waters.

The general pattern of plaice migration has been established from trawl surveys (Wimpenny 1953) and conventional tagging experiments in the Southern Bight of the North Sea (see review by Harden Jones 1968) and the English Channel (Houghton and Harding 1976). In autumn, maturing plaice leave the Leman Ground and more northerly feeding areas and migrate south to spawning areas centred on the Hinder Ground and in the eastern English Channel. On the Hinder spawning grounds, peak spawning occurs in late January and February (Simpson 1959; Harding et al. 1978), whilst peak spawning in the eastern English Channel occurs in early January (Houghton and Harding 1976). Subsequently, spent plaice return north to their summer feeding areas in late winter and spring. The timing of these migrations appears to be well structured both by age and sex. Extensive midwater trawling experiments in the Dover Strait have shown that males complete their pre-spawning migration earlier, and their post-spawning migration later, than females (Harden Jones et al. 1979; Arnold and Metcalfe 1996) confirming earlier suggestions (Hefford 1909, 1916; Simpson 1959) that males spend longer on the spawning ground than females. These experiments also suggest that immature females follow the mature fish in a 'dummy run' migration that may help them learn the location of the spawning grounds (Arnold and Metcalfe 1996).

Recently, a range of sophisticated telemetric techniques has revealed details of the mechanism by which these fish migrate. Sonar tracking studies of plaice equipped with transponding acoustic tags (Greer Walker et al. 1978; Metcalfe et al. 1992) and experiments with electronic data storage tags (Metcalfe and Arnold 1997, 1998) have established that these migrations are made by selective tidal stream transport. This behaviour is characterized by a circatidal pattern of vertical movement in phase with the tidal streams (Fig. 8.6). The fish leave the sea bed and move into midwater at about the time of slack water (Greer Walker et al. 1978) and swim down-tide (Metcalfe et al. 1990; Buckley and Arnold 2001) for the major part of the ensuing north-going or south-going tide. As the tide turns again, the fish return to the sea bed where they re-
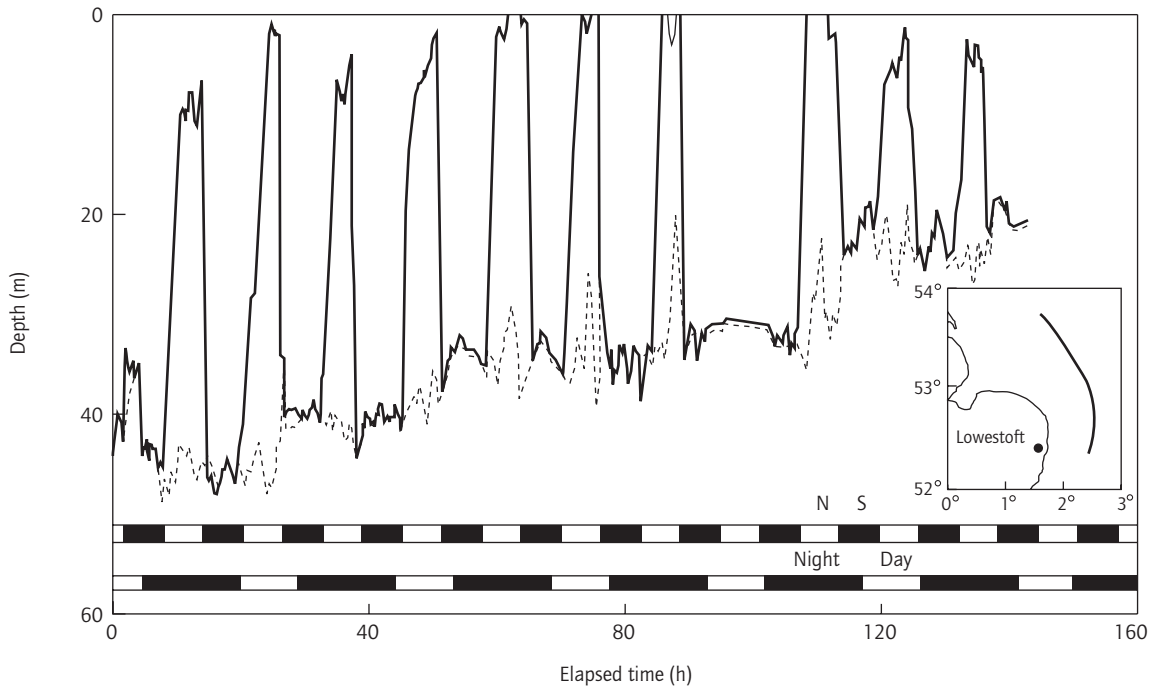
Fig. 8.6 The vertical movements (solid line) of a 44-cm maturing female plaice tracked in the southern North Sea in January 1991 in relation to the depth of the sea bed (broken line) and the direction of the tidal stream. The bars along the abscissa indicate the periods of north-going (N) and south-going (S) tidal streams and the periods of day and night respectively. Inset: the ground track of the same fish as it moved north between 25 and 31 January 1991. (Source: from Metcalfe et al. 1992.)

main for the duration of the opposing tide. This behaviour allows fish to move at speeds of up to 25 km day^{-1} between feeding and spawning grounds while reducing the cost of migration by between 20% (Metcalfe et al. 1990) and 40% (Weihs 1978) compared with swimming continuously over the same distance. Other species such as cod (Arnold et al. 1994), sole (Greer Walker et al. 1978), eels (McCleave and Arnold 1999) and possibly mackerel (Castonguay and Gilbert 1995) may also use selective tidal stream to aid migration.

While selective tidal stream transport can clearly reduce the energetic cost of migration, it may also provide a reliable transport mechanism for fish that are otherwise unable to navigate between feeding and spawning areas. However, recent evidence (Metcalfe et al. 1999) indicates that in areas of the North Sea where tidal stream speeds

are slow, such as the German Bight, plaice appear to migrate by directed swimming close to the sea bed rather than by using tidal streams. These results support the idea that metabolic cost determines the choice of migratory mechanism, and that plaice only exploit tidal streams where these are sufficiently fast to reduce the cost of migration, thereby enhancing the energy available for reproduction (Metcalfe et al. 1993).

Knowledge that plaice in the Southern Bight use tidal streams for migration has allowed development of computer simulation models that predict rates and scales of geographical movement by combining patterns of behaviour with tidal stream vectors (Arnold and Cook 1984; Arnold and Holford 1995). Although early models (Arnold and Cook 1984) relied on generalizations about fish behaviour, the recent use of electronic data storage

tags has provided the detailed information about how behaviour changes in time and space needed to develop more realistic models. Such models should help to predict seasonal movements of fish populations in relation to fishing effort, and allow effective assessment of management options such as marine protected areas and the potential effectiveness of quota management (Metcalfe et al. 1998, 1999; Sparre and Hart, Chapter 13, Volume 2).

8.3.2 *Diadromous fish*

Diadromous fish comprise a small (2.6% in 1997) but important part of the world commercial catch of finfish. Myers' (1949) definitions of the three different kinds of diadromous migration given earlier appear distinct and explicit, but the distinctions between categories (e.g. potamodromy or oceanodromy on the one hand and diadromy on the other) are not always clear. In particular, there are many fish from diverse higher taxa that move between fresh water and the sea but with no particular pattern with regard to either season or life-history stage. There are also others that make similar movements on a short time-scale, such as diurnally or tidally. These fish are not truly diadromous and some movements scarcely qualify as migration at all. Such species are probably best described as facultative wanderers. Although there is a continuum from facultative wanderers to more strictly diadromous fishes, we can still use diadromy and associated terms in an informative and heuristic way. The same is true for the terms 'carnivore' and 'herbivore' or 'benthic' and 'pelagic', which are not always totally explicit but are still useful as general descriptors.

Anadromous fish

Anadromous fishes include lampreys of the families Petromyzontidae, Geotriidae and Mordaciidae, the Acipenseridae (sturgeons), Salmonidae (salmons, trouts, chars and white-fishes), Osmeridae (northern smelts) and Retropinnidae (southern smelts), Aplochitonidae (Tasmanian whitebait), Salangidae (icefishes), Clupeidae (shads and herrings), Engraulidae (anchovies), Ariidae (forktailed catfishes), Gasterosteidae (sticklebacks), Gadidae (cods), Percichthyidae (temperate basses) and Gobiidae (gobies) (McDowall 1988).

By far the best-known examples of anadromy are the various species of salmon (genera *Oncorhynchus* and *Salmo*; Groot and Margolis 1991). These fish typically spawn in the gravels of headwater streams, occasionally at low elevations. After the eggs hatch, the young, known as alevins, remain in the spawning gravels for some weeks before emerging to live and feed in the streams. Behaviour after emergence varies with species. In pink or chum salmon (*O. gorbuscha* and *O. keta*), there is a rapid downstream movement and the alevins go almost immediately to sea. At the other extreme, parr of Atlantic salmon (*S. salar*) may spend several years feeding and growing in fresh water before moving to sea as smolts. Duration of life at sea, where most growth takes place, varies from just 2 years in pink salmon to as many as 5–6 years in chinook salmon (*O. tshawytscha*) (Groot and Margolis 1991). When salmon at sea approach maturity, they migrate towards land and enter the mouths of rivers. They move upriver over a period of weeks to months, during which time they do not feed and energy is transferred from the body to the maturing reproductive organs. In most species of Pacific salmon, spawning is followed inevitably by death; in some other species the spent adults may recover and mature again in subsequent years.

Lampreys follow a similar life cycle. Duration of the juvenile stage in fresh water is typically several years, as is the marine phase, during which time the submature lampreys are parasitic on marine fishes (Hardisty and Potter 1971). A distinctive feature of the return and upstream migration of the southern pouched lamprey (*Geotria australis*) is that sexual maturity is not attained until about 18 months after the adult leaves the sea, and there is no feeding in fresh water at all (Glova 1995). Osmerid smelts in northern cool temperate waters (Scott and Crossman 1973) and retropinnid smelts in Australia and New Zealand (McDowall 1990) are also anadromous, although the duration of freshwater life is brief. Adults, which are close

to maturity when they enter fresh water, spawn and die, and the larvae move swiftly to sea after hatching.

Catadromous fish

Catadromous fishes include Anguillidae (freshwater eels), some Galaxiidae (galaxiids and southern whitebaits), some Clupeidae, Engraulidae, Mugilidae (grey mullets), Centropomidae (snooks), Percichthyidae, Bovichtidae (southern rock cods), Scorpaenidae (scorpionfishes), Kuhliidae (flagfishes), Terapontidae (therapons), Lutjanidae (snappers), Cottidae (sculpins), Gobiidae and Pleuronectidae (flounders) (McDowall 1988).

The life cycles of the 15 species of anguillid eels (family Anguillidae) are very similar. Mature fish spawn at sea, usually in tropical to subtropical waters and often over great oceanic depths; invariably they die after spawning (Bertin 1956; Tesch 1977). The eggs hatch as distinctive, leaf-shaped, leptocephalus larvae that feed and grow in the sea for a year to two, gradually making their way back to the shores of countries from which their parents originated, probably propelled largely by oceanic currents. Leptocephali metamorphose in coastal waters, first to become slender and typically eel-shaped glass eels, and then into elvers that make their way into rivers from the sea. As elvers, and subsequently as yellow eels, they gradually penetrate upstream, feeding and growing over a period of many years. Age at maturity varies widely, being arguably greatest in the New Zealand longfin eel (*Anguilla dieffenbachii*), in which the female may be 80 or more years old before maturing and migrating to sea (Jellyman 1995).

Some mullets (family Mugilidae) are also catadromous. They spawn at sea and the larvae are initially marine. Small juveniles may invade freshwater rivers and remain there until maturity, when there is a downstream migration to the sea. Details of mullet life histories after first spawning are poorly understood, but there may be a return migration to fresh water of post-spawning adults (McDowall 1988).

The Australian barramundi (*Lates calcarifer*) is also catadromous and undertakes similar migrations. Upstream penetration in some rivers of Papua New Guinea is substantial, for example up to 800 km in the Fly River (Roberts 1978). An interesting and distinctive feature of this species is that only the males live in fresh water. The females are sex-reversed males that have left fresh water and remain in estuaries and tidal reaches (Moore 1982; Moore and Reynolds 1982).

Amphidromous fish

Amphidromy occurs among members of the Galaxiidae, Aplochitonidae (South American peladillos), Prototroctidae (southern graylings), Clupeidae, Pinguipedidae (New Zealand's torrentfish), Cottidae, Eleotridae (sleepers) and Gobiidae (McDowall 1988).

Amphidromy is the least widely recognized subcategory of diadromy, but nevertheless represents a clearly distinct pattern of migration. A typical example in the Northern Hemisphere is the Japanese ayu (Okada 1960; Kawanabe 1969). Spawning takes place in fresh water during autumn and the demersal eggs develop and hatch there. The larvae move immediately to sea, where they live for several months, before returning to fresh water during spring at a size of 50–70 mm. The fish grow and mature over the summer, before spawning and dying the following autumn. A very similar life history is evident in a number of southern galaxiids. Spawning occurs in autumn or early winter. Newly hatched larvae emigrate to sea where they feed and grow over the winter, before returning to fresh water at a length of 40–50 mm the following spring. In the New Zealand inanga (*Galaxias maculatus*), which like the ayu is an annual species (McDowall 1990), maturation takes place over the first summer and the adults spawn and die the following autumn (McDowall 1990). However, in other amphidromous galaxiids, maturation may not take place until the second or even third autumn depending on sex. In these species a substantial number of fish survive spawning and may spawn repeatedly over subsequent years (McDowall 1988, 1990).

Of the 250 species of diadromous fishes, about half are anadromous, one-quarter are catadromous

and one-quarter are amphidromous (McDowall 1988, 1998a). Anadromous fishes occur most frequently in cool-temperate and subpolar waters, catadromous fishes occur most frequently in warm-temperate to tropical waters, and amphidromous species are most common on oceanic islands in tropical to cool temperate waters (McDowall 1988).

The evolution of these three forms of diadromy may be related to optimization of life-history strategies in differing geographical ranges. Anadromy is favoured in cooler regions where biological productivity is greater in the sea than in fresh water. The sea is therefore a better feeding and growing biome because growth is more rapid, survival is usually higher, size at maturity is larger and fecundity is usually greater. Catadromy is favoured in warmer regions because biological productivity is greater in fresh water than in the sea, so that the main trophic life stage occurs in fresh water for the same reasons that anadromous fish spend their main trophic life stage at sea (Gross et al. 1991). Amphidromy may be favoured on oceanic islands because it either provides a mechanism for fish to colonize the fresh waters of islands when these become habitable or favours recolonization of these waters following perturbations, such as volcanism or drought, which cause local extirpation of island stream faunas (McDowall 1995, 1998a).

8.4 MIGRATORY MECHANISMS

8.4.1 *Orientated swimming*

Although water currents clearly play a major role in migrations of some stocks of fish, particularly in the open sea (Arnold 1981), there is also evidence that some species move independently of water currents. Atlantic cod have been shown to migrate across the cold (<0 °C) waters of the Newfoundland Shelf by swimming along deep 'highways' of warm (2–2.5 °C) oceanic water (Rose 1993). Tracking studies involving blue sharks (*Prionace glauca*, Carey and Scharold 1990) and bluefin tuna

(Lawson and Carey 1972) equipped with acoustic tags indicate that these fish can maintain a consistent heading in the open sea for hours or even days, moving independently of the water current.

The observation that fish can use external directional clues and move independently of water currents has led to controversy as to the relative importance of environmental transport by water currents and orientated swimming in migrations, particularly for large and active species like salmon and tuna. There are, as yet, insufficient data available about movements of individual fish in the open sea for it to be possible to resolve this question. However, it is likely that there is no single answer, and the importance of each type of movement differs for different stocks of fish and for different life-history stages. It seems probable that there is a trade-off between the costs of migration, such as increased energy expenditure and risk of predation, and the benefits, which can include improved survival and reproductive success. If this is so, the cost–benefit trade-off for any particular stock of fish will vary depending on the complex of environmental and biological factors experienced by that particular stock. For example, in the North Sea plaice exploit tidal streams during their pre- and post-spawning migrations in areas where currents are fast enough for them to be able to save energy (Metcalfe et al. 1990). However, more recent evidence already described suggests that, in areas where the tidal streams are slow, plaice swim in a directed way across the sea bed instead of using the tidal streams.

8.4.2 *Navigation and homing*

Our initial discussion of migration implied a strong element of 'to and fro-ness', and therefore a return movement during some part of the migratory cycle. This leads to some important questions. To what extent is the return movement an active process? To what extent does it involve homing to 'a place formally occupied instead of going to equally probable places' (Gerking 1959)? What mechanisms are used to locate 'home'? The literature on navigation and homing in fish is extensive, and numerous scholarly reviews, both

specific and general, are available (e.g. Dittman and Quinn 1996). Suffice to say, there is evidence for a whole range of homing and navigational abilities in a wide variety of fish species.

At one end of the spectrum, there is clear evidence for very precise homing abilities in some species. For example, adults of both Pacific and Atlantic salmon are able to return to the gravel bed in which they themselves were spawned several years earlier. Such feats of homing have been shown to depend on the young fish learning features of their 'home' before they leave for the sea, and subsequently using celestial, geomagnetic and olfactory clues to aid their return from the high seas to their natal river (Hasler 1971).

In comparison, European and Japanese eels spawn in the open sea in locations which ensure that most of their progeny will eventually be carried to the continental shelves by drifting passively with ocean currents. However, unlike salmon, elvers arriving on the continental shelves have no prior experience of the freshwater habitats they are about to enter, and it seems very unlikely that individuals can identify and ascend the same rivers that their parents left several years previously.

For migratory fish that live entirely at sea, like cod and plaice, conventional tagging studies provide evidence that adults return to the same spawning grounds in successive years (de Veen 1962 quoted by Harden Jones 1968 and Cushing 1990). Considering the vast numbers of individual fish involved and the comparatively small number of available spawning grounds, it is inevitable that some fish will spawn on grounds where they themselves were spawned. However, there is as yet no evidence, comparable with that for salmon, to suggest that adults use a specific homing mechanism to locate their natal spawning grounds. In contrast, there is growing evidence that in marine species like herring, local population persistence is ensured by recruiting individuals 'learning' migration patterns and spawning areas from adults of the stock to which they recruit, rather than by natal homing (McQuinn 1997). Such a mechanism would be consistent with observations of 'dummy run' migrations in which pre-spawning recruits follow mature adults. Dummy run migrations

have been suggested for plaice in the North Sea (Arnold and Metcalfe 1996), immature Arcto-Norwegian cod migrating from the Barents Sea to the Norwegian coast (Trout 1957; Woodhead 1959) and Newfoundland cod making inshore feeding migrations after spawning off the edge of the continental slope (Rose 1993). If young fish learn migration routes by following older ones, loss of older fish from a stock may lead to changes in the pattern of migration. The migration pattern of Norwegian spring-spawning herring (*Clupea harengus*) changed dramatically after adult stocks were depleted in the 1960s (Dragesund et al. 1980) and there is concern that the migrations of Newfoundland cod may have altered, possibly irrevocably, as a result of the severe population declines due to overfishing in the 1990s (Rose 1993).

From an experimental point of view, our understanding of the migrations of salmon is helped by the fact that the young fish (smolts) can be tagged before they go to sea. As a result, it is possible to identify with some accuracy how many fish return to their natal river and how many arrive at spawning sites in other rivers. However, acquiring comparable data for fish that spawn in the open sea is much more difficult since there is not yet a technique for marking eggs or larvae in a way that allows the individual fish to be reidentified as adults.

Why do some fish exhibit greater precision in their homing abilities than others? Presumably, the level of precision will be a function of the trade-off between enhanced reproductive success and the increased cost involved in homing to one specific spawning site as opposed to another. For example, the relatively small additional cost incurred by an adult salmon in selecting one river, as opposed to another a few miles further up the coast, may be significantly outweighed by the higher reproductive success achieved by spawning at a site previously proved to be good. On the other hand, recent studies of the migrations of Norwegian spring-spawning herring suggest that homing *per se* is not a successful strategy and that the selection of spawning grounds depends on the condition of the fish, the cost of migration and the probability of larval survival (Slotte and Fiksen 2000). The evolution of homing in some anadro-

mous species is usually regarded as a mechanism that allows fish to return to spawn in habitats that are capable of producing large numbers of progeny. However, because it limits levels of gene flow between populations, homing may also be a mechanism that enables local populations of diadromous species to become adapted to local conditions (Dittman and Quinn 1996). Such a situation has been demonstrated for populations of some Pacific salmon (Hendry and Quinn 1997).

8.5 TECHNIQUES

Understanding fish migration is clearly important to rational management and conservation of fish stocks, but obtaining the necessary information is frequently difficult. Fishers can provide useful information about seasonal appearances and disappearances of fish, and fisheries statistics can give a general picture of seasonal changes in population distribution. However, such information rarely suffices to describe the migrations of a particular species, and much more detailed information about the behaviour and movements of individuals and populations is needed.

Tagging, and other simple methods of marking, have been used since the mid-17th century (Walton and Cotton 1898) as a means of increasing our understanding of fish biology. Tagging tells us where individual fish are at two times in their life, when caught and tagged and when recaptured. If tagging and recapture are separated by a suitable amount of time, which can be months or even years, conventional tagging can provide information on stock identity, movements, migration rates and routes, abundance, growth and mortality.

There are many methods for marking or tagging fish (see Parker et al. 1990; Jennings et al. 2001). Branding or fin clipping is a quick and simple way to mark large numbers of fish, while chemical tags such as tetracycline, an antibiotic that is deposited specifically in calcified areas and fluoresces under ultraviolet light, can easily be applied to large numbers of fish and remain as a permanent mark. Alternatively, various types of tag can be attached to, or placed in, the fish. External tags include

Petersen discs used to tag plaice and other flatfishes, while internal tags include the tiny coded wires that are used for the mass marking of young salmon.

Simple tagging can be very useful for describing gross patterns of population movement, but the method tells us very little about *how* fish migrate. Population movements derived from tagging studies rely on commercial fishermen reporting details of the time and location of recapture of tagged fish and the results of such studies are inevitably an integration of both fish behaviour and fishing activity, which confounds any analysis of population movements. Tagging data can be adjusted for spatial variations in fishing effort, where this is known, but movements of fish into unfished or unfishable areas, or changes in fish behaviour that alter availability or catchability, cannot easily be accounted for. It is only by understanding the movements and behaviour of individuals over short (hours and days), medium (days and weeks) and long (seasons and years) time-scales that we can reveal the mechanisms fish use to move about. Understanding these mechanisms allows us to be predictive rather than simply descriptive.

Since the late 1960s electronic tags that transmit radio or acoustic signals have increasingly been used to track the movements of individual free-ranging fish for limited periods. Such work has yielded substantial advances in our understanding of how some species of fish such as the plaice migrate. However, this technique is limited because, in most applications, only one fish can be followed at a time, each fish can only be followed for a short period, often only a few days, and seagoing work aboard research vessels is expensive. More recently, substantial advances in microelectronic technology have permitted the successful development of electronic 'data storage' or 'archival' tags that are small enough to be attached to fish. These devices record and store environmental and behavioural data and, because there is no need for human observers to follow the fish, now make it possible to monitor the behaviour and movements of many fish simultaneously over entire migrations (Metcalfe and Arnold 1997, 1998). A variety of such devices are now being used to study the movements of species as diverse as plaice

(Metcalfe et al. 1994; Metcalfe and Arnold 1997), salmon (Walker et al. 2000), tuna (Gunn 1994; Gunn et al. 1994; Block et al. 1998) and others.

Although most data storage tags currently measure only simple environmental variables such as depth from pressure, internal and external temperature and ambient daylight, the data can nonetheless be used to derive detailed information about the movements of fish. On the European continental shelf, times of high and low water and tidal range derived from pressure measurements can be used to locate fish whenever they remain stationary on the sea bed for a full tidal cycle or more (Metcalfe and Arnold 1997, 1998). In the open sea, records of ambient daylight can be used to derive latitude from daylength and longitude from the time of local noon (Gunn et al. 1994; Hill 1994; Hill and Braun 2001; Metcalfe 2001). The development of further onboard sensors that can monitor more complex variables, such as compass heading, swimming speed or feeding activity, will do much to increase our understanding of migration of many more species of fish (Arnold and Dewar 2001; Righton et al. 2001).

Despite such technical advances, the use of data storage tags with many species remains limited because the prospect of the fish being caught and the tags returned is very low. To avoid the need to rely on a commercial fishery and to increase the probability of data recovery, a major area of development has been the 'pop-up' tag. These tags are attached externally and have a release mechanism that causes the tag to detach from the fish at a predetermined time and 'pop-up' to the sea surface where the data can be recovered by airborne radio or satellite (Nelson 1978; Hunter et al. 1986). Such devices are now commercially available and are being deployed on large pelagic species such as tuna (Block et al. 1998; Lutcavage et al. 1999). Although data transmission capabilities are currently very limited, further developments in this field give the prospect of much improved data recovery rates in the future, while further miniaturization will allow the technology to be applied to small species.

8.6   DISTRIBUTION AND GENETICS

Migratory fish tend to have much wider geographical distributions than non-migratory species, and a single species may exist as a number of distinct populations spread over a wide area. In some instances, particularly when they are separated by large distances, different populations may have sufficient integrity in the medium to long term that they respond independently to the effects of exploitation. In such cases these populations can be regarded as discrete 'stocks', which can be managed separately. If there is little or no transfer of individuals between these populations, they may also become genetically distinct. However, the transfer of only a few individuals can often lead to loss of genetic heterogeneity, even though exploitation of one population may have no effect on the other. Genetic analysis can thus be of value when it indicates that a population consists of more than one stock, but difficulties arise when it fails to provide evidence of stock separation (Ward, Chapter 9, this volume).

Among marine species, for example, Atlantic cod are found in continental shelf waters throughout the North Atlantic from the eastern seaboard of Canada and the USA to the coast of Norway and into the Barents Sea. However, while there are few obvious physical barriers to mixing, cod do not form one large mixed population and a number of separate stocks have been identified. Widely separate populations, such as Barents Sea and Canadian cod, have been shown to be genetically distinct, and isolation by distance is clearly a major factor maintaining stock separation (Hutchinson et al. 2001). Early genetic studies of North Sea cod suggested that this population was a single stock (Jamieson and Thompson 1972). However, more recent studies involving microsatellite DNA analysis have shown that there is significant genetic substructuring of the North Sea cod population (Hutchinson et al. 2001), with three or four genetically distinct groups: one off Bergen, one in the Moray Firth, one off Flamborough and one in the Southern Bight. The close proximity of these

different North Sea groups suggests that some behavioural and/or environmental factors must play a role in maintaining the genetic integrity of each (Hutchinson et al. 2001). Although the temporal stability of this genetic substructuring needs to be assessed, the results suggest that current assessment of North Sea cod may need to be re-evaluated.

Diadromy has particular implications for the evolution, biogeography and ecology of fish species, populations and communities, with diadromous species tending to have more widespread distributions than closely related non-migratory species. Although not all diadromous species are widely dispersed, those that are, and particularly those found on both sides of the major northern temperate oceans, are diadromous. For example, Pacific salmon of the genus *Oncorhynchus* are found on both sides of the northern Pacific (Scott and Crossman 1973; Groot and Margolis 1991), whilst the Atlantic salmon is present on both sides of the Atlantic (MacCrimmon and Gots 1979). The same is true of some sturgeons of the family Acipenseridae and some smelts of the family Osmeridae in northern cool temperate waters (Scott and Crossman 1973). The same applies in the Southern Hemisphere. Examples are the anadromous southern pouched lamprey and the diminutive catadromous inanga, which share an extraordinarily wide distribution that involves all or most of western Australia, eastern Australia, Tasmania, Lord Howe Island, New Zealand, the Chatham Islands, southern South America and the Falkland Islands (McDowall 1990).

Within regions, distributions and the amount of within-species genetic structuring have been shown to relate to diadromy. Species that have diadromous life stages tend to demonstrate less genetic structuring than those that do not (Allibone and Wallis 1993; Bernatchez and Wilson 1998; McDowall 1999). This difference is attributed to the capacity for gene flow amongst separate populations of diadromous species. Gene flow is inhibited in non-diadromous species, whose populations are geographically isolated in separate freshwater habitats. These differences have implications for patterns of speciation. Low gene flow

inhibits the development of genetic differences between diadromous populations and thus inhibits speciation.

There are several corollaries of this principle. One is that the phylogenetic relationships, and narrower distributions, of non-diadromous species can often be explained in terms of the recent geological histories of the areas they occupy (McDowall 1996, 1998a; Mooi and Gill, Chapter 3, this volume). Moreover, the existence of diadromy gives fish species a capacity for restoration of populations in areas perturbed by such events as glaciation (Milner 1987; Main 1989; Milner and Bailey 1989; Bernatchez and Wilson 1998), volcanic eruptions (Leider 1989; McKnight and Dahm 1990; McDowall 1996), drought (McDowall 1995) and defaunation resulting from pollution. Diadromous species re-establish populations in such waterways by migration upstream from the sea once habitats again become habitable. Another corollary is that the upstream distributions of diadromous species may be limited by the presence of natural or artificial barriers that exclude fish from habitats located further upstream. Some diadromous species demonstrate astonishing ability to migrate upstream. Chinook salmon in the Pacific northwest of North America may migrate upstream for more than 3000 km (Healey 1991), while Atlantic salmon are known to penetrate 2500 km inland (Hasler 1971). Equally astonishing are the climbing abilities of the small migratory juveniles of catadromous anguillid eels and amphidromous gobies and galaxiids, which are capable of climbing huge natural falls and the faces of dams (McDowall 1990; Fitzsimons and Nishimoto 1995). Such swimming and climbing abilities are at the extreme end of a continuum. At the other end are species that do not penetrate far upstream (McDowall 1993), some of which scarcely penetrate beyond estuarine waters. These more limited movements are presumably a combination of poor swimming or climbing ability and a low instinctive drive to move far upstream.

Where regional freshwater fish faunas are dominated by diadromous species, there is a variation in species richness along the length of river systems, with greatest richness at the downstream end.

Thus, as one moves up the length of a river, the pattern of species richness closely resembles the change in species richness predicted by the 'river continuum concept' (Vannote et al. 1980; Minshall et al. 1985). However the similar patterns of species richness have quite different causal mechanisms (McDowall 1998b). Running parallel to declining species richness as one moves up a river, there is a decline in fish abundance, driven by the same causes. Moreover, the fact that fish faunas in rivers are dominated by diadromous species means that the assembly of fish communities (Drake 1990, 1992) is, in substantial measure, driven externally by the processes that control upstream invasion. Consequently, the community existing at any point up a river system is the product of interactions between local characteristics that determine which species the habitat is suited for and those factors such as distance and obstacles that determine which species are able to reach such habitats.

Indices of biotic integrity (IBI) are increasingly being used in freshwater ecology and resource management. Karr (1991) defined biological integrity as a 'balanced, integrated community of organisms having a species composition comparable to that of a natural habitat of the region'. Karr (1991) used attributes such as species composition, species richness, fish abundance, trophic composition, fish reproductive guilds and fish condition to evaluate habitat quality and anthropogenic effects. However, where fish faunas are strongly influenced by invasion through diadromy, there is a natural downstream–upstream attrition of the fish fauna. This means that depending on how far upstream they are and what impediments to migration are present, similar habitats may have very different fish faunas. Consequently, use of the IBI in river systems dominated by diadromous species is likely to fail, unless multipliers can be developed that compensate for the effects of distance inland and the degree of difficulty in reaching various habitats under study (McDowall and Taylor 2000).

8.7   FISHERY APPLICATIONS

Stock assessment involves routine fishing or acoustic surveys, during which it is normally assumed that the fish are stationary (but see Sparre and Hart, Chapter 13, Volume 2). However, this is rarely true, and migration can be a major source of error in acoustic surveys (MacLennan and Simmonds 1991). By properly understanding the spatial and temporal pattern of migrations, surveys may be appropriately adapted or the effects of migration on the abundance estimates otherwise taken into account.

Migration is also a key factor in the identification of stock units in relation to exploitation. For instance, a particular species may be caught in one area at one time of the year and in another area at another time. Such a situation could result either from one stock migrating between the two areas and being exploited twice, or from two separate stocks migrating in from two other areas at different times. Understanding stock identity is therefore important in predicting the effects of changes in the levels and/or patterns of exploitation.

Similarly, migration is a critical element in the effectiveness of management by 'closed areas' or 'no-take zones' (Polunin, Chapter 14, Volume 2). Clearly, while a fish remains within a closed area it is protected from fishing, but once it moves outside it becomes vulnerable. It is therefore necessary to understand the spatial and temporal patterns of fish movement and fishing effort if we are realistically to assess the conserving effect of this method of management.

8.8   CONCLUSIONS

As world fisheries continue to be heavily exploited, with drastic reductions in catches or even closures of entire fisheries (such as the Newfoundland cod in the 1990s) being necessary to conserve stocks, there is an increasing need for rational management that takes more account of fundamental biology. This applies not only to traditionally exploited species like cod and tuna but also to newly developing commercial fisheries, like those for deepwater species such as orange roughy (*Hoplostethus atlanticus*) and round-nosed grenadier (*Coryphaenoides rupestris*). For most of these species we know little of their migratory be-

haviour or of the environmental factors that affect it.

Fortunately, management agencies are becoming increasingly aware of the need to understand fish migration, not just because it is interesting but because it is fundamental to many basic elements that underpin fisheries management. It is hoped that this will lead to improved future support for the study of fish migration. However, the need to understand migration is of little value without the necessary tools, so continuing to improve methodologies will be important too. The successful application of telemetry techniques to the study of fish migration should help to ensure that, as technology develops, smaller, cheaper, more sophisticated electronic tags become available. Such devices, combined with other techniques used to study population movement such as genetics and otolith microchemistry, can only improve our understanding of how and why fish migrate, and where they go.

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9 Genetics of Fish Populations

ROBERT D. WARD

9.1 INTRODUCTION

The well-publicized collapses of many well-known fish stocks, such as those of Peruvian anchoveta (*Engraulis ringens*), North Sea herring (*Clupea harengus*) and Newfoundland cod (*Gadus morhua*) (Beverton 1990; Hutchings and Myers 1994), have led to demands for more effective and more sustainable management. Fishery managers are now primarily aiming for resource sustainability and the recovery of severely depleted populations. Their decisions are based on stock assessments, together with socioeconomic and sometimes political considerations. Stock identification is an integral element (Carvalho and Hauser 1994; Begg et al. 1999); indeed a recent check-list of stock assessment methods (Deriso and Quinn 1998) listed information on spatial distribution or stock structure as the number one item.

Determining the stock or population structure of any fish species is a complex task. There are many approaches that can be taken, including genetic analyses, phenotype analyses to detail growth rates, age composition, morphometrics and microconstituents in calcified structures, together with parasite loads and tagging returns. While these different approaches generally complement each other and assist in a better understanding of stock structure, their reconciliation into a unified model can be challenging (McQuinn 1997).

Genetic analyses are not only useful in helping to define stock structures of commercial fishes; they are also important in other areas of concern to fisheries managers, including conservation and enhancement programmes and the validation of species identification. In this chapter, the genetic tools currently available are described, with their strengths and weaknesses, and examples given of their uses in specimen identification, population structure analyses and conservation and enhancement programmes. The chapter finishes with a short section on the genetics of sex determination in fish, and some concluding remarks.

9.2 GENETIC TOOLS

Genetic analysis of fish populations is not new. Serological approaches were first adopted in the early 1930s (see de Ligny 1969) but failed to gain widespread acceptance. The genetic tools now used are based on electrophoretic analysis of proteins and DNA. Table 9.1 summarizes their properties, albeit in a somewhat simplified and subjective fashion, and should be read in conjunction with the following subsections. Table 9.2 summarizes their uses in different areas of fisheries science.

9.2.1 Allozyme analysis

The first genetic tool to be widely adopted for fish population analysis was protein electrophoresis. One of the earliest studies was Sick's (1961)

Table 9.1 The major current genetic tools used in fisheries science, with some general comments on their properties. The comments are necessarily partly subjective and sometimes oversimplified. For example, the costs of microsatellite analysis are significantly less when primer sequences are already available than when they have to be developed anew. The suitability of these tools in different areas of fisheries science is summarized in Table 9.2.

	Basis	PCR based	Speed	Expense	Genetics	Tissue required	Number of markers	Variability of markers	Coding/ non-coding	Comments
Allozymes	Electrophoretically detectable protein variation	No	*****	*	Codominant	Fresh, frozen	***	**	Coding	Still an excellent tool if suitable tissue available
MtDNA-RFLP	Fragment size variation following restriction enzyme digestion	No	**	***	Haploid, maternally inherited	Fresh, frozen, preserved	*	**	Mostly coding	Effectively a single marker
MtDNA-PCR-RFLP	As above, but using PCR products	Yes	***	***	Haploid, maternally inherited	Fresh, frozen, preserved	*	**	Mostly coding	Effectively a single marker
MtDNA sequencing	Nucleotide sequence variation	Usually	***	****	Haploid, maternally inherited	Fresh, frozen, preserved	**	**	Mostly coding	Effectively a single marker
Randomly amplified polymorphic DNA (RAPD)	DNA fragment size variation following use of primers of random sequence	Yes	****	**	Dominant	Fresh, frozen, preserved	*****	***	Mostly non-coding	Reproducibility a concern; highly sensitive to PCR conditions
Microsatellite	Variation in number of tandem repeats of dinucleotide/ tetranucleotide motifs	Yes	***	***	Codominant (some recessive null alleles)	Fresh, frozen, preserved	*****	*****	Non-coding	Development time a deterrent; scoring problems not unknown
Minisatellite	As above but tandem repeats longer	Sometimes	***	***	Codominant	Fresh, frozen, preserved	***	***	Non-coding	Usually scored with Southern blots; not popular
Amplified fragment length polymorphism (AFLP)	Presence/absence of fragments after selective amplification	Yes	****	**	Dominant	Fresh, frozen, preserved	*****	***	Mostly non-coding	Still novel for fish; multiple bands can hinder cross-gel comparisons
Exon-primed intron-crossing PCR (EPIC)	Sequence or size variation in introns	Yes	***	**	Codominant	Fresh, frozen, preserved	***	***?	Non-coding	Still novel, but with considerable potential

PCR, polymerase chain reaction; RFLP, restriction fragment length polymorphism; mtDNA, mitochondrial DNA.

Table 9.2 Suitability/uses of the current genetic tools in fisheries science. Columns graded * to *****; for example allozymes are very suitable for species identification and somewhat less so for aquaculture genetics. Scorings are overall scores; for example mtDNA sequencing is a very powerful approach to species identification but given its expense is rated below the mtDNA-PCR-RFLP approach. Scores marked with a ? indicate that these approaches have been little explored as yet, but that these are likely scores based on the properties of these markers. Column headings are broad; for example, aquaculture genetics embraces diversity estimation, pedigree analysis and gene mapping studies. Some tools might be better in some subcategories than others; for example AFLPs will likely be of more use in aquaculture in mapping than studies of gene diversity.

	Species identification	Population genetics	Systematics	Aquaculture genetics
Allozymes	*****	***	***	***
MtDNA-RFLP	****	**	***	*
MtDNA-PCR-RFLP	*****	***	***	**
MtDNA sequencing	****	**	*****	*
RAPD	***	**	*	**
Microsatellite	*	****	*	*****
Minisatellite	*	***	*	**
AFLP	***?	**	*?	***
EPIC	**?	****?	**?	***?

AFLP, amplified fragment length polymorphism; EPIC, exon-primed intron-crossing PCR; mtDNA, mitochondrial DNA; PCR, polymerase chain reaction; RAPD, randomly amplified polymorphic DNA; RFLP, restriction fragment length polymorphism.

examination of haemoglobin variation in whiting (*Merlangius merlangus*) and cod (Gadus morhua). The subsequent advent of enzyme-specific histochemical staining made it possible to examine a large range of enzymes, a procedure often referred to as allozyme analysis. The seminal studies of Lewontin and Hubby (1966) and Harris (1966) showed that genetically determined allozyme variation was widespread in *Drosophila* and human populations. Fish populations were soon shown to be no different, and for the first time a simple, quick and reliable genetic method was available for examining fish population structure. Practical details may be found in Richardson et al. (1986), Whitmore (1990), Manchenko (1994) and Hillis et al. (1996).

Allozyme analysis remains a highly attractive approach, when fresh or frozen tissue is available, in terms of speed and cost. Many allozymes are tissue-specific, so the availability of different tissues including muscle, liver and nerve (eye) is advantageous. Significant disadvantages include low average degrees of variability which, when coupled with the limited number of loci that can be assessed (usually <50), can give little variation for screening purposes. There is also a lingering debate over whether the variation detected is or is not selectively neutral. Lewontin (1974) gives a classic account of this controversy. Population genetic interpretation is generally based on the null hypothesis of selective neutrality, so that population differences are held to reflect reproductive isolation and genetic drift. However, it is possible that some of the amino acid differences responsible for allozyme separation affect function in some way; if this is so, then population differences might reflect differences in selection pressures rather than isolation.

A modification of protein electrophoresis is isoelectric focusing (see Whitmore 1990), where proteins are electrophoretically separated on a pH gradient gel on the basis of their surface electrical charge alone, rather than size and charge as in conventional electrophoresis. They are sharply 'focused' at their isoelectric point, the pH at which the protein has a net surface charge of zero.

9.2.2 DNA analysis

The ability to examine DNA variation directly, rather than indirectly through protein variants, came with the recognition and isolation of restriction enzymes. There are many such enzymes, which cut or 'restrict' DNA at enzyme-specific nucleotide sequences, usually of four or six bases. Unfortunately, with the constant development of new analytical DNA techniques, comprehensive manuals are lacking. Two good sources of information are Hillis et al. (1996), who provide an overview of molecular techniques and data analysis, and Caetano-Anollés and Gresshoff (1997), who provide details on selected methods of DNA marker analysis and their applications, including methods not discussed here. A brief outline of some of the major and more commonly used methods in fisheries population genetics follows; other approaches are included, briefly, in Tables 9.1 and 9.2.

Fig. 9.1 Inheritance of nuclear DNA and mitochondrial DNA. The male parent has genotype a/b at a nuclear DNA locus, and mitochondrial haplotype X. The female parent has genotype c/d at the nuclear DNA locus, and mitochondrial haplotype Y. The offspring have one of four nuclear DNA genotypes (a/c, a/d, b/c and b/d) but all have the mitochondrial DNA haplotype Y.

Mitochondrial DNA

Most initial DNA analyses were of mitochondrial DNA (mtDNA), largely because this genome (usually about 16–18 kb) is much smaller than nuclear DNA (nDNA) and was easier to examine with the techniques available some 10–15 years ago. Mitochondrial DNA was extracted and cut with restriction enzymes; the resulting fragments were separated by electrophoresis and visualized. This is a restriction fragment length polymorphism (RFLP) analysis.

Mitochondrial DNA is inherited differently from nDNA (Fig. 9.1): it is only inherited from the maternal parent, with very rare exceptions, and is haploid in nature. The genetically effective population size of mtDNA is thus, other factors being equal, only one-quarter that of nDNA, which is inherited from both parents and is diploid in each parent. This makes it potentially a more sensitive indicator of genetic drift than nDNA. Furthermore, its overall rate of evolution is about an order of magnitude faster than single-copy nDNA. The non-coding control region (d-loop) of mtDNA evolves more rapidly than coding segments, making it possible to choose a relatively variable region for population studies or a relatively conserved region for taxonomic or systematic studies.

However, mtDNA also has significant disadvantages. Principal among these is that it is a non-recombining genome and best treated as a single character, whereas nDNA assessment can be based on many independent characters (loci).

Polymerase chain reaction

Analyses of DNA variation, both mtDNA and nDNA, were considerably enhanced by the development of polymerase chain reaction (PCR) techniques. PCR analysis allows the repeated amplification of a DNA region lying between two DNA primers, the primers generally being sequences of around 20 bp that are complementary to sequences in the target DNA. These techniques typically allow the amplification of a DNA region, flanked by the complementary primer sequences, that is some hundreds of base pairs long, although

regions of several thousand base pairs can now be amplified successfully. Once the target fragment has been amplified, it can be examined for size or sequence variation.

This general approach is very flexible and lends itself to a wide variety of adaptations and modifications. Many of these relate to primer design and make it possible to target different classes of mtDNA or nDNA sequence. The amplified fragments can be assessed by a wide variety of methods, including RFLP analysis, sequencing, size analysis, single-strand conformational polymorphisms and dot plots. Furthermore, very little tissue is needed as the target DNA is amplified many-fold from the small amount initially available. This permits non-invasive and non-lethal sampling. DNA can be extracted and amplified from old fish scales (Nielsen et al. 1999) or museum specimens (Pichler and Baker 2000), permitting historic surveys of changes in genetic variability. Tissue can be stored at room temperature in alcohol or other chemicals such as dimethyl sulfoxide, simplifying the logistics of sampling and freight. PCR analyses have now largely supplanted non-PCR analyses.

Microsatellites

Microsatellites are nDNA regions of repeated sequences where the repeat sequence or motif is short, 2–5 bp. An example is TCTCTCTC, which is a 2-bp or dinucleotide repeat. The total microsatellite length is usually less than 300 bp (Tautz 1989). Microsatellites are flanked by non-repeat sequences that are conserved within species, making it possible to design PCR primers which will amplify the microsatellite region. Microsatellite variability arises principally from variation in the number of repeats of the motif, leading to size changes in the PCR product that can be identified on electrophoresis gels. Microsatellites are usually in non-coding regions and thus likely to be selectively neutral. The mutation rate of microsatellite loci is very high, and consequently dozens of alleles per microsatellite locus are not uncommon. Allele data are most readily collected using primers with fluorescent labels and an automated DNA sequencer, although non-automated approaches are also popular. Unfortunately, primers tend to be specific to an individual species or species group, as mutations that accumulate in the flanking region quickly reduce the binding ability of the primers. Microsatellite primers generally have to be developed anew for each species or species group; this time-consuming development phase can require several months of skilled labour.

Microsatellites provide an abundant supply of hypervariable codominant markers for fish studies (O'Connell and Wright 1997). This is an advantage in pedigree or mapping studies, but too many very low frequency alleles can reduce the power of population structure analyses. Scoring of genotypes can sometimes prove difficult, especially when there are many alleles of similar size and when PCR products of a single allele produce multiple bands on gels, a phenomenon known as band 'stuttering' or 'laddering'. Non-amplifying or 'null' alleles have also been recorded; these can arise from mutations in the primer site so that a particular allele is not amplified or from the PCR process not amplifying a long allele as well as a short allele. Null alleles are recessive alleles. In population surveys, an individual heterozygous for an expressed allele and a null allele will usually be mistakenly scored as homozygous for the expressed allele.

Randomly amplified polymorphic DNA

Another PCR technique, less widely used in fisheries, is the analysis of randomly amplified polymorphic DNA (RAPD; Welsh and McClelland 1990; Williams et al. 1990). Primers of random nucleotide sequence, typically around 10–20 bp, are used to amplify anonymous segments of DNA. Variation in primer binding sites leads to variation in PCR products, which are again scored from size variation in electrophoresis gels. This is a quick and relatively simple technique, although amplification occurs in conditions of low stringency and repeatability of observations requires careful attention to all aspects of the procedure. It is a dominant/recessive system, and DNA fragments

of any particular locus in any individual are generally scored as present (genotypes + + or + −) or absent (genotype − −).

Amplified fragment length polymorphism

Amplified fragment length polymorphism (AFLP; Vos et al. 1995) constitutes a third major marker class. In this procedure, genomic DNA is digested with two restriction enzymes, *Eco*RI and *Mse*I, and suitable adapters ligated on to the fragments. Primers are then used that recognize these adapters and also have additional terminal selective bases, which can be used to discriminate between and then amplify particular subsets of fragments. By changing these selective bases, different sets of fragments can be recognized. Like the RAPD approach it does not require prior sequence information, but unlike the RAPD approach primer specificity is high and stringent annealing conditions can be used. Repeatability is therefore higher. It can produce large numbers of polymorphic markers on a single gel. One disadvantage of AFLP is that, like RAPD, it is generally scored as a dominant/recessive system. Mueller and Wolfenbarger (1999) give a short general account of the methods and uses of AFLP.

Exon-primed intron-crossing PCR

A further PCR variant makes use of the fact that many genes in higher organisms are made up of exon and intron sequences. Exons are expressed whilst introns are intervening sequences that do not code for any product. Generally the exon regions, which code for amino acids in protein genes, are highly conserved, but the intervening non-coding sequences can accumulate mutations. Thus conserved primers that anneal to adjacent exon regions can be created which amplify the variable DNA from introns; this is exon-primed intron-crossing PCR (EPIC). Intron variation can be assessed by RFLP analysis, fragment size electrophoresis or any other appropriate technique. EPIC analysis has the advantage that a particular pair of exon primers may be relatively universal. This means that they are usable over a wide range

of distantly related species (e.g. Quattro and Jones 1999).

9.2.3 Uses

A somewhat subjective attempt to summarize the abilities of these different tools in four areas of fisheries science is provided in Table 9.2. Allozymes and mtDNA analysis are excellent tools for species identification. Allozymes and microsatellites are perhaps the best tools for population genetics, although neither rates the full five-star category. Allozymes have limited variability and lingering uncertainties concerning the relative roles of selection and drift, whilst microsatellites can have too much variability and scoring difficulties. Systematics and aquaculture are important areas of fish genetics not otherwise covered here. Mitochondrial DNA sequencing is perhaps the best current tool for systematics but may in future be equalled or bettered by nDNA sequencing. Microsatellites are probably the best overall tool for aquaculture applications and would be used to provide measures of diversity in hatchery stocks, to assess pedigrees and to map genomes. AFLPs yield large numbers of markers very quickly for mapping purposes.

9.3 STATISTICAL TOOLS

The development of hypervariable markers has rendered traditional statistical methods for analysing genotype and allele frequencies inappropriate or at least lacking in power. Traditional approaches cannot deal with very small cell or sample sizes, and require the pooling of rare genotypes or alleles. The new methods typically use computer-intensive resampling techniques that do not require data pooling (Rousset and Raymond 1997). Many of the statistical packages for analysing molecular data are briefly described in Hillis et al. (1996) and Schnabel et al. (1998). Most implement Monte Carlo or other methods for dealing with hypervariable loci and small cell sizes. Maximum likelihood and coalescence methods are being explored as alternatives to tradi-

tional ways of handling gene frequencies and estimating gene flow rates (e.g. Neigel 1997; Beerli 1998; Luikart and England 1999).

9.4   SPECIMEN AND SPECIES IDENTIFICATION

Accurate species identification is vital for scientific research, for catch recording and for labelling in the marketplace. Accurate catch identification is necessary to monitor species managed under quota systems; some species are morphologically very similar yet under quite different management regimes. Accurate labelling is necessary for consumer confidence in fish products. Cases of fish substitution or mislabelling do occur, more commonly where fish are marketed as fillets rather than as whole fish. Compliance officers require a tool that provides unequivocal specimen identification and which will be acceptable to a court of law. Finally, eggs and larvae may be virtually impossible to identify morphologically, yet accurate identification may be required for research or assessment purposes.

Molecular genetic methods have proven invaluable in all these areas, and indeed have sometimes led to the recognition of previously unrecognized sibling species (see Ward and Grewe 1994 for examples). The premise underlying genetic identification of species is straightforward: if two taxa are reproductively isolated from each other and warrant species status, they are likely to have accumulated sufficient genetic differences during their isolation to be genetically distinguishable. If the two taxa are sympatric, genetic differentiation provides strong evidence of species separation; if they are allopatric, then large genetic differences again suggest two discrete species, but small differences could be compatible with either two recently diverged species or limited gene flow between populations of a single species.

The method chosen should ideally target a genetic marker of low intraspecies variability but high interspecies variability. Contemporary levels of variation generally correlate with evolutionary rate so it is difficult to find such a marker. However, some markers show little variation within species but enough variation between species to make them suitable for species identification.

Allozyme analysis is a satisfactory method of identifying fish tissue, provided that the material is either fresh or frozen. The methods are sufficiently sensitive to be able to identify fish eggs and larvae (see Ward and Grewe 1994 for examples). A fast and simple method for fish identification involves Coomassie blue staining of the major white muscle proteins after electrophoresis (Shaklee and Keenan 1986). The use of a cellulose acetate matrix rather than starch or acrylamide can speed the time required to less than 1 h. A recently published identification guide for Australia's domestic seafood includes cellulose acetate-based protein fingerprints of about 380 species (Yearsley et al. 1999). Where possible, multiple specimens of each species were examined so that at least the more common intraspecies variants were detected where present. This simple test cannot differentiate all members of some closely related species groups; in such instances supplementary allozyme or DNA tests are required.

Isoelectric focusing of muscle proteins has been used to identify red snapper (*Lutjanus campechanus*) fillets (Huang et al. 1995) and caviar from various sturgeon species (Chen et al. 1996), and can be used to discriminate snapper cooked in a variety of ways (Hsieh et al. 1997). The cooked flesh of ten commercially important species was examined in nine laboratories using the two electrophoretic methods SDS polyacrylamide and urea isoelectric focusing. With the exception of some closely related salmonids, all species could be identified (Etienne et al. 2000). Isoelectric focusing methods have also been used in the US-based Regulatory Fish Encyclopedia (Office of Seafood and Office of Regulatory Affairs, Food and Drug Administration, 1993–2000, see the website: http://vm.cfsan.fda.gov/~frf/rfe0.html).

DNA-based methods can be used when specimens cannot be identified by protein or allozyme electrophoresis. Examples would be when species are genetically so similar that diagnostic proteins

cannot be found, when insufficient tissue is available or when specimens have been preserved in such a way as to destroy protein integrity or enzyme activity. Early cases of fish identification using PCR amplification of mtDNA, followed by sequencing or RFLP analysis, are given in Ward and Grewe (1994). More recent examples are billfish (Chow 1994; Innes et al. 1998), tunas (Ward et al. 1995), flatfish (Cespedes et al. 1998), fish eggs (caviar) (DeSalle and Birstein 1996) and starfish larvae (Evans et al. 1998). Rehbein et al. (1999) used single-strand conformation polymorphism of mtDNA to identify a variety of raw and canned fishery products.

Nuclear DNA identification is less common, although RAPD has been used for tilapias (Dinesh et al. 1993; Bardakci and Skibinski 1994), barbels (Callejas and Ochando 1998) and a variety of other fishes (Partis and Wells 1996). PCR amplification of 28S RNA from nDNA has been used to identify spiny lobster (*Jasus edwardsii*) phyllosome larvae (Silberman and Walsh 1992). PCR-based analysis of DNA is also commonly used for identifying pathogenic and infectious organisms of fish. An example is mycobacterial identification using RFLP analysis of 16S ribosomal RNA (Talaat et al. 1997). A combination of mtDNA and nDNA analyses was used to track an individual hybrid blue/fin whale, *Balaenoptera musculus* × *B. physalus*, from the time of harpooning off Iceland in 1989 to sale in Japan as raw meat in 1993 (Cipriano and Palumbi 1999). Multilocus typing of hypervariable microsatellite loci, although not used in this study, lends itself particularly well to identification and tracking of individuals.

Genetic tests reveal that misidentification or mislabelling of fish fillets is not uncommon. Huang et al. (1995) showed that 70% of a sample of claimed red snapper (*Lutjanus campechanus*) fillets in Florida were from congeneric species. Mislabelling of fish fillets in Australian outlets has also been recorded (Partis and Wells 1996; R.D. Ward, personal observation). Allozyme identification of material has been used in law courts in the USA (Harvey 1990) and Australia (C. Keenan, personal communication). J.E. Seeb et al. (1990) used allozyme analysis to locate a king crab catch

(*Paralithodes camtschatica*) to an area closed to fishing rather than to the claimed open area.

One point worth making here is that for many population genetic surveys, tissue samples are collected by third parties or relatively untrained personnel. In such situations checks on the species identity of the tissue fragments prior to population analysis are highly desirable. This can be done quickly by mtDNA examination, which might also provide data on population structure to complement any nDNA analysis.

9.4.1 Identifying and studying fish hybridization

Hybridization between fish species is not uncommon (Verspoor and Hammar 1991) and genetic analysis is invaluable for determining hybrid status; allozymes often make excellent diagnostic markers. F_1 hybrids can be readily recognized as they are heterozygous for all nuclear loci discriminating the two parental species. The female parent, and by elimination the male parent, of known F_1 hybrids can be identified using mtDNA markers. Backcross hybrids will be heterozygous for some diagnostic loci but homozygous for others characterizing the species with which the F_1 hybrid has crossed. Examples of the use of biochemical genetics in hybridization studies are given in Verspoor and Hammar (1991) and Ward and Grewe (1994); some recent examples of the joint use of nDNA and mtDNA markers include the cyprinid genus *Luxilus* (Dowling et al. 1997), the salmonid genus *Salvelinus* (Wilson and Bernatchez 1998), the percichthyid genus *Macquaria* (Jerry et al. 1999) and the scorpaenid genus *Sebastes* (Seeb 1998).

9.5 FISH POPULATION GENETICS

Population genetics is a vast field. It includes measurements of levels of variation within and between populations, the development of mathematical and simulation models of how genes

mutate, differentiate and evolve, and studies of the forces changing gene frequencies, i.e. the relative roles of genetic drift and selection. Here I am mostly concerned with the assessment and interpretation of genetic variation within and between fish populations. Nei (1987) and Hartl and Clark (1997) provide good guides to the principles and applications of population and evolutionary genetics.

Levels of genetic diversity vary among classes of fish. Marine fish show higher levels of average allozyme heterozygosity (h) per locus than anadromous fish (see Metcalfe et al., Chapter 8, this volume), which in turn show higher heterozygosity than freshwater fish ($h = 0.059$ vs. 0.052 vs. 0.046, respectively, Table 9.3, Ward et al. 1994). The same pattern holds for microsatellite heterozygosities (average marine $h = 0.79$, 12 species; anadromous $h = 0.68$, 7 species; freshwater $h = 0.46$, 13 species; see DeWoody and Avise 2000). Microsatellite heterozygosities are an order of magnitude greater than allozyme heterozygosities. This is largely because microsatellites are intrinsically more variable than allozymes, with much higher mutation rates. In addition, the allozyme datasets include monomorphic loci whereas microsatellite studies are generally biased towards the more polymorphic microsatel-

lites; the monomorphic microsatellites, which admittedly are rather uncommon, tend to go unreported. The greater heterozygosity of marine fish over freshwater fish may reflect their larger effective population sizes, which in turn may reflect their larger and more connected environment.

A comparison of the genetic make-up of different samples or subpopulations allows an assessment of the degree of genetic connectivity between subpopulations (Fig. 9.2). A summary of allozyme genetic diversity levels among samples or subpopulations of fish (Table 9.3) shows that, on average, about 5% of loci are expected to be heterozygous in a sample (H_S). The total heterozygosity (H_T), that is, the expected heterozygosity derived from allele frequencies averaged across populations, is a little higher, at about 6%. The proportion of genetic diversity attributable to differences among samples is the statistic F_{ST} (or G_{ST}), and can be estimated by $(H_T - H_S)/H_T$ (see Wright 1969 and Nei 1987 for further details). Where there is no differentiation among samples, F_{ST} will be zero. Across all fish species, F_{ST} is about 0.13, indicating that about 13% of the observed allele frequency variation arises from population differentiation.

There is a striking difference in the proportion

Table 9.3 Comparison of allozyme diversity levels among different classes of animals and between different groups of fish. Details are given of number of species, mean number of subpopulations sampled per species, mean number of loci sampled per species, and mean values of H_T (total heterozygosity), H_S (average sample heterozygosity) and F_{ST} (proportion of total genetic diversity attributable to sample differentiation). Standard errors are given. See text for further explanation. Fish data are from Ward et al. (1994); data for other vertebrates are updates of information in Ward et al. (1992). Requirements for inclusion are that 15 or more loci have been examined in 15 or more individuals per sample or subpopulation.

Class	Number of species	Number of subpopulations	Number of loci	H_T	H_S	F_{ST}
Fish	113	6.60 ± 0.46	28.08 ± 0.81	0.062 ± 0.004	0.053 ± 0.003	0.132 ± 0.016
Marine	57	6.40 ± 0.62	29.19 ± 1.22	0.064 ± 0.004	0.059 ± 0.004	0.062 ± 0.011
Anadromous	7	13.14 ± 3.12	27.43 ± 1.86	0.057 ± 0.007	0.052 ± 0.008	0.108 ± 0.044
Freshwater	49	5.90 ± 0.53	26.88 ± 1.18	0.062 ± 0.007	0.046 ± 0.005	0.222 ± 0.031
Amphibia	49	5.53 ± 0.57	22.59 ± 0.75	0.146 ± 0.012	0.097 ± 0.008	0.308 ± 0.033
Birds	28	4.75 ± 0.65	29.21 ± 1.34	0.059 ± 0.006	0.054 ± 0.006	0.078 ± 0.021
Mammals	83	4.82 ± 0.37	27.89 ± 0.85	0.077 ± 0.005	0.057 ± 0.004	0.207 ± 0.023
Reptiles	33	5.58 ± 0.73	23.73 ± 1.36	0.115 ± 0.014	0.086 ± 0.010	0.222 ± 0.036
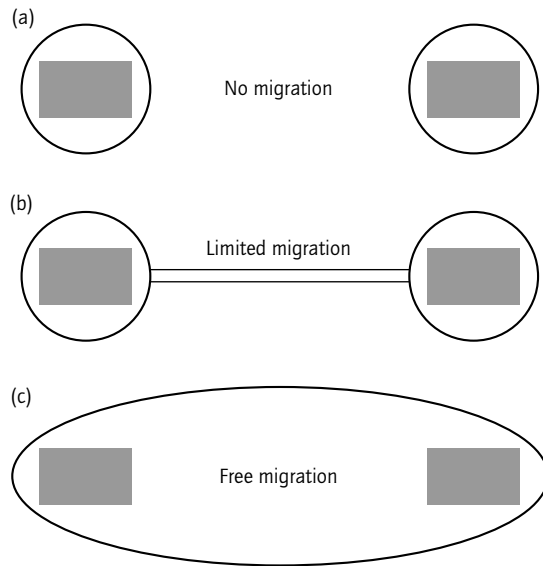
Fig. 9.2 A simplified scheme of three types of migration pattern between two fished areas (denoted by shaded boxes). In (a) interchange is effectively zero. An example would be lake populations of freshwater fish; F_{ST} would be expected to be greater than 0.1. In (b) there is limited migration. An example would be fish populations occupying different tributaries of the same catchment, or marine fish from widely separated areas; F_{ST} would be expected to approximate the 0.01–0.10 zone. In (c) there is panmixia. An example would be fish from a single spawning site dispersing to different fishing grounds, or a widely ranging non-homing migratory species; F_{ST} would not be significantly different from zero. In practice, the size of F_{ST} would depend on the extent of contemporary and historical gene flow.

of genetic variation attributable to sample differences between marine and freshwater species. In marine species, the mean F_{ST} is 0.062, much less than the 0.222 of freshwater species (Table 9.3). In fact, these mean values are inflated by the relatively high values of a few species: the median F_{ST} value for these 57 marine species is only 0.020, one-seventh that of the 49 freshwater species at 0.144 (Waples 1998). Anadromous fish show intermediate levels of differentiation.

These differences in levels of differentiation between populations of marine and freshwater fish

undoubtedly reflect differences in levels of gene flow. Freshwater species occupy lakes or isolated river catchments; gene flow rates between such populations are expected to be low and levels of differentiation are expected to be high. Marine fish occupy habitats with fewer barriers to dispersal, and many have long-lived pelagic larvae that can drift widely in current systems. As a result, gene flow levels among populations are expected to be high. The expected negative correlation between dispersal ability and F_{ST} has been demonstrated for ten marine shorefishes and seven coral-reef fish species by Waples (1987) and Doherty et al. (1995) respectively. However, not all marine larvae disperse over long distances and current eddies may assist larval retention; the recruitment of locally spawned larvae, even of coral-reef fish, can be substantial (Jones et al. 1999; Swearer et al. 1999). This is of particular relevance to the value of marine protected areas as described by Polunin (Chapter 14, Volume 2).

The mean F_{ST} of marine fish is similar to that of birds, while amphibia, which are generally restricted to ponds and lakes for breeding, show even more population differentiation than freshwater fish (Table 9.3). Clearly dispersal ability does have a major role in determining the degree of genetic connectivity between populations.

The data in Table 9.3 are based on allozyme analysis; there are not, as yet, similar F_{ST} summaries using mtDNA or microsatellite data. Freshwater fish show generally higher levels of mtDNA haplotype divergence than marine species (Billington and Hebert 1991), but interpopulation summaries are lacking. Carvalho and Hauser (1998) list F_{ST} values from microsatellite studies of five marine fish species; the mean is 0.017 (range 0.035–0.006), less than the mean value of the marine fish allozyme data but similar to the median. F_{ST} values were tabled for only one freshwater and two anadromous species. These admittedly very limited data indicate that F_{ST} values for microsatellites may well be rather similar to those from allozymes. This should not be surprising, as at equilibrium F_{ST} is approximately equal to $1/(1 + 4N_e m)$ (Wright 1969), where N_e is effective population size and m is migration rate. F_{ST} is then

almost entirely dependent on the absolute numbers of migrants ($N_e m$). However, if mutation rates (u) are high relative to gene flow rates, m may be substituted by ($m + u$) (Wright 1969). In such a situation, increased population differentiation might be detected for loci with high mutation rates, such as microsatellites. Be that as it may, the particular advantages of microsatellites to population analysis are probably in providing high levels of polymorphism even in species with low levels of allozyme polymorphism, so providing enhanced power to detect differentiation, and in providing markers that are more likely to be selectively neutral than allozymes.

The relationship between F_{ST} and numbers of migrants, $N_e m$, is beguilingly simple. However, it is based on an island model of migration and only holds under certain conditions. Some of these conditions are that m has to be much less than 1 and the same for each population, N_e has to be constant both spatially and temporally, alleles must be selectively neutral, and populations must be at equilibrium between migration and drift. Rarely if ever will these conditions be met. For example, populations of fish are constantly expanding and contracting, and sometimes merge or separate. The time required to go halfway to equilibrium is approximately $2m + \frac{1}{2}N_e$ (Crow 1986). Therefore, while small populations approach the new equilibrium quite quickly following a change in state, large populations, which are typical of many marine species, will take a long time. Cases of equilibrium may well be rare. Clearly, $N_e m$ estimates derived from F_{ST} estimates are at best expected to be crude approximations, and frequently may have little basis in reality. They become even less meaningful when the large standard errors attached to F_{ST}, which reflect sampling error from numbers of individuals and numbers of loci, are translated into standard errors attached to $N_e m$. In such a situation, even when all the assumptions of the relationship hold, distinguishing a true $N_e m$ of 10 ($F_{ST} = 0.024$) from a true $N_e m$ of 1000 ($F_{ST} = 0.00024$) can be problematic. These issues are discussed further by Waples (1998) and Bossart and Prowell (1998). Waples (1998) suggests that the best single strategy for distinguishing F_{ST} noise

from signal, a particular problem for marine species showing little differentiation, is to replicate samples over time.

F_{ST} statistics are based on genotype and allele frequencies. With microsatellites, allele size information, determined as the number of repeat units, is also available. Alleles with similar sizes at a locus are considered to be genetically more similar than alleles with disparate sizes, and this size, or genetic relatedness, information along with frequency information can be included in the analytical genetic distance framework. Such an analysis of population subdivision is an R_{ST} analysis (Slatkin 1995; Goodman 1997). However, R_{ST} variances are higher than F_{ST} variances (Slatkin 1995) and R_{ST} may be more sensitive to unequal sample sizes (Ruzzante 1998). In addition, R_{ST} analyses assume that microsatellite mutations occur in a stepwise size fashion, but the validity of this assumption is questionable. R_{ST} and F_{ST} analyses can yield different statistical results (e.g. O'Connell et al. 1998; Shaw et al. 1999). Because of these and other issues, O'Connell and Wright (1997) recommended that analyses of microsatellite variability in fishes be based on conventional F_{ST} statistics.

The above discussion focuses on the use of F_{ST} methods for partitioning genetic variation. Recently, new approaches for studying migration patterns have been proposed that do not assume symmetrical migration rates or equal population sizes. These are often based on maximum likelihood methods and coalescence theory (e.g. Neigel 1997; Beerli 1998; Luikart and England 1999) and are expected to provide improved estimates of population parameters.

9.5.1   *Stock structure analysis*

From a fisheries manager's point of view, a stock is a group of fish that will react independently to exploitation from other such groups and which consequently should be managed independently. In practice, assessments of stock structure are difficult and often contentious. Different types of information may appear to delineate different stocks and may contradict existing management bound-

aries. Stocks may expand or collapse, and the dynamics of stock interactions are rarely if ever understood. However, managers ignore stock structure issues at their peril and must consider such information, even if incomplete, in their stock assessments.

Perhaps the most commonly quoted biological definition of a stock is that of Ihssen et al. (1981): 'a stock is an intraspecific group of randomly mating individuals with temporal and spatial integrity'. The implication is that there is restricted gene flow with other such groups and that there is genetic differentiation between stocks. These issues are considered further in, for example, Carvalho and Hauser (1994). However, marine fish generally show less genetic population differentiation than anadromous species, which in turn show less differentiation than freshwater populations (Table 9.3) (Metcalfe et al., Chapter 8, this volume). Consequently, determining the stock structure of marine species is more challenging than for anadromous or freshwater species. Findings of no significant genetic differentiation between samples of commercial marine fish are quite common (e.g. Ward and Elliott 2001). Such results are of little value to managers, being consistent with models of population structure ranging from complete mixing (panmixia) to 1% or less exchange. Some examples of genetically based fish stock structure analysis follow.

Chum salmon (*Oncorhynchus keta*)

Atlantic and Pacific salmonids have been targeted for population/stock analysis, largely because of their commercial importance and the threatened nature of some stocks and also because of their interesting anadromous life histories. Shaklee et al. (1999) review how genetic data have been used by agencies in the Pacific northwest to manage four species of Pacific salmon; here one of these, the chum salmon, is considered.

Chum salmon have the most extensive natural distribution of Pacific salmonids, ranging from Korea and Japan north to Alaska and south to Oregon. They mature in the North Pacific, forming mixed aggregations before returning to natal rivers to spawn. Determining the stock composition of these frequently fished mixed aggregations is an important management objective. Once genetic stock differences have been described, stock components in mixtures can be quantified using maximum likelihood mixed-stock analysis (MSA; see Shaklee et al. 1999 for references).

Much of the chum salmon MSA is based on a database comprising approximately 20 allozyme loci typed in more than 250 collections from Japan, Russia, Alaska, British Columbia and Washington, with sample sizes generally in the vicinity of 100 per collection (Seeb and Crane 1999a). There is a northern lineage with three genetic subgroups, Japan, Russia and northwestern Alaska, and a southern lineage with three subgroups, Alaskan Peninsula/Kodiak, southeastern Alaska/northern British Columbia/Prince William Sound and southern British Columbia/Washington. A detailed examination of western Alaska and Alaskan Peninsula populations using 40 allozyme loci revealed an overall F_{ST} of 0.061 for this region alone (Seeb and Crane 1999b).

There is also a less comprehensive mtDNA database. This shows that a particular mtDNA haplotype is very common in Japan (~0.80), uncommon in Russia and Alaska (frequencies of 0.13 and 0.07 respectively) and absent from British Columbia and Washington (Park et al. 1993).

About 2000 chum salmon caught incidentally in Alaskan Peninsula sockeye salmon fisheries in 1993 and 1994 were genotyped for allozymes and mtDNA (Seeb and Crane 1999a). The subsequent MSA estimated that most (~60%) were bound for northwestern Alaska streams but stocks from Japan (~15%) and from other Asian, Alaskan, British Columbian and Washington stocks were also harvested (Table 9.4). This information is currently being used in conservation and management decisions.

At present there has been relatively little work with microsatellites in chum salmon. However, eight populations ($n > 50$ per population) from the Yukon River catchment were examined for 24 polymorphic nDNA loci (18 allozymes, one gene intron, five microsatellites) and for mtDNA (Scribner et al. 1998). As expected, the different

Table 9.4 Estimated contributions of Pacific Rim chum salmon from different regions to an Alaskan Peninsula fishery (Seeb and Crane 1999a). Standard deviations in parentheses. Sample sizes from 395 to 399 per collection. Fish were examined for 23 allozyme loci. The 1994 sample 21–25 June was also examined for mitochondrial DNA variation.

Region	1993		1994		
	13–20 June	22–29 June	17–20 June	21–25 June	26–30 June
Japan	0.17 (0.05)	0.15 (0.04)	0.13 (0.04)	0.09 (0.03)	0.16 (0.04)
Russia	0.06 (0.07)	0.07 (0.07)	0.19 (0.07)	0.06 (0.09)	0.15 (0.07)
NW Alaska (summer)	0.62 (0.10)	0.57 (0.10)	0.51 (0.09)	0.72 (0.10)	0.54 (0.08)
Yukon (autumn)	0.00 (0.01)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)
Alaskan Peninsula	0.04 (0.03)	0.13 (0.05)	0.07 (0.05)	0.10 (0.05)	0.05 (0.04)
SE Alaska	0.06 (0.05)	0.05 (0.02)	0.03 (0.01)	0.02 (0.01)	0.04 (0.01)
British Columbia	0.04 (0.02)	0.03 (0.01)	0.04 (0.02)	0.00 (0.01)	0.03 (0.02)
Washington	0.01 (0.01)	0.00 (0.01)	0.02 (0.02)	0.00 (0.01)	0.00 (0.01)
Unknown	0.003	0.000	0.003	0.000	0.005

markers showed different average heterozygosities (haplotype diversity for mtDNA): allozymes 0.250, nDNA 0.592, mtDNA 0.063. Estimates of F_{ST} were however highly concordant across marker classes: allozymes 0.010 ± 0.003, nDNA 0.011 ± 0.004 and mtDNA 0.016. These F_{ST} estimates were significantly greater than zero, and were largely attributable to differences between drainages in the Yukon catchment. The addition of microsatellite data to the existing allozyme and mtDNA database will increase MSA power but will be costly.

Cod (*Gadus morhua*)

The Atlantic cod is a demersal marine fish that in 1997 was the ninth largest single-species fishery, at 1.36 million tonnes (FAO 1999). Despite the importance of the resource and detailed stock assessments, a population collapse caused its commercial extinction off Newfoundland and Labrador in 1992 (Hutchings and Myers 1994). Concern about the North Atlantic cod fisheries has stimulated numerous genetic examinations of population structure (see Shaklee and Bentzen 1998).

The largest allozyme survey (Mork et al. 1985) found very limited differentiation between east and west Atlantic cod ($F_{ST} = 0.014$; see Pogson et al. 1995), which suggested that gene flow was high enough to prevent the formation of genetically differentiated stocks below the scale of ocean basins. Conclusions from mtDNA studies have ranged from a lack of differentiation across the Atlantic (Smith et al. 1989) to heterogeneity and restricted gene flow between east and west (Carr and Marshall 1991; Dahle 1991). Pogson et al. (1995) examined anonymous nDNA markers by RFLP analysis and found significant differentiation among Atlantic samples ($F_{ST} = 0.069$). They suggested that the allozyme homogeneity reflected balancing selection for expressed loci, while the RFLP heterogeneity reflected restricted gene flow of neutral markers. Mork et al. (1985) had suggested effectively the reverse: the homogeneity of most allozymes reflected extensive gene flow, the heterogeneity of a few allozymes reflected selection. Galvin et al. (1995) examined a single minisatellite locus, finding significant allele frequency differences across the Atlantic ($F_{ST} = 0.03$) and significant differences between Newfoundland and Nova Scotia. The overall picture then is of limited but significant genetic differentiation within the North Atlantic, with allozymes showing less differentiation than nDNA markers.

There have also been detailed examinations of the stock structure of particular regions of the

Atlantic, in particular the Norwegian coast. Here interest has focused on 'arctic' cod living in the Barents Sea in the northeastern Arctic and 'coastal' cod inhabiting Norwegian coastal and fjord areas. These cod spawn in the same period and on the same grounds. They differ in allele frequencies for *HbI* (haemoglobin) (Frydenberg et al. 1965; Dahle and Jørstad 1993), for an intron of *SypI* (synaptophysin) (Fevolden and Pogson 1997) and in four microsatellite loci (Dahle 1995). One allozyme locus, *Ldh-3*, showed differentiation, but up to 12 other allozymes (Mork et al. 1985; Mork and Giaever 1999) and ten cDNA clones (Fevolden and Pogson 1995) did not; no mtDNA differentiation was detected (Arnason and Palsson 1996). The *SypI* differentiation was remarkably high (F_{ST} = 0.40), with evidence of selection at it or a linked region (Fevolden and Pogson 1997); interestingly, rather similar levels of *SypI* differentiation were observed between two groups of Icelandic cod (F_{ST} = 0.20; Jónsdóttir et al. 1999). *Ldh-3* and *HbI* might also be subject to selection (Mork and Giaever 1999). It is not easy to reconcile these data into a single satisfying and unambiguous picture of population structure, and at present levels of gene flow among populations in this region remain debatable. For details of the physiological consequences of the different haemoglobin genotypes, see Brix, Chapter 4, this volume.

Another region to have attracted considerable attention is the northwestern Atlantic (Ruzzante et al. 1999). Four to six microsatellite loci were examined in samples of larval cod, inshore and offshore cod, and cod from adjacent banks. Significant fine-scale differentiation has been detected, although F_{ST} levels were very low (generally, over all loci, <0.02, R_{ST} values tended to be a little higher). It was suggested that oceanographic structures, in the form of gyres and currents, and spatiotemporal differences in spawning were barriers to gene flow between neighbouring and even contiguous populations. This evidence of small-scale stock structuring should be considered in management plans aimed at rebuilding these depleted stocks. Counter-intuitively, the single region examined from the eastern Atlantic (Barents Sea) showed little differentiation from these northwestern samples: allele frequencies at only one of six microsatellites were distinguishable (Bentzen et al. 1996). It was suggested that convergent mutations at these highly mutable loci might have erased differentiation more readily detected at less mutable markers such as allozymes and mtDNA, and that therefore microsatellites might be less suitable for broad-scale surveys than allozymes or mtDNA.

One important point to be made from these various analyses is that relying on data from one marker or even one class of marker can lead to erroneous or misleading conclusions. It is clearly desirable to have data from as many markers as possible, yet there is then the possibility of different markers appearing to give conflicting results. Interpretation of likely population structures can become difficult or controversial. More needs to be known about the relative levels of selection and mutation for different classes of marker, and this information is rarely available. Markers that are neutral with respect to selection are desirable. While microsatellites probably fit this requirement, they have some disadvantages such as sometimes being too variable and/or difficult to score unambiguously; furthermore their underlying mutation processes and consequent effects on population differentiation need to be understood better.

Yellowfin tuna (*Thunnus albacares*)

The yellowfin tuna is another valuable fishery, ranking 11th in 1997 with 1.13 million tonnes (FAO 1999). The yellowfin tuna, like other tunas, is a fast-swimming highly migratory pelagic species, whose genetic population structure in the major oceans has been quite extensively studied.

Some genetic diversity parameters are summarized in Table 9.5. Portions of the data permitted a hierarchical analysis of genetic variation, with the overall genetic diversity partitioned into within- and between-ocean components. The within-ocean component almost entirely reflects a within-Pacific component, there being fewer samples from the Atlantic and Indian oceans.

All F_{ST} estimates are low and many are not sta-

Table 9.5 Heterozygosity and F_{ST} estimates for yellowfin tuna.

Oceans	Marker	Het	No. of collections	F_{ST}	F_{SO}	F_{OT}	Reference
P, A	MtDNA (12)	0.85	6	−0.021	−0.015	−0.006	Scoles and Graves (1993)
P, I, A	MtDNA (2)	0.68	9	0.010**	0.012*	−0.002	Ward et al. (1997)
P, I, A	Allozyme (4)	0.36	8	0.025**	0.027**	−0.002	Ward et al. (1997)
P	MtDNA (12)	0.85	5	−0.015			Scoles and Graves (1993)
P	MtDNA (2)	0.68	6	0.012*			Ward et al. (1997), Grewe and Ward (unpublished data)
P	Allozyme (4)	0.36	6	0.027**			Ward et al. (1997)
P	Microsatellites (6)	0.78	5–8	0.002*			Grave and Ward (unpublished data)
I	MtDNA (2)	0.71	2	0.009			Ward et al. (1997)

P, Pacific Ocean; A, Atlantic Ocean; I, Indian Ocean. Marker: mtDNA (whole genome assayed by RFLP methods, with the given number of restriction enzymes), allozyme and microsatellites (number of polymorphic loci examined). Het, overall heterozygosity (genetic diversity for mtDNA). F_{ST}, proportion of total genetic variation attributable to sample differences; F_{SO}, proportion of within-ocean genetic variation attributable to sample differences; F_{OT}, proportion of total genetic variation attributable to ocean differences. The F_{ST} parameter for the single-ocean studies is analogous to the F_{SO} parameter for the multiple-ocean studies. F estimates are from Hauser and Ward (1998) and used the AMOVA package (Excoffier et al. 1992). Significance of F parameters: *, $P < 0.05$; **, $P < 0.01$.

tistically significant (Table 9.5). The maximum F_{ST} value for mtDNA was a barely significant 0.012, and this related to differentiation within the Pacific Ocean; there was no detectable differentiation between oceans. The maximum F_{ST} value over the four polymorphic allozymes examined was 0.027; again this was within the Pacific Ocean and again there was no detectable differentiation between oceans. In fact, this allozyme differentiation reflects differentiation within the Pacific Ocean of only one (*Gpi-A*) of four polymorphic loci, with eastern samples being separable from western-central samples (Ward et al. 1997). So far microsatellite variation has only been examined in the Pacific Ocean, where a preliminary data examination shows a very low F_{ST} of about 0.002.

The finding of no differentiation for either mtDNA or allozymes between oceans suggests either that there is significant gene flow between the Atlantic and Indo-Pacific oceans, and yellowfin tuna are indeed found around the Cape of Good Hope, or that the sampling regime has failed to detect the existence of presumably low amounts of interoceanic differentiation.

Within the Pacific Ocean, extensive mtDNA (Scoles and Graves 1993; Ward et al. 1997), allozyme (Ward et al. 1997) and microsatellite (Ward and Grewe, unpublished data) surveys have shown very little differentiation for any marker other than the allozyme *Gpi-A*. The F_{ST} value for this locus is about 0.10; other markers are 0.01 or less. Perhaps the most likely interpretation of these data is that the *Gpi-A* differentiation within the Pacific reflects selection. The low but just statistically significant differentiation of mtDNA and microsatellites suggests that there might be some weak genetic structuring of the Pacific Ocean yellowfin population but that, in general, gene flow is preventing any strong signals.

It should be noted that, contrary to yellowfin, there is striking mtDNA differentiation between Pacific and Atlantic populations of albacore (*Thunnus alalunga*) and bigeye (*Thunnus obesus*) tunas (Chow and Ushiama 1995; Alvarado Bremer et al. 1998). Their interocean F_{ST} values are about 0.10 and 0.20 respectively (see Hauser and Ward 1998). Extrapolation of population structure from one species to another, even when they have similar ecologies, ranges and life-history attributes, is therefore fraught with danger (Graves 1998).

Furthermore, for the bigeye tuna, analyses of seven microsatellite loci and one nDNA locus (a creatine kinase intron) have shown very little Atlantic–Indo-Pacific differentiation (R.D. Ward, personal observation), although so far only about 100 specimens have been examined. Yet again, different marker classes appear to reveal different patterns of population heterogeneity. Consistent differences between nDNA and mtDNA patterns might reflect the greater sensitivity of mtDNA variants to bottleneck effects or sex differences in dispersal.

9.5.2 Effects of fishing on genetic diversity

Genetic diversity is a rich and irreplaceable part of our heritage. The loss of genetic diversity is highly undesirable, whether the loss is in the form of species extinction or of intraspecific variability. Can fishing itself lead to the loss of genetic variation? The answer must be yes, since fishing reduces population size from pre-fishing levels and some variation will therefore be lost by genetic drift (see also Reynolds et al., Chapter 15, Volume 2).

In fact, heterozygosity is lost relatively slowly. The expected proportion of the original heterozygosity remaining after a bottleneck of size N for one generation is $1 - \frac{1}{2}N$. A single male and female will thus retain 75% of original heterozygosity, although the loss of heterozygosity compounds with successive generations of size N. A short-term bottleneck will have much less drastic effects than a long-term bottleneck. Allele loss, however, will be more striking. Regardless of how many alleles existed at a locus in an ancestral population, a single male and female cannot retain more than four alleles. Rare alleles are likely to be rapidly lost in a bottleneck.

Loss of diversity is commonly observed in hatchery fish and shellfish; it is an expected consequence of genetic drift in small numbers of broodstock. Significant losses arising from fishing pressures will be more noticeable in populations that are already relatively small before fishing; freshwater fish could be particularly vulnerable.

Some weak salmonid subpopulations in a mixed ocean fishery could drop to small N_e values, where N_e is the biologically effective population size. Fortunately, most wild fisheries are of marine species where populations are generally very large and where there is appreciable gene flow among populations. In such a situation, fishing is unlikely to cause such a massive decrease in population size that an experimentally detectable amount of variability will be lost by drift, at least given sample sizes of the order of 100. A fishery that did reach low population levels would likely become uneconomic to exploit, although bycatch harvesting could continue as other species become targeted. The major goal of fisheries management is to maintain populations at levels permitting sustainable exploitation. However, it would be erroneous to consider marine species as 'immune' to genetic depletion (see Ryman et al. 1995 for a full discussion), especially if the genetically effective population size of some species is much less than the apparent size (Hedgecock 1994).

There was some early evidence of a decrease in allozyme heterozygosity concomitant with fishing pressure in the large deepwater orange roughy (*Hoplostethus atlanticus*) fisheries off New Zealand. This was not attributed to a population bottleneck but to fishing removing larger and putatively more heterozygous fish (Smith et al. 1991). However, there is no clear relationship between size and heterozygosity in orange roughy (Ward and Elliott 1993), and studies over a longer time period found no correlation between fishing pressure and genetic heterozygosity (Smith and Benson 1997). There was no detectable change in the allozyme heterozygosity of Hawaiian populations of the spiny lobster (*Panulirus marginatus*) either before or after expansion of the fishery (L.W. Seeb et al. 1990).

Loss of mtDNA diversity has been observed for the New Zealand endemic species Hector's dolphin (*Cephalorhynchus hectori*) (Pichler and Baker 2000). A PCR-sequencing protocol was used to compare the mtDNA of museum and contemporary specimens. The North Island population over the last 20 years has declined from three mtDNA lineages (diversity, $h = 0.41$) to one ($h = 0$),

and the east coast South Island population from nine lineages ($h = 0.65$) to five ($h = 0.35$). Note that values of h can in principle range from 0, where all individuals are identical, to 1, where all individuals are different. It was suggested that this loss of diversity resulted from a population decline caused by dolphin entanglement in gill-nets, a loss exacerbated by very low gene-flow rates among populations. The mtDNA F_{ST} of four populations was high at 0.47, implying little population mixing). Mitochondrial DNA diversity is especially sensitive to drift, as a single male and female mating will transmit only one mtDNA haplotype, and the small fragmented populations of this species make it particularly vulnerable to genetic loss.

9.5.3   Genetic effects of stocking

There are two major classes of stocking programmes for fish:

1 those where exotic species are introduced to areas where they have never naturally existed;
2 those designed to enhance pre-existing fisheries. The latter may be enacted to replace a locally extinct stock, to rebuild a collapsed stock or to augment a natural population for recreational fishing. While stocking programmes may have major benefits, they may also have very significant detrimental outcomes (see Cowx, Chapter 17, Volume 2). Introduction of exotic species can lead to the elimination of native species, hybridization with native species, habitat alteration and the spread of disease. Stock enhancement programmes can introduce disease and can deleteriously affect the gene pool of native fish. Cowx (1998) provides a recent collection of papers on fish stocking.

Introductions of exotic species to habitats occupied by a closely related species can lead to hybridization and introgression, problems readily monitored by species-diagnostic loci. In Arizona, the gene pool of the Apache trout (*Oncorhynchus apache*) has been threatened by hybridizations with introduced non-native cutthroat *(O. clarki)* and rainbow (*O. mykiss*) trout (Carmichael et al. 1993). All wild populations of the leon springs pupfish (*Cyprinodon bovinus*) have been introgressed by introduced sheepshead minnow (*C. variegatus*);

a single captive population appears free of foreign genes (Echelle and Echelle 1997). Introduced species may outcompete native species to the point that inbreeding becomes a problem in the native species – an indirect genetic effect.

Stock enhancement programmes do not introduce exotic species but can nevertheless have unintended deleterious effects. Such programmes may reintroduce strains from the target area or introduce strains from another part of the species' range. These strains are very likely to hybridize and introgress with native fish. Again, the fate of introduced fish can be monitored if they carry unique strain-specific markers. Allozyme studies have confirmed introgression, for example in European brown trout (*Salmo trutta*) restocking programmes. In Spain, local stock heterogeneity is being eroded by introductions of hatchery-reared fish (Machordom et al. 1999), and in Switzerland introduced trout of Atlantic basin origin are replacing native Adriatic strains *S. trutta fario* and *S. trutta marmoratus* (Largiader and Scholl 1995). Clearly, where possible, enhancement should be of local rather than exotic strains. Even then, the introduced strains are likely to be of hatchery origin and therefore will have undergone some change in genetic make-up with respect to ancestral populations.

One undesirable consequence of such hybridization is that locally coadapted gene complexes, which will be a particular genetic make-up favoured by selection in that location, can break down, reducing fitness. Such outbreeding depression has been recorded for pink salmon (*Oncorhynchus gorbuscha*) (Gharrett and Smoker 1991). Hatchery-bred rainbow trout, marked by a rare allozyme variant, had a reproductive success only 28% that of wild trout, but so outnumbered native fish that 62% of smolts were offspring of naturally spawning hatchery trout (Chilcote et al. 1986). There is 'compelling evidence' that hatchery production of at least three species of Pacific salmonids lowers fitness, and that when such fish hybridize with wild fish, the productivity and viability of the naturally spawning populations declines substantially (Reisenbichler and Rubin 1999).

There may also be indirect genetic effects of enhancement programmes. One example concerns introductions of Atlantic salmon (*Salmo salar*) genetically resistant to but carrying an ectoparasite; the recipient population was susceptible, causing heavy mortality of native fish (Bakke 1991).

A particular threat to the genetic integrity and viability of wild fish populations may come from the deliberate or accidental release of genetically engineered or transgenic fish (Reichhardt 2000). Such fish are likely to be engineered for higher growth rate by elevating growth hormone (GH) levels. The effects of such fish on native populations remain unknown. They are often assumed to have reduced viability, but GH-enhanced transgenic coho salmon (*Oncorhynchus kisutch*) showed a marked competitive feeding advantage over non-transgenic fish (Devlin et al. 1999). Thus, depending of course on other fitness-related traits, escaped GH transgenic fish may be able to compete successfully in the wild with native non-transgenic fish. Even if the transgene does lower viability, modelling studies (Muir and Howard 1999) have shown that it can still spread if it simultaneously increases male mating success, for example by yielding faster-growing larger males. This can, in principle, lead to local extinction. It seems that in order to minimize the genetic effects of escapees on local populations, commercial producers of transgenic fish will have to guarantee that the transgenic product is sterile. This might be achievable through the production of triploid fish or by inclusion of a transgene for repressible sterility (Grewe et al. submitted). Containment facilities would still be advisable; the release of large numbers of voraciously feeding, rapidly growing, GH-enhanced fish could seriously disrupt the functioning of natural ecosystems, even if the fish were sterile.

9.5.4   Conservation genetics

The desirability of retaining or conserving genetic diversity is now widely accepted. Once lost, diversity cannot be restored. Unfortunately, we often have little knowledge of the extent of diversity within a species or how this diversity is partitioned among populations. Without this information, it is not possible to assess the effectiveness or appropriateness of conservation measures. Some quantification of the extent of genetic population structuring of threatened or vulnerable species is therefore desirable. However, if this structuring is extensive, as is frequently the case for freshwater and anadromous species but less so for marine species (Ward et al. 1994), it may not be feasible to enact conservation measures to protect all components. Pacific salmonids, for example, are separated into numerous genetically distinct populations through their strong homing behaviour. Allendorf et al. (1997) consider that more than 300 native stocks of these salmonids are at risk in the Pacific northwest and suggest how they may be prioritized for conservation actions using ranks based on the genetic and ecological consequences of extinction. Such actions might include habitat protection, reduction in harvesting rate, stock enhancement using strains from the stock to be protected or, if that is not possible, the most closely related population, or translocation to a new habitat. Some genetic effects associated with the last two issues have already been considered. Another concern is the need to maintain genetic diversity levels as high as possible in any translocated population. The minimum effective population size of a hatchery or transplanted stock should be, whenever possible, around 50–100 animals. A high population size and diversity permits some measure of adaptive evolution and reduces the deleterious effects of inbreeding.

Ryman et al. (1995) review the many threats to genetic diversity in fish and suggest three responses to these threats: (i) to ensure that those involved in operations such as wild harvesting, aquaculture and ocean ranching are aware of possible incompatibilities with conservation objectives; (ii) to require a risk assessment before any potentially threatening activity commences; and (iii) to accept that whoever proposes a threatening activity is responsible for providing the burden of proof of the likely impact of that action. Further aspects of conservation are discussed by Reynolds et al. (Chapter 15, Volume 2).

9.6   GENETICS OF SEX DETERMINATION IN FISH

Reproductive mechanisms in fish are highly variable (reviewed by Devlin and Nagahama 2002). While most reproduce sexually, some are asexual. Some of the asexual species consist of all-female gynogens, whereby matings with a male of a related species are necessary to initiate embryogenesis but the male does not contribute genetic material. Examples are the gynogenetic *Poecilia formosa* (sailfin molly), whose embryogenesis is initiated by sperm from *Poecilia latipinna* in mixed-species shoals (Schlupp and Ryan 1996), and gynogenetic minnows of the *Phoxinus eos-neogaeus* complex. In the latter, examinations of DNA variability have revealed only one clone or genotype in more than 400 gynogenetic fish sampled (Elder and Schlosser 1995). Another type of asexual reproduction is hybridogenesis. In *Poeciliopsis*, the all-female hybridogenetic *P. monacha-lucida* biotype arose as an interspecific hybrid of *P. monacha* and *P. lucida*. Subsequent maintenance of this biotype relies on matings with males of *P. lucida*, but the *lucida* genome is discarded during oogenesis (Schultz 1969; Vrijenhoek 1994).

Among sexual fish species, there is a wide range of sex-determining systems, including both genetic and environmental mechanisms. Genetic mechanisms in fish are varied, with Tave (1993) listing nine types. Fifteen fish species had the XX/XY chromosome type with homogametic females and heterogametic males; five had the ZZ/ZW type with homogametic males and heterogametic females; eight had other sex chromosome systems; and two had autosomal sex determination. The XX/XY system is found in many aquacultured species, including channel catfish, salmonids and carp. Often the sex chromosomes are not morphologically differentiated and cannot be identified by chromosome staining techniques; in such cases the system has to be inferred from sex-reversal or other genome manipulations. For example, a ZZ/ZW mechanism has been shown in *Leporinus* and *Clarias* by direct chromosome staining (Pandey and Lakra 1997; Molina

et al. 1998) and inferred in *Acipenser* and *Rhodeus* by ploidy and gynogenesis manipulations (Kawamura 1998; Van Eenennaam et al. 1999). The lake trout (*Salvelinus namaycush*) is one of the few salmonids with morphologically differentiated sex chromosomes, and the sex-determining region appears to lie on the short arm of the Y chromosome (Reed et al. 1995). Given the difficulty of distinguishing sex chromosomes in most salmonids, and the importance of sex manipulations in aquaculture production, there have been considerable efforts put into isolating salmonid Y-specific probes. These are now available for five different *Oncorhynchus* species (Devlin et al. 1994; Donaldson and Devlin 1996; Nakayama et al. 1999), although not yet for Atlantic salmon.

Environmental sex determination, principally through temperature, has been suggested for a range of fish from lampreys (Beamish 1993) to eels (Krueger and Oliveira 1999) and atherinids (Strussmann et al. 1997). In the cichlid genus *Apistogramma*, pH as well as temperature is a significant determinant of sex in some species (Romer and Beisenherz 1996). There is evidence that environmental factors often overlay or modify the outcomes of a genetic switch (e.g. Conover et al. 1992; Strussmann et al. 1997; Abucay et al. 1999). Finally, some fish are protandrous hermaphrodites, with sex changing from male to female with age (e.g. sea bass or barramundi, *Lates calcarifer*; Guiguen et al. 1993), while some are protogynous, with sex changing from female to male (e.g. bluehead wrasse, *Thalassoma bifasciatum*; Kramer and Imbriano 1997).

9.7   CONCLUSIONS

It should be clear from the discussion in this chapter that genetic analyses have a great deal to offer in the study of fish populations. The range of tools is ever-expanding as new ways to harness the power of PCR analysis are brought on-line. These different tools are suited to different problems, and I have tried to outline both their benefits and limitations. The focus has been on the uses of genetics in fish identification and population structure analy-

sis, but molecular genetic studies have also made numerous contributions to other areas such as systematics and aquaculture.

Genetic identification of unknown or disputed samples is usually unambiguous and simple; protein or mtDNA-based tests are very suitable. The analysis of population structure is far more demanding. Interpretation of frequently large and complex datasets can be difficult, and estimates of gene-flow levels are at best likely to be only crude approximations to true values. Increasing the number of markers in a study will increase resolving power, but the attributes of the various markers need to be carefully considered in reaching any conclusion. These include mode of inheritance, mutation rate, degree of selective neutrality and likelihood of scoring errors. Ideally, selectively neutral nDNA and mtDNA markers would be jointly deployed, in sample sizes of 100 or more.

Genetic analysis is of course not the only option for examining fish population structure. The many other tools that can be applied include examination of life-history traits and morphometric and meristic variation, tagging returns (Metcalfe et al., Chapter 8, this volume), parasite loads and microchemical variation of hard parts. The various genetic and non-genetic tools all have their attendant advantages and disadvantages but all provide valuable and complementary information and every type of available information should be considered when drawing up models of population structure. Physical data, such as bathymetry and direction and strength of eddies and currents, should also be factored into likely population models. Such a coordinated multidisciplinary approach is much to be encouraged, albeit challenging, but may be too resource-demanding for studies of any other than the major fisheries.

Finally, genetic diversity once lost from a species can never be regained. Careful husbandry of our genetic resources requires the continued deployment of genetic analyses for cataloguing, monitoring and conservation.

ACKNOWLEDGEMENTS

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10 Behavioural Ecology of Reproduction in Fish

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10.1 GENERAL INTRODUCTION

Fish exhibit an enormous diversity of reproductive behaviour. Indeed, this diversity far exceeds that found in birds, mammals, reptiles or amphibians. For example, forms of parental care range from none at all in the majority of fish species, to live-bearing, mouth brooding or biparental guarding of free-swimming young. Courtship behaviour is also diverse, with either males or females being the dominant competitor when attracting the opposite sex. Social behaviour also varies greatly, from extended monogamy to promiscuity, from co-operative breeding to solitary nesting, from group spawning to pair spawning. Finally, fish also exhibit at least five major forms of hermaphroditism, including self-fertilization, which is unique among vertebrates.

In this chapter we attempt to make sense of this diversity in reproductive behaviour by using general concepts from the field of behavioural ecology. This approach focuses on the individual, examining costs and benefits resulting from interactions with other individuals and the environment in order to make inferences about evolution. First, we give a brief theoretical background to the understanding of breeding systems. Then we use this to explain the diversity of parental care and sexual selection in fishes. The latter emphasizes differences between the sexes in courtship roles, competitiveness, mate choice and numbers of mates. This leads to the last section on links between breeding behaviour and responses of populations to human exploitation. Our review is mainly restricted to teleost fishes and is biased towards species with parental care, for the simple reason that most of the present-day knowledge on these issues comes from studies of such species. Our chapter complements many of the others in this volume, especially the review of life histories by Hutchings (Chapter 7, this volume), which covers alternative life histories stemming from reproductive conflict.

10.2 INTRODUCTION TO BREEDING SYSTEMS

The term 'breeding system' (or mating system) is used when describing an animal's mating behaviour and parental care (Emlen and Oring 1977; Reynolds 1996). It applies to groups of animals, including populations or species. Breeding system classification focuses on variation in various kinds of behaviour. These typically include:
1 form and duration of parental care by each sex;
2 form and duration of any pair bonds;
3 number of mates (both 'genetic' and 'social');
4 forms of courtship, coercion and competition (including competition among sperm from different males);
5 breeding resources defended and offered;
6 extent of mate choice (including choice among sperm from different males).

10.2.1 A general framework

The fundamental difference between the sexes is the size of the gametes. Females produce few, large eggs, whereas males produce a vast number of tiny sperm. Sperm is a rapidly renewable resource, and males of most species could presumably fertilize hundreds of females over their lifetime if given the chance. Females, in contrast, must devote considerable time and energy to each ovum before fertilization. In some species, the basic difference between the sexes is further increased through parental care. Female mammals, for example, usually devote more of their time and energy to care of offspring than males do. As a result, the potential rate of reproduction is much lower in females than males. The potential reproductive rate is defined as the number of independent offspring that could be produced per unit time by members of one sex if given unlimited access to members of the opposite sex (reviewed in Kvarnemo and Ahnesjö 1996). The more females a male can fertilize, the higher his reproductive success will be. In females, on the other hand, reproductive success is normally related to access to resources and not to the number of mating partners. Thus, the lifetime reproductive success of males is limited by access to females, while females are not limited by access to males. This difference between the sexes leads to an imbalance in the number of individuals of each sex that are ready to mate, termed the 'operational sex ratio' (Emlen and Oring 1977). Typically, the operational sex ratio is male-biased because males are recycling into the mating pool faster than females. Thus, there is an excess of males and a shortage of females willing to mate at any given time. This has profound implications for sexual selection. It would pay males to compete for and court as many females as possible, whereas females can afford to be more selective of their
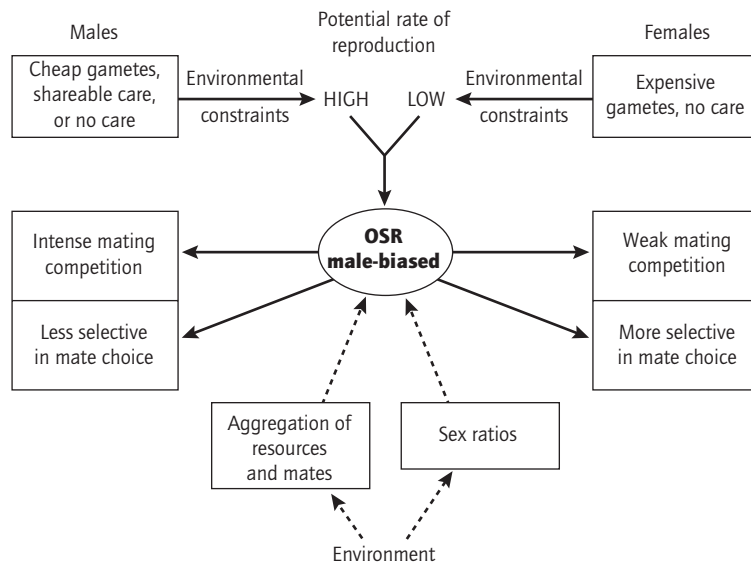
Fig. 10.1 Framework for understanding breeding systems, based on a 'typical' fish where females do not provide parental care. The upper boxes under each sex indicate time or energy devoted to offspring (gametic development and parental care). Differences between the sexes cause a disparity in potential reproductive rates, which in turn leads to a male-biased operational sex ratio (OSR). The operational sex ratio affects mating competition and choosiness (lower boxes). Thus, sexual selection acts more strongly on males. The environment can affect potential reproductive rates and operational sex ratios. (Source: after Reynolds 1996; reproduced by permission of Elsevier Science.)

mates. A schematic view of this is shown in Fig. 10.1, which exemplifies the breeding system of a typical fish. In fish, males are most often the sex providing parental care (see Section 10.3). However, they can often care for several clutches simultaneously, retaining a higher potential reproductive rate than females. Thus, despite providing parental care, males still have much to gain from competing with each other for mates and courting females.

10.2.2   *Role of the environment*

The environment can influence mating systems and sexual selection in several ways. It may, for example, influence the costs and benefits of time and energy devoted to different activities. Many studies have shown that predation pressure can reduce the intensity of sexual selection, either by relaxing mate choice (e.g. Forsgren 1992) or by increasing the costs of attracting a mate. This shifts the optima for ornamental traits and courtship towards less conspicuous forms, exemplified by studies of Trinidadian guppies, *Poecilia reticulata* (reviewed in Endler 1995; Houde 1997). Predation pressure may also play a key role in the provision of parental care. It may increase the benefits to the offspring of receiving parental care, as well as the costs to the parents of providing it. In the biparental convict cichlid, *Cichlasoma nigrofasciatum*, males sometimes desert their broods and this happens most often at sites with the lowest brood predation pressure (Wisenden 1994). Environmental factors can also affect the operational sex ratio, which in turn can have strong effects on mating competition and mate choice. For example, differential mortality rates between the sexes can bias the operational sex ratio towards the sex least prone to predation. Males of the viviparous Amarillo fish, *Girardinichthys multiradiatus*, are more often caught by snakes than are females, biasing the sex ratio towards females (Macías Garcia et al. 1998). The operational sex ratio can also be affected by temperature through differential effects on the potential reproductive rates of the two sexes (Kvarnemo 1994; Ahnesjö 1995). Egg-guarding male sand gobies, *Pomatoschistus minutus*, have a much faster potential reproductive rate in warm water when egg development is faster, while the female potential reproductive rate is not so strongly affected by temperature (Kvarnemo 1994). Thus, warmer water 'causes' more fighting in male gobies (Kvarnemo 1998).

Another important component of the environment is the spatial and temporal distribution of resources critical for breeding. If these are economically defendable, there are greater opportunities for polygyny (Emlen and Oring 1977). For example, if large numbers of female bluehead wrasse, *Thalassoma bifasciatum*, arrive at a spawning site on a coral reef, the dominant male is unable to defend all females and additional males participate in spawnings (Warner and Hoffman 1980). Likewise, in the Japanese medaka, *Oryzias latipes*, the highest variation in male mating success was found when females arrived asynchronously (Grant et al. 1995). Similarly, if resources such as nest sites are spatially aggregated and therefore can be defended by a single male, this male can attract more mates than if the nesting sites were widely dispersed and hence impossible to monopolize. This has been shown in experiments with the sand goby, a species which exhibits male parental care in defended nest sites. Polygyny and the potential for sexual selection were highest when nest sites were large and females arrived asynchronously (Lindström and Seppä 1996). In the same species, nest abundance has implications for the mode of sexual selection. In areas with few nest sites, male competition is strong and the potential for female choice is low, while the opposite is true in areas with a high availability of nest sites (Forsgren et al. 1996a). In a field study of the slimy sculpin, *Cottus cognatus*, Mousseau and Collins (1987) found that the abundance of nest substrates in lakes seemed to affect whether a population was monogamous (many sites) or polygynous (few sites). The importance of 'environmental constraints' is indicated in two places in Fig. 10.1; environmental factors may affect each sex's potential rate of reproduction or may directly affect the operational sex ratio. This can have profound implications for sexual selection.

10.3   PARENTAL CARE

Parental care can be defined as any behaviour that increases the fitness, defined in terms of development and survival, of an animal's offspring (see Clutton-Brock 1991). This should be in the interest of the parent but, as we shall see, engaging in parental care may not be as straightforward as one might think.

10.3.1   *Diversity of care in fish*

Fish vary substantially in their parental care. A complete lack of care is most common, followed by paternal care, biparental care and maternal care (Blumer 1982). Parental care occurs in about 20% of all teleost families and is widely distributed phylogenetically. However, it is more common among freshwater than marine families (Blumer 1982). Among fish with parental care, male care is most common, occurring in two-thirds of the families (Gross and Shine 1981). The forms of care provided by fish are also diverse, from defence of eggs to more advanced forms such as guarding and feeding of the larvae after hatching. The most common form of parental care is brooding the eggs on a substratum. In this case, care may consist of actions directed at the eggs, such as fanning them to provide oxygen, and defence of the eggs against predators. Other types of care are mouth brooding and carrying the eggs, externally or internally. Comprehensive overviews of parental care in fish have been provided by Blumer (1982) and Gross and Sargent (1985).

10.3.2   *Costs of care and filial cannibalism*

Parental care is often costly in terms of reducing the parent's residual reproductive value, defined as its expected future reproductive success. These fitness costs are difficult to measure (Clutton-Brock 1991) but can sometimes be approximated by measurements of time and energy devoted to care. In fish, there are a number of ways in which parental care can be costly to the parent (reviewed in Smith and Wootton 1995; Sargent 1997). Care-giving may increase predation risk due to conspicuousness or reduced agility. In a pipefish, *Nerophis ophidion*, where males brood their young on their body, parental males were much more likely to be preyed upon than non-caring males (Svensson 1988). Caring can also be energetically costly or reduce feeding, leading to deterioration in body condition and thereby increasing the risk of death through disease or starvation. In the river bullhead, *Cottus gobio*, body condition of parental males declined over the breeding season and this may have accounted for a peak in male mortality observed during the second part of the breeding season (Marconato et al. 1993). Caring may also be costly by extending the time to next breeding or by reducing future fecundity. In an experiment with Galilee St Peter's fish, *Sarotherodon galilaeus*, a biparental mouth brooder, parental care has been shown to decrease growth and increase the number of days until the next reproductive cycle in both males and females (Balshine-Earn 1995). In addition, care also decreased subsequent fecundity in females. Care can also be costly to males in terms of lost mating opportunities (see Section 10.3.3).

Parents may sometimes consume their progeny, which is termed 'filial cannibalism' (Rohwer 1978) and is especially prevalent in fish (Dominey and Blumer 1984). Consumption may include the whole clutch or only part of it. Filial cannibalism in fish with parental care is now viewed as an adaptive behaviour that maximizes the parent's lifetime reproductive success, instead of as an abnormal behaviour (FitzGerald 1992). Caring males may compensate for the costs of care by cannibalizing part of their progeny in order to remain in sufficient physical condition to complete care of the current brood (Marconato et al. 1993) or to be able to care for future broods (Rohwer 1978). Guardian males may also eat their entire clutches, especially when these are smaller than usual and the value of the clutch is lower than the costs of care (Petersen and Marchetti 1989). In a feeding experiment with the common goby, *Pomatoschistus microps*, which exhibits paternal care, whole clutch cannibalism was associated with unusually

small clutches, while partial clutch cannibalism was associated with a low feeding regime (Kvarnemo et al. 1998). Cannibalism by guarding males may generate conflicts of interests between the sexes, and adds another factor that females should take into account when choosing a mate.

10.3.3   Who cares?

Which sex should provide care? This depends on sex-specific costs and benefits of care. If parental care can be provided by a single parent alone, both sexes would gain the same benefits from being the sole care-giver, provided that the male has not been cuckolded. However, the costs of providing care may differ between the sexes, and this difference may explain why male care is common in fish (Sargent and Gross 1993). The costs of care are related to the options available to each sex if it did not engage in parental care. In fish, female fecundity is often closely related to body size (Hutchings, Chapter 7, this volume). Thus, it is important for females to allocate resources to growth. In addition, females have to produce costly eggs. There-

fore, the cost for a female of providing care may be considerable in terms of lowered future fecundity. In males, reproductive success is usually not equally strongly related to size. Thus, males would not pay such a high 'fecundity cost' as females by providing care (Sargent and Gross 1993). If, however, males lose opportunities for additional matings by providing care, this could be very costly for them. However, in substrate-spawning fish with egg guarding, males can usually care for clutches from several females simultaneously. Thus, males are able to court and attract multiple mates and provide care at the same time. Important in this context is that guarding of eggs is often 'shareable', meaning that it is no more energetically demanding to defend a nest containing thousands of eggs than a nest containing only a few eggs. In other taxa like mammals and birds, the investment in offspring is substantial and less shareable among offspring. This may explain why uniparental male care is much more common in fish than in birds and mammals. Furthermore, females in many species of fish prefer nests containing other females' eggs (reviewed by Reynolds and Jones 1999).
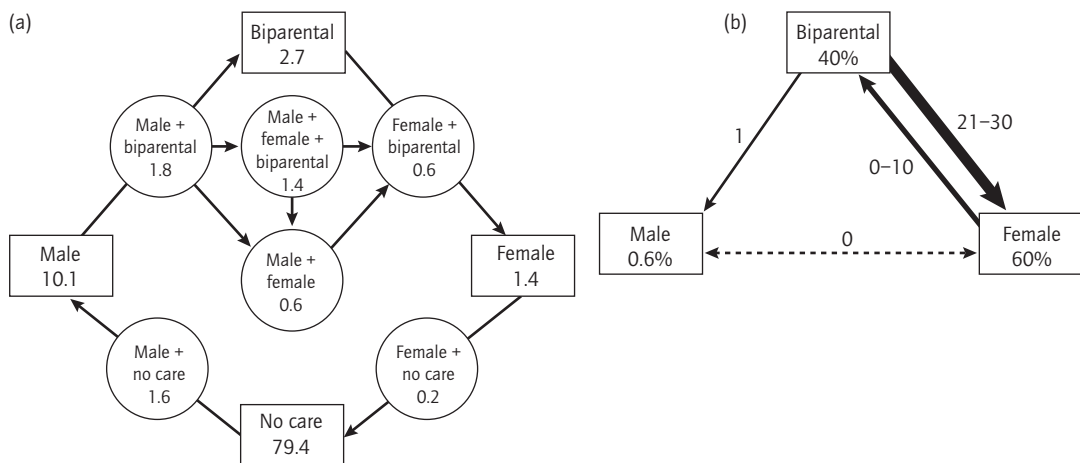
Fig. 10.2   (a) Hypothetical evolutionary transitions (arrows) between parental care states in teleost fishes. Numbers in boxes show the percentages of the 422 families surveyed by Blumer (1982) that have various forms of care. Circles show families that exhibit more than one form of care. (Source: after Gross and Sargent 1985; reproduced by permission.) (b) Evolutionary transitions between biparental care and female care among Cichlidae, based on 182 genera. Figures show number of transitions and arrow widths are proportional to this number. (Source: after Goodwin et al. 1998.)

Evolutionary changes in the amount of parental care provided by each sex have been reviewed for fish and compared with other vertebrates by Reynolds et al. (2002). Figure 10.2a shows hypothesized directions of transitions for fish based on a review by Gross and Sargent (1985). It has been suggested that male care has most often evolved from no care. Then females may, in some cases, be selected to join males due to selective advantages of biparental care. Biparental care might be unstable if males are then selected to desert their mates in search of new mating opportunities, which may be the case in mouth brooders where multiple clutches cannot be cared for simultaneously. The benefits and costs associated with this decision have been explored in a game-theory framework (Maynard Smith 1977), including a model developed specifically for cichlid fishes (Balshine-Earn and Earn 1997). Indeed, studies of fish have provided the first experimental evidence demonstrating that males do desert broods in response to the availability of new mating opportunities (Keenleyside 1983; Balshine-Earn and Earn 1998). Female care, too, may be unstable through evolutionary time if the benefits are outweighed by the costs of uniparental female care, expressed as decreased survival and fecundity. This leads to the interesting proposition that parental care may be a cyclical phenomenon, at least in species where the costs of care are substantial and roughly equal for both sexes (Gross and Sargent 1985). The hypothesis that maternal care follows biparental care was supported by Goodwin et al. (1998), who examined evolutionary transitions in cichlid fishes (Fig. 10.2b). In cichlids biparental care seems to be the ancestral state, and female care is the most common form of uniparental care.

10.4   SEXUAL SELECTION

Darwin (1871) developed the theory of sexual selection to account for the evolution of secondary sexual characters. He was concerned about how traits such as the train of the peacock, *Pavo cristatus*, could evolve, as they seemed to confer no survival advantage. The answer, Darwin suggested,

lies in differences in reproductive success caused by competition over mates. This may concern either number or quality of mates. Individuals that carry traits that increase their reproductive success will successfully spread their genes to the next generation. Members of one sex, usually the males, may compete with each other by contests or other forms of rivalry. This competition may lead to the evolution of large body size, weapons or status badges. Sexual selection may also take place if members of one sex, usually the females, mate preferentially with certain individuals of the opposite sex. Mate choice may lead to the evolution of ornamental traits in the other sex, such as gaudy coloration, long fins and complex courtship displays.

Darwin's ideas about female mate choice met strong resistance (reviewed by Cronin 1991), and it took almost 100 years until these theories were accepted. During the last decades it has been shown that mate choice is indeed common in many species belonging to different taxa and that it constitutes a strong selective force (reviewed by Andersson 1994). Fish have featured prominently in this research. While sexual selection has now been demonstrated conclusively, many questions remain unanswered. Researchers are still asking what specific benefits are gained through mate choice, how these are related to ornamentation and courtship, how genetic variation in secondary sexual traits can be maintained, and how conflicts between the sexes over matings have shaped behaviour (Andersson 1994).

10.4.1   *Competition for mates*

Competition may occur over mates, spawning sites or nests. Direct fighting is one common form of competition in fish, although they have not evolved as many weapons as other vertebrates. The hooked jaws (kype) of many salmonids and the large fangs of male crystal gobies, *Crystallogobius linearis*, come to mind. Other weaponry like teeth, saws and stinging rays seem not to be primarily sexually selected. In fish, fighting commonly occurs by bites and chases, behaviours that perhaps do not require specialized weapons. As large body

size may be advantageous in fights, it may be under intense sexual selection. Consequently, in many fish species males may be larger than females, in spite of the fact that females are subjected to natural selection for larger body size because of fecundity advantages (Hutchings, Chapter 7, this volume).

A bewildering array of threat signals have evolved in fish: morphological structures like the orange caudal fin of the damselfish *Chrysiptera cyanea* (Gronell 1989), colours like the red belly of three-spined sticklebacks, *Gasterosteus aculeatus* (Candolin 1999), or sounds as in the croaking gourami, *Trichopsis vittata* (Ladich 1998). Even electrical signals may be used in this context, as in the electric knife fish *Eigenmannia virescens* (Hopkins 1974). Status signals may serve as honest indicators of competitive ability, even if there is no energetic cost of producing or displaying them because individuals showing dishonestly large status badges ('cheaters') will be exposed to escalated fights with opponents bearing a similar-sized but honest badge (e.g. Maynard Smith and Harper 1988). Information about the opponent and the environment can be crucial in determining whether fighting will occur or not (e.g. Lindström 1992; Johnsson and Åkerman 1998). In fact, fights can themselves provide important information on how to proceed (e.g. Oliveira et al. 1998).

Male mating success may not translate directly into fertilization success. If females mate with more than one male, male fertilization success may also depend on factors like sperm number and sperm quality, and select for increased sperm production. Accordingly, across fish species there is a strong correlation between degree of sperm competition and relative testes size (Stockley et al. 1997). The pipefish *Syngnathus typhle*, with a paternity confidence of 100%, has minute testes, whereas species with intense sperm competition like paddlefish *Polyodon spathula*, minnows *Phoxinus phoxinus*, silversides *Menidia beryllina* and perch *Perca fluviatilis* and *P. flavescens* have large testes and/or large sperm numbers (Stockley et al. 1997).

10.4.2 Mate choice

Benefits of mate choice

Mate choice can be defined as any behaviour that increases the likelihood of mating with certain members of the opposite sex. Theories to explain the evolution of mate preferences can be divided into those yielding either genetic or non-genetic benefits (reviewed in Andersson 1994). The magnitude of the benefits of choosiness will be proportional to the amount of variation in mate quality of the opposite sex (Owens and Thompson 1994; Johnstone et al. 1996).

The nature of potential genetic benefits has been much debated. According to Fisherian models (Fisher 1930) male ornaments are merely arbitrary traits that females find attractive. Ornamented males thus have a high mating success and selective females gain through the production of attractive sons, so long as ornament expression is heritable. If female preference is also heritable, the ornamental trait and the preference will become associated in the offspring. This may lead to a self-reinforcing runaway process causing exaggeration of the ornamental trait. Evidence has been found for positive genetic correlations between female preferences and preferred male ornaments, such as in the three-spine stickleback (Bakker 1993). However, a positive genetic correlation between preference and ornament is predicted not only by Fisherian models but also by good genes models (below).

Good genes models, also known as viability indicator models, suggest that male ornament expression signals the genetic quality of the bearer. By mating with males with extravagant ornaments females gain indirect benefits through the production of offspring that grow more quickly, are more viable or are more fecund (carrying 'good genes'). In most of these models, the trait is thought to be costly to produce or carry and only males of high quality can afford to have such a 'handicap' (Zahavi 1977). Thus, the handicap will act as an honest signal. A special case of this was proposed by Hamilton and Zuk (1982), suggesting that ornamental traits reflect the bearer's re-

sistance to parasites. A mechanism for how this might work was suggested by Folstad and Karter (1992) in their immunocompetence handicap model: the primary androgenic hormone, testosterone, stimulates ornament expression at the same time as it interferes with the immune system. Thus, only high-quality healthy males would afford a high ornament expression associated with high androgen levels. Another type of genetic benefit comes from mating with an individual having a very different genotype, thereby obtaining complementary genes for the offspring (Jennions 1997). Whether this occurs in fish is an open question. Wedekind (1996) speculated that this might explain strong individual preferences among female roach.

Mating preferences may also have evolved through direct selection. Here, females gain direct (non-genetic) fitness benefits that increase their survival or reproductive success. Examples of direct benefits are access to a safe and resource-rich territory, nuptial gifts and provision of high-quality parental care (reviewed in Andersson 1994).

Numerous studies of mate choice have been carried out on fish, which provide good model systems that are often suitable for experimental manipulations. Many of these studies have been concerned with what type of benefits females might gain through their choice of mate. Whether females are able to pick a mate with good genes is still a controversial question (Andersson 1994). One example from fish comes from an experiment on guppies, where Reynolds and Gross (1992) (Fig. 10.3) found that matings with preferred large males produced offspring that had a higher growth rate and daughters with a higher reproductive success. However, recent findings on the same species suggest that another component of male attractiveness, their ornamentation, may be related to lower offspring survival (Brooks 2000). In a pipefish, both male and female choice resulted in higher offspring quality in terms of ability to escape predation. In addition, female choice resulted in higher offspring growth rate (Sandvik et al. 2000). There might, however, be other explanations than good genes for these results, such as
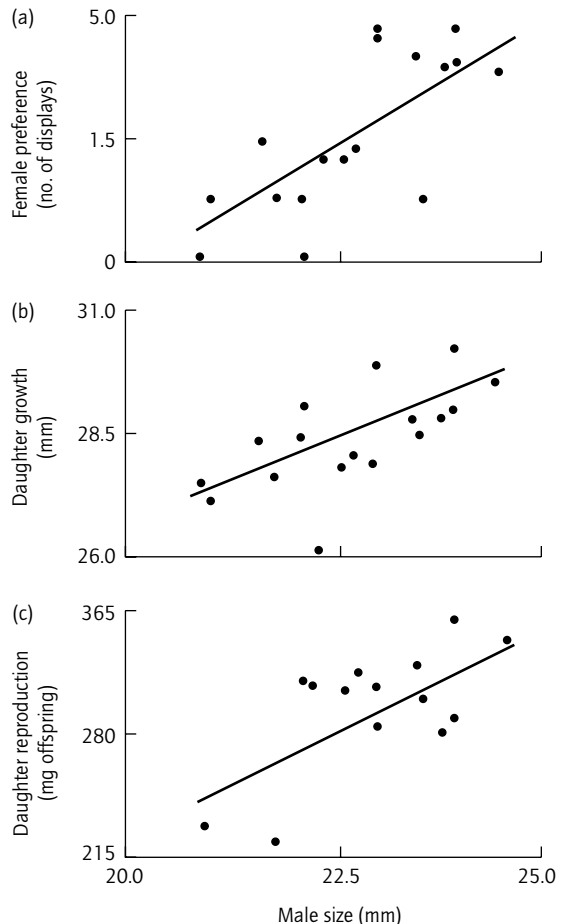
Fig. 10.3 Results from an experiment designed to test for potential genetic benefits in female mate choice by Trinidadian guppies. (a) Females prefer larger males (total length). (b) These same males sire faster-growing daughters (total length at a standard age of 78 days). (c) These daughters have higher reproductive output over their first two broods (sum of dry weight at birth). Each data point represents the mean preference or offspring performance of two females tested per male. The scales are log-transformed with labels in original units. (Source: from Reynolds and Gross 1992.)

differential allocation into eggs or parental care depending on the attractiveness of the partner (reviewed in Sheldon 2000). Several studies, for example on guppies (Houde and Torio 1992) and

sticklebacks (Milinski and Bakker 1990, but see Fitzgerald et al. 1993), have shown that fish avoid parasitized mates. This preference might render genetic benefits in terms of parasite resistance genes passed on to the offspring (Hamilton and Zuk 1982). However, females may also gain direct benefits by avoiding contagious parasites or by avoiding males that are too sick to provide adequate parental care (see also Barber and Poulin, Chapter 17, this volume).

Evidence for direct benefits of mate choice through high-quality parental care comes from several correlational studies (e.g. Downhower and Brown 1980; Côté and Hunte 1989). Choice for parental ability has also been confirmed in experiments where confounding variables such as female quality and clutch size were controlled (Knapp and Kovach 1991; Forsgren 1997a). In the study of the bicolor damselfish, *Stegastes partitus*, by Knapp and Kovach (1991), females were apparently able to select good fathers by using courtship intensity as a cue.

Mate sampling and costs of mate choice

Several models of search behaviour have been developed to describe how animals should search for mates (see Luttbeg 1996 and references therein). However, very few empirical studies on taxa other than birds have been devoted to this problem (reviewed in Gibson and Langen 1996). Female sand gobies appear to use a threshold criterion when selecting potential partners (Forsgren 1997b). Males were inspected sequentially until one advertising above a certain threshold courtship intensity was encountered and mating occurred. In the bicolour damselfish (Knapp 1993) and the blenny *Aidablennius sphynx* (Kraak and van den Berghe 1992), females seemed to assess the success of earlier laid eggs and avoided nests where eggs had disappeared.

Search costs should reduce choosiness (Crowley et al. 1991) and several studies of fish have demonstrated this. In an experiment on sticklebacks, females became less choosy if time costs and energy expenditure were increased (Milinski and Bakker 1992). In the upland bullie, *Gobiomor-*

phus breviceps, heavily parasitized females were less selective than less parasitized females, apparently because they had depleted energy stores and were in poor physical condition (Poulin 1994; Barber and Poulin, Chapter 17, this volume). In several experiments, increased predation risk has been found to result in decreased choosiness (e.g. Forsgren 1992; Berglund 1993). Although choosiness apparently is very cost sensitive and may disappear if search costs are high, females may be willing to pay some costs to obtain preferred mates. In redlip blennies, *Ophioblennius atlanticus*, some females travelled quite extensive distances in search of mates, enduring severe attacks from damselfish whose territories they crossed in the process. However, these females obtained higher quality mates than females with a more restricted search (Reynolds and Côté 1995). In the damselfish *Stegastes nigricans*, females changed the number of spawning visits depending on the distance to the males' territories, probably in order to minimize costs in terms of intrusions to their own territories and attacks from heterospecifics (Karino and Kuwamura 1997).

Ornaments and other choice cues

Many examples from fish show that females base their mate choice on male characteristics (reviewed in Andersson 1994). Examples of male traits that may have evolved through female choice include coloration (Milinski and Bakker 1990; Houde 1997), elongated fins (Bischoff et al. 1985; Basolo 1990), body size (Côté and Hunte 1989; Reynolds and Gross 1992) and courtship displays (Knapp and Kovach 1991). If these are honest signals of male quality, only high-quality males should be able to develop and carry highly elaborated versions of the traits (Zahavi 1977). Elaborate traits can indeed be costly, as evidenced by the well-studied colour ornaments of male guppies (reviewed in Endler 1995; Houde 1997; see also Olson and Owens 1998 for a discussion of costs of carotenoid colours). Also, in the Amarillo fish elaborate traits are costly, as males with a morphology attractive to females were more likely to be captured by predatory snakes (Macías Garcia

et al. 1994). Honest signalling may work if the optimum trait expression is different for individuals of different quality. This can come about if poor-quality males pay higher costs than high-quality males for a certain trait expression (Johnstone 1997). To date this has not been conclusively demonstrated in any fish. There are, however, data supporting the idea that ornaments are expressed in a condition-dependent way. For example, parasitized males have been found to develop a less bright carotenoid-based breeding coloration in sticklebacks (Milinski and Bakker 1990) and guppies (Houde and Torio 1992). Females may also gain reliable information from cues that are honest by design rather than through costs (Hasson 1997), such as body size or visible parasites.

Females may also base their choice on aspects other than the male himself. Many fish have resource-based breeding systems, with males defending a spawning site. Without experimental manipulations it is often difficult to assess the importance of territory and male characteristics in mate choice, although there are studies indicating that the breeding site, in addition to male characteristics, is an important cue in mate choice (e.g. Kodric-Brown 1983). This was also the conclusion from an experiment with the river bullhead (Bisazza and Marconato 1988). In European bitterling, *Rhodeus sericeus*, females base their initial interest in males on the male's courtship display, but the final spawning decision is based on the quality of spawning site that the male is defending (Candolin and Reynolds 2001). These fish spawn in living freshwater mussels (Unionidae) and females prefer mussel species that yield the highest survival to their embryos (Mills and Reynolds 2002). In a removal experiment conducted in the wild, Warner (1988a) demonstrated that female bluehead wrasse chose particular spawning sites instead of male characteristics. Also, elaborate nest constructions may be attractive themselves (e.g. Jones and Reynolds 1999; Östlund-Nilsson 2001). An extreme form of extrabodily ornaments are found in some cichlids in the African rift lakes, where males construct impressive sand bowers to attract females (McKaye et al. 1990). As mentioned

in Section 10.3.3, females of several different fish prefer to spawn in nests already containing eggs from other females. Several hypotheses have been proposed to explain this, including mate choice copying, a predator dilution effect and high parental investment (see Jamieson 1995). An increased egg survival, resulting from the two latter mechanisms, might be a more likely explanation than mate choice copying (Jamieson 1995; Forsgren et al. 1996b).

It is not only males who carry extravagant ornaments; females of many species are conspicuous in one way or another. In many fish, for example, females are brightly coloured. The function of female ornaments in species with conventional sex roles (see Section 10.4.3) is poorly understood in general, and most of our knowledge comes from studies on birds (Amundsen 2000). Traditionally, female ornaments have been assumed to be functionless, existing solely because of a genetic correlation between male and female traits, in cases where both sexes have similar ornamentation. Alternatively, female ornaments may have been selected for by male choice or female competition (see Section 10.4.3). Recent experiments have demonstrated that males are attracted to colourful females in both sex-role reversed pipefish (Berglund and Rosenqvist 2001) and conventional-role gobies (Amundsen and Forsgren 2001). If female ornaments have evolved through male choice for direct or indirect benefits, the ornaments should provide information about female quality. There is evidence from Arctic charr, *Salvelinus alpinus*, that the intensity of the carotenoid-based coloration is informative of immunocompetence or health in both sexes (Skarstein and Folstad 1996).

Interactions between male competition and female choice

Males successful in male competition should be in better condition and might also have higher viability than unsuccessful males. It is therefore generally believed that females should benefit by mating with winners of male competition (reviewed in Berglund et al. 1996). Thus, female

choice may be facilitated by male competition, as suggested for sticklebacks (Candolin 1999; but see Nilsson and Nilsson 2000). There is some evidence from fish that females do prefer dominant males (Järvi 1990; Bisazza and Marin 1991) and that they may gain direct benefits from such matings (Bisazza et al. 1989). However, there is also some evidence suggesting that females neither prefer dominant males nor gain any direct benefits by mating with these males as opposed to less dominant ones (Forsgren 1997a). Thus, female choice and male competition need not work in concert. In such cases, male competition may constrain female choice. Commonly, dominant males have a mating advantage over other males (Kodric-Brown 1992; but see Houde 1988). It is, however, often difficult to disentangle the effects of male competition and female choice in order to assess the importance of each selective mechanism independently of the other. Very little is known about the interactions between these two sides of sexual selection (Qvarnström and Forsgren 1998).

10.4.3   Sex roles

Sex differences in mating competition largely depend on the operational sex ratio (Kvarnemo and Ahnesjö 1996; see Section 10.2.1). Species where males are most competitive over matings are said to have conventional sex roles (Vincent et al. 1992). This does not necessarily imply that male mate choice and female competition over matings are absent in these species. These behaviours are, however, usually less obvious and have often been overlooked in studies of sexual selection (Cunningham and Birkhead 1998). When male potential reproductive rate is not so high and female variation in quality is substantial, males are expected to be choosy. In fish, several studies have demonstrated male choice for large and more fecund females (reviewed in Andersson 1994). Female competition over males is expected if there is a shortage of males or if variation in male quality is large (reviewed in Berglund et al. 1993). In the latter case females are expected to compete over the most preferred males, so showing competitive mate choice. An example of male shortage comes

from a population of the peacock blenny, *Salaria pavo*, where nest sites are scarce (Almada et al. 1995). In this species, males take up nests and provide uniparental care. Accordingly, nest-holding males are hard to find and females compete intensely for access to these males. Females may also compete over resources necessary for reproduction as in the coho salmon, *Oncorynchus kisutch*, where females compete over oviposition sites (Fleming and Gross 1994).

Although most species have conventional sex roles, there are examples from different taxa, including fish, where the sex roles are reversed. Here females are the predominant competitors over matings. For example, in the pipefish *Syngnathus typhle*, the form and extent of male parental care decreased the relative potential reproductive rates of males below that of females (Berglund et al. 1989) (Fig. 10.4). This, in turn, influenced the operational sex ratio so that willing females were in excess (Berglund and Rosenqvist 1993). This caused males to be choosier and females more competitive (Berglund 1991). Consequently, females should be subject to stronger sexual selection than males, and females more than males should evolve behaviours and structures aiding them in mating competition (e.g. Berglund et al. 1997). Several other fish species also exhibit sex-role reversal, for example the pipefish *Nerophis ophidion* (Rosenqvist 1990), the black-chinned tilapia, *Sarotherodon melanotheron* (Balshine-Earn and McAndrew 1995) and the goby *Eucyclogobius newberryi* (Swenson 1997). Note that paternal care *per se* does not cause sex-role reversal: the majority of caring fish species have exclusive paternal care but sex roles are typically not reversed (Fig. 10.1). This is probably because the usual forms of care, such as guarding and fanning, allow the male to accept several clutches and does not depress his potential reproductive rate below that of the females. Even the extreme form of paternal care found in pipefishes and seahorses does not necessarily cause sex-role reversal: seahorses typically have conventional sex roles (Vincent et al. 1992; Vincent 1994).
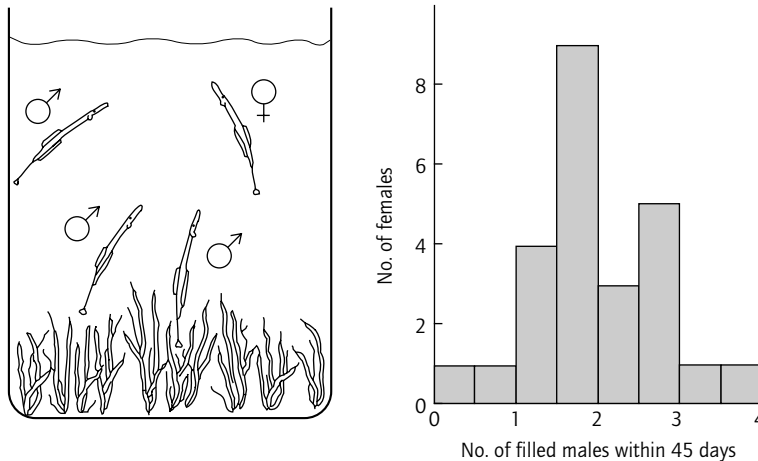
Fig. 10.4 Potential reproductive rate in females of the pipefish *Syngnathus typhle*. Females could fill on average two males during the time of an average male pregnancy (45 days) when provided with an excess of mates. Thus, females have a potential reproductive rate twice as high as that of males. (Source: after Berglund et al. 1989; reproduced by permission of the University of Chicago Press.)

10.5   MATING PATTERNS

The diversity of mating patterns, ranging from promiscuity to monogamy, is to a large extent explained by sex differences in mating competition and resource distribution. Often, females distribute themselves according to resources, such as food, shelter or breeding sites, while males distribute themselves according to female distribution. Males may compete for the resources females need or try to monopolize females directly (Emlen and Oring 1977; Reynolds 1996). As resources vary in space and time, mating patterns may too, depending on economic defendability (see Section 10.2.2). This may, for example, explain the occurrence of 'resource-defence polygyny'. While this scheme explains broad mating patterns, additional information about parental care and sex differences in costs and benefits of mate choice and competition are needed to understand the details of interactions between the sexes (Reynolds 1996).

Promiscuous group-spawning is common in many pelagic fish, probably because resources are widely distributed in time and space and not economically defendable. Many commercial fish species may fall into this category, such as herring, *Clupea harengus*, which gather in large numbers to spawn. There are probably few options for exercising mate choice or engaging in intrasexual com-

petition except for sperm competition. This may explain the lack of sexual dimorphism in this species.

Leks are areas where males aggregate and display to females, which come there to mate only (Höglund and Alatalo 1995). Females receive nothing but sperm from the males, and do not leave eggs or young on the males' territories. A spectacular example is the bower-building cichlid, *Cyrtocara eusinostomus*, in Lake Malawi, where up to 50 000 males may display simultaneously along a 4-km long arena. After mating, the female, who does all the brooding, leaves the lek with the eggs in her mouth (McKaye et al. 1990). Cod, *Gadus morhua*, may provide another example, with aggregated males courting females vocally and by fin displays (Nordeide and Folstad 2000).

Resource-defence polygyny is common in fish because, in many species, males defend a spawning site or build a nest where females lay their eggs. This is widespread among, for example, gobies, sticklebacks, labrids and damselfish. Female-defence polygyny is much rarer but has been found in two simultaneously hermaphroditic sea basses, the barred serrano, *Serranus fasciatus*, and the lantern bass, *S. baldwini*. Males defend groups of female-acting hermaphrodites with small and collectively defendable home ranges (Petersen 1987). In *S. fasciatus*, groups of females form with the

dominant individual acting as a pure male. Subordinates spawn as females but retain their functional testes without using them much. However, these 'females' may streak: a subordinate can hide close to a pair about to spawn and dash in to release sperm at the right time (Petersen 1990). For a review of alternative mating tactics see Hutchings (Chapter 7, this volume).

A few fish species are monogamous. In the Midas cichlid, *Cichlasoma citrinellum*, parents stay together to defend their territory both against other Midas cichlids and to protect their larvae from predators, including conspecifics. A single parent is unlikely to be able to accomplish this successfully (e.g. Keenleyside 1991). Monogamy is a fixed trait in this species: even if the sex ratio and density are experimentally manipulated to promote polygyny, monogamy reigns (Rogers 1987).

Biparental care is, however, not the only factor that promotes monogamy. Males may be kept from access to several females by dominant males and may have to resort to monogamy or not mate at all, as in the cichlid *Lamprologus brichardi* (Limberger 1983). In marine fishes, monogamy is commonly associated with difficulties in finding and keeping more than one mate. Monogamy may be influenced by territoriality, low population density, and restricted or slow movement. In two species of coral-dwelling hawkfishes, *Neocirrhites armatus* and *Oxycirrhites typus*, males were monogamous if suitable corals were small or rare, but maintained groups of females among large or abundant corals (Donaldson 1989). In the simultaneous hermaphrodite *Serranus fasciatus*, pairs spawn monogamously under low population densities, taking turns to act as males and females (Petersen 1990).

Reproductive synchrony between males and females may select for monogamy. In the pipefish *Corythoichthys intestinalis* (Gronell 1984) and in two seahorses, *Hippocampus fuscus* and *H. whitei* (Vincent et al. 1992; Vincent and Sadler 1995), females need to hydrate their eggs for some time before depositing them in the male brood pouch. Under monogamy, the female hydrates eggs while the male broods the previous clutch. Once the male has given birth, the pair is ready to mate

anew. A female cannot search for a new mate while retaining hydrated eggs, as these must be released within a short period. However, one can wonder whether preparatory periods select for monogamy or whether monogamy permits the female to have preparatory periods. Whatever the reason, seahorses and monogamous pipefish seem to be examples of animals where 'pure' genetic monogamy can be found, as evidenced by microsatellite analysis in the Western Australian seahorse *H. angustus* (Jones et al. 1998).

Communal breeding has evolved in several fish species with parental care and is especially common in the Cyprinidae and the Cichlidae (Taborsky 1994; Wisenden 1999). Two common forms are 'non-reproducing' helpers that assist a reproducing couple in raising their offspring, and parental fish that adopt and raise other individuals' offspring (alloparents). Several advantages have been proposed to explain 'helping'. If helpers are related to the individuals they assist, kin selection may explain this phenomenon. Thus helpers propagate their own genes by helping relatives, as in the cichlid *Lamprologus brichardi* (Taborsky and Limberger 1981). Helpers may also benefit by being included in a group and gain access to shelters or feeding sites if such are scarce (Taborsky 1984). Further, helpers may reproduce by stealing fertilizations from the territorial male, as in the cichlid *Neolamprologus pulcher* (Dierkes et al. 1999). Alloparents may benefit if larger schools of offspring reduce the per-capita predation by diluting the risk or by confusing the predator (reviewed in Pitcher and Parrish 1993). In addition, predation risk may be diverted from the parent's young to the alien young, as in convict cichlids (Wisenden and Keenleyside 1993). However, alloparenting need not always be adaptive but can simply be misdirected care, as when mouth-brooding cichlids are parasitized by the catfish *Synodontis multipunctatus* (Sato 1986).

Some species of fish do not have sex at all. Examples include some minnows of the genus *Phoxinus* and the topminnow genus *Poeciliopsis*. The latter contains both sexual and asexual species. The asexual all-female species were formed by hybridization between two sexual top-

minnow species and are triploid. Sperm from one of the ancestral species is still required to initiate reproduction but is not incorporated into the offspring (Vrijenhoek 1979). Males of the ancestral species still benefit from spawning with the asexual females because females of their own species copy the mate choice of the asexual females (Schlupp et al. 1994). These fish are often infected by trematode larvae (*Uvulifer* sp.) and may develop the black spot disease. Theory attempting to explain why sex is advantageous suggests that asexuals should be more parasitized than sexuals, and that variation in parasite level should be higher in sexuals. This has been confirmed for an assemblage of one sexual and two asexual topminnow species (Lively et al. 1990). Further, when the sexual species was inbred following a population bottleneck, parasite levels rose, suggesting that a lowered genetic variability increases susceptibility.

10.6 REPRODUCTIVE BEHAVIOUR AND LIFE HISTORIES

Reproductive behaviour is intimately linked with life histories because the time and energy devoted to mating behaviour and parental care usually incur costs in terms of decreased future survival and fecundity. It is a matter of semantics whether one considers parental care to be a component of life histories. Below we address briefly some areas of reproductive behaviour that have close links to life histories. Life histories are reviewed in detail in Hutchings, (Chapter 7, this volume).

10.6.1 Sex change and hermaphrodites

Many coral-reef fish and some temperate species are sequential or simultaneous hermaphrodites. Sequential hermaphrodites may change sex from male to female, female to male, or both ways. Simultaneous hermaphrodites produce eggs and sperm at the same time and may either cross- or self-fertilize. This feature of life histories could be

driven either by sexual selection or by natural selection for fecundity advantages.

Protogyny, in which individuals start as females and then switch to males, is the commonest form of hermaphroditism, exemplified by groupers (Epinephilinae), parrotfishes (Scaridae) and many wrasses (Labridae). This sexually selected life-history trait is explained by the 'size-advantage model' (Fig. 10.5; Ghiselin 1969; reviewed in Warner 1988b). In species with strong competition
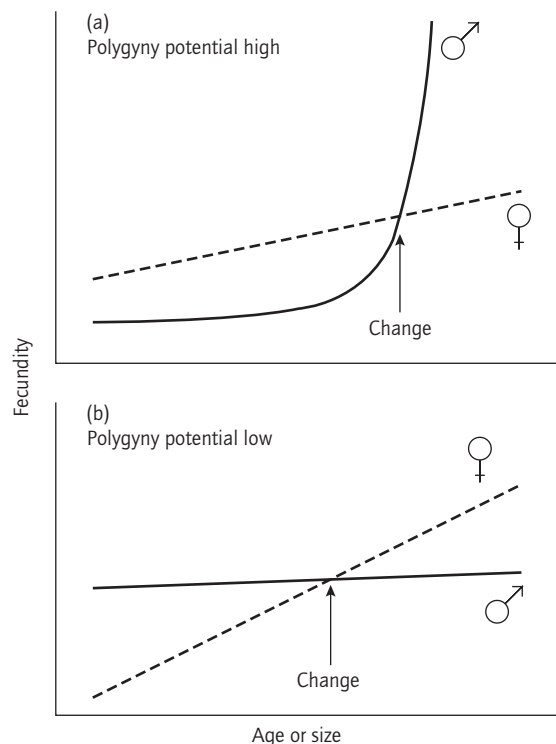
Fig. 10.5 The size-advantage model of sex change. (a) When only large males can defend resources or females, it pays to start life as a female and change sex when a competitive size/age is reached (protogyny). (b) When there is a low potential for polygyny, female fecundity usually increases more rapidly with size than male fecundity. It pays to start out as male and change to female when reaching some size/age threshold (protandry). These scenarios assume that costs of changing are not prohibitive. (Source: after Berglund 1997; © Oxford University Press 1997.)

among males for females, small males may be at a strong disadvantage. Then it may pay individuals to start out as females and remain so until they reach a sufficient size to compete successfully as males (Fig. 10.5a). At this point the gains from reproducing as a male outweigh the lower-risk, lower-benefit option of reproducing as a female, including the time and energy costs of switching over their gametic function. So they switch to males. Experiments have shown that when dominant males are removed, the largest female in an assemblage may initiate sex change within hours and become fully functional within days (Ross 1990).

Protandry, in which sex changes from male to female, usually occurs in species where sexual selection through male–male competition is less important, for instance when breeding resources are less aggregated. Individuals are then selected to switch from male to female when the benefits of higher fecundity associated with larger body size outweigh the benefits of remaining a male (Fig. 10.5b). This has been suggested to explain protandry in the anemonefish *Amphiprion akallopisos* (Fricke 1979). If the female of a pair is removed, the top-ranking male changes into a female and the next highest ranking male (or an immigrant if there are no more males) fertilizes the eggs (Fricke and Fricke 1977).

Some goby species take the elements of the size-advantage model one step further and switch in both directions. In some species this is advantageous if moving between territories is risky: after mate loss, a flexible attitude to sex increases partner availability and reduces mate search costs, as individuals can mate with whichever sex is available (Nakashima et al. 1996; Munday et al. 1998). Thus, there is no sharp borderline between sequential and simultaneous hermaphroditism: when changing occurs rapidly we call it simultaneous hermaphroditism (e.g. St Mary 1994).

If a male, above some certain body size, gains nothing by allocating further resources to sperm production, he may instead allocate new resources to egg production: we now have a simultaneous hermaphrodite. Male size advantages may be circumvented by low mate encounter rates and a

behaviour called egg trading. Eggs are more expensive to produce than sperm, so a pair benefits from sharing the heavy task of egg production, taking turns spawning as a male and as a female. However, if a 'female' allows its partner to play the 'cheap' male role, how can 'she' know that 'she' can be a 'he' next time? In other words, how is reciprocation achieved in this obvious conflict between the sexes? This is a classic problem in studies of human social conflict, known as the Prisoner's dilemma (Axelrod and Hamilton 1981). It falls in the domain of game theory, because an individual's best response depends on what others in the population do (see also discussion of game theory by Hannesson, Chapter 12, Volume 2). Hamlets, *Hypoplectus nigricans*, have solved this dilemma in the same way that a computer tournament eventually solved it, using the 'tit-for-tat' strategy, i.e. always start by cooperating and then do what your partner did in the previous round (Fischer 1980; Leonard 1993). Each member of the pair takes turns acting as a female and as a male. By allowing a male-acting fish to fertilize only a small parcel of eggs (egg trading) and then withholding eggs unless the other individual reciprocates by acting female, any loss due to cheating is reduced (Fischer 1980).

There is one species of self-fertilizing hermaphrodite, the killifish *Rivulus marmoratus* (Cyprinodontidae). Indeed, this is the world's only known self-fertilizing vertebrate, although pure males and outcrossing may occur (Lubinski et al. 1995).

10.7 REPRODUCTIVE BEHAVIOUR AND EXPLOITATION

There are numerous links between the reproductive behaviour of fish and exploitation (Vincent and Sadovy 1998; Reynolds and Jennings 2000). For example, fishers in many parts of the world take advantage of predictable spawning aggregations of fish, and managers often incorporate this information into their plans. Reproductive behaviours

may affect the vulnerability of fish to capture, as well as the resilience of populations in responding to exploitation. Other forms of exploitation, such as fish farming and sea-ranching, may also affect fish populations. Here, altered or relaxed selection pressures may lead to altered behaviour, morphology and life history, which in turn may affect survival and reproduction (e.g. Petersson and Järvi 1997). For example, hatchery populations of female coho salmon have lost a number of secondary sexual characters (Fig. 10.6). Obviously, loss of naturally and sexually selected traits due to domestication can have implications for the conservation of wild populations, when cultured fish escape or are released (Fleming 1994).

10.7.1 Timing and location of spawning

Fish species that form spawning aggregations in locations accessible to fisheries are particularly susceptible to overexploitation (see Reynolds et al., Chapter 15, Volume 2). This includes many anadromous species such as salmonids and sturgeons that are targeted in estuaries and rivers. It also applies to the Peruvian anchoveta, *Engraulis*

ringens, the Canadian cod and Atlantoscandian herring, which have all experienced crashes largely due to overfishing. Large species of groupers in the Indo-Pacific may aggregate in the thousands at traditional sites. Unrestricted fishing access to these sites can result in rapid depletions (Sadovy 1993, 1994). Orange roughy, *Hoplostethus atlanticus*, gather in large spawning aggregations at underwater peaks, i.e. seamounts. Here they are vulnerable to trawling, which has proved to be a considerable threat since large-scale fisheries began in New Zealand during 1978. Aggregated spawning behaviour, combined with a slow life history (average age at maturity about 32 years; Fenton et al. 1991), has led to rapid declines (see also Ward, Chapter 9, this volume). The elaborate sand bowers built by male haplochromine cichlids in Lake Malawi (see Sections 10.4.2 and 10.5) are destroyed by trawlers, thereby disrupting spawning even for the surviving males (see illustrations in Ribbink 1987).

In some parts of the world, fishers take advantage of limited spawning sites by attracting fish to artificial sites where they can be caught. An example is the use of bundles of sugar cane, palm fronds or banana leaves by fishers in the Caribbean target-
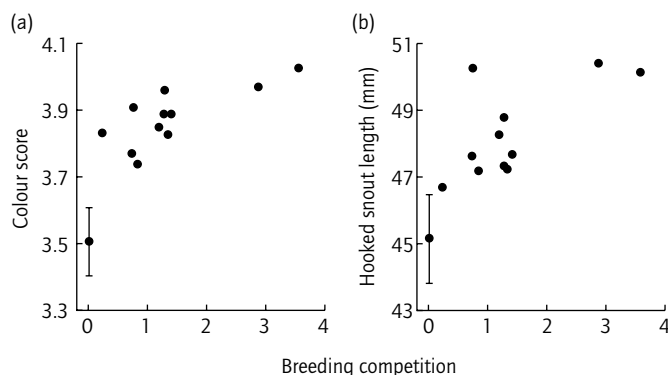
Fig. 10.6 Relationships between breeding competition and (a) intensity of red breeding coloration and (b) hooked snout length for 11 wild populations and five hatchery populations (mean ± SE) of female coho salmon. Breeding competition for the wild populations was measured as the average female population size (measured over 3–38 years) divided by the spawning capacity of the stream. For hatchery populations, breeding competition was assumed to be zero since spawning occurs artificially and independently of natural breeding competition. Correlations are significant even if only the wild populations are included. (Source: after Fleming and Gross 1989; reproduced by permission.)

ing flying fish. The fish are caught during their frantic spawning activities, often while attempting to spawn on the mesh of the nets themselves. Artificial reefs are also used to attract fish, and may under certain circumstances increase productivity (Pickering and Whitmarsh 1997).

10.7.2 Sex change and sex-specific fisheries

An understanding of behavioural ecology is essential in order to predict the effects of sex change and sex-specific fisheries on the resilience of populations to fishing pressures (Vincent and Sadovy 1998; Petersen and Warner 2002). Most sex-changing reef fishes change from female to male when they reach a large size (Section 10.6.1). If this switch is under social control, i.e. triggered by the loss of large males, then one might expect that the loss of males would not impair productivity. However, there are at least two reasons why we should not take much comfort from this idea. First, intensive fishing may not allow sufficient time for females to change sex (Vincent and Sadovy 1998). This may explain why males of one species, the gag grouper, *Mycteroperca microlepis*, have become proportionally much rarer in the Gulf of Mexico and the southeastern Atlantic (e.g. McGovern et al. 1998). Second, although the social control of sex change is understood in some small species of reef fishes that live in permanent social groups, little is known about mechanisms of sex change in large groupers that come together only for spawning. No conclusions can be drawn about implications of male-biased fishing for stock productivity until we understand better how female-biased the sex ratio needs to become before sperm becomes limiting (see Petersen and Levitan 2001; Petersen and Warner 2002). The evidence from small reef fishes such as the bluehead wrasse is that although group spawnings may have more than ten times as much sperm released as pair spawnings (Shapiro et al. 1994), this difference does not greatly affect fertilization success (Marconato et al. 1997). However, frequently spawning male bluehead wrasse release less sperm per mating, resulting in lower fertilization success

(Warner et al. 1995). It remains to be seen whether these results apply to species of conservation concern such as groupers.

Sex-specific fisheries may also result from spatial and temporal segregation of the sexes (reviewed in Vincent and Sadovy 1998). As with considerations of sex change, this is apt to be most important where the sex that is targeted has the lower potential reproductive rate, and hence may limit population productivity. For example, in the coral trout, *Plectropomus areolatus*, females are caught selectively before spawning, leading to male sex-biases in spawning aggregations and male harassment of females that may hinder spawning (Johannes et al. 1994). In some migratory species such as plaice, *Pleuronectes platessa*, sexual selection is probably responsible for males arriving at spawning grounds before females (Arnold and Metcalfe 1996), leading to sex-specific fisheries during migration.

Anglers may have adverse effects on male fish that provide parental care. For example, North American male smallmouth bass, *Micropterus dolomieu*, will bite anything that comes near their nests, including hooks. Hook-and-release rules during the spring spawning season may allow males to survive (see Cowx, Chapter 17, Volume 2). However, an experimental study showed that when anglers 'played' fish to exhaustion (2 min), it took the males four times longer to return to their nests than when they were played briefly (<20 s) (Kieffer et al. 1995). Even a brief absence of the male can lead to breeding failure due to predation by other species as well as neighbouring males.

10.8   CONCLUSIONS

As we have seen, fish are excellent model organisms for studying important questions in behavioural ecology, displaying a wide variety of complex reproductive behaviours. Today, most of our knowledge of these questions comes from studies of shallow-water teleost fish with parental care. Indeed, researchers have relied very heavily on a handful of model species, such as sticklebacks

and guppies. We know surprisingly little about the behavioural ecology of reproduction in fish without parental care. Absence of parental care is typical of many pelagic fish, including some of the most abundant and economically important fish species on earth, such as cod and anchovetas. Whether those species fit into the general picture, for example, with widespread sexual selection, is basically unknown. An improved knowledge of the behavioural and reproductive dynamics of such species, focusing on the adaptive decisions made by individual fish, is clearly needed. We believe that increased communication and collaboration between behavioural ecologists, fisheries biologists and nature conservationists would be very fruitful and could greatly increase our knowledge and improve resource management.

ACKNOWLEDGEMENTS

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Part 3

Fish as Predators and Prey

11 Fish Foraging and Habitat Choice: A Theoretical Perspective

GARY G. MITTELBACH

11.1 INTRODUCTION

Fish come in a variety of shapes and sizes, and their diversity in form and the range of environments that they occupy is unparalleled amongst the vertebrates. Fish as different in size as minnows, paddlefish (*Polyodon* spp.), and whale sharks (*Rhincodon typus*), make their living feeding off tiny zooplankton in the open waters of lakes, rivers and oceans. Pike (*Esox* spp.) and anglerfish (*Lophius* spp.) lie in ambush for other fishes, while tuna and swordfish (*Xiphias gladius*) cruise continuously in search of prey. Within a single coral reef there is a diversity of feeding modes that can stagger the imagination. For example, some wrasses (Labridae) make a living cleaning the parasites off other fishes, parrotfish (Scaridae) crunch corals between their massive jaws and turn them into sand, pipefishes (Syngnathidae) and seahorses (*Hippocampus* spp.), with mouths shaped like soda-straws, extract tiny invertebrates from their protective crevasses, and triggerfish (Balistidae) blow over sea urchins with a powerful jet of water and then feast on their soft undersides.

How do we make sense of such a bewildering array of feeding niches and foraging behaviours? One way would be to classify fish by foraging mode or prey type, such as planktivore, molluscivore and piscivore, and then examine the feeding behaviours exhibited by fish in each group. In contrast to this empirical approach, one might attempt to develop general theories of foraging behaviour based on evolutionary principles common to all fishes.

The diversity of nature presents a challenge to both approaches and there is room for empiricist and theoretician alike. In writing this chapter, however, I have thrown my lot in with those who use models of adaptive behaviour to attempt to provide a general framework for understanding foraging behaviours. This field of study is sometimes referred to as optimal foraging theory, because optimality models have been used to formulate hypotheses about adaptive behaviour. A more empirical approach is taken by Juanes et al. (Chapter 12, this volume) for piscivores and by Krause et al. (Chapter 13, this volume) for prey. However, optimal foraging theory should not be confused with the notion that natural selection has somehow led to the evolution of animals that are 'optimal' in their behaviours. Rather, as Stephens and Krebs (1986, p. 213) note, 'Optimality models . . . are yardsticks against which to compare nature; they are not claims about what nature must be like'.

Below, I first discuss the question of diet choice in fishes, including the development of optimal foraging models, and the potential use of foraging models to predict fish feeding rates and growth in natural habitats. I then consider problems of habitat selection, using the construct of the ideal free distribution (Fretwell and Lucas 1970; Fretwell 1972) and theories of optimal habitat selection based on balancing foraging gains and predation risks to understand how fish might choose among foraging habitats. Finally, I discuss how habitat selection by predator and prey may relate to such important population- and community-level

processes as cascading effects and the response of trophic levels to changes in environmental productivity. Mathematical descriptions of theory are kept to a minimum and I focus instead on providing a conceptual understanding of the theory and its predictions, and a summary of the main empirical tests that have involved fish. Fortunately, fish have played a predominant role in the development and testing of adaptive models of foraging behaviour.

11.2 FORAGING BEHAVIOUR AND DIET CHOICE

11.2.1 *Feeding preference*

Most fish are selective foragers: they prefer to feed on some prey types and not on others (Gerking 1994). Preference can be defined as the difference between the proportion of a prey type in the diet and the proportion of that prey type in the environment. Although feeding preference can be measured by a variety of mathematical indices (Confer and Moore 1987), the index developed by Manly (1974) and further extended by Chesson (1978, 1983) is the most widely accepted. The Manly–Chesson index calculates the selectivity for prey type i as:

$$\alpha_i = \left(d_i/N_i\right)\Big/ \sum_{j=1}^{k} \left(d_j/N_j\right) \qquad (11.1)$$

Where i = 1, 2, . . . , k and k is the number of prey categories, d_i is the number (or proportion) of prey of type i in the diet, and N_i is the density (or proportion) of prey of type i in the environment. The index α_i ranges from 0 to 1. Prey types that are consumed in proportion to their abundance in the environment (i.e. no preference) have $\alpha_i = 1/k$; $\alpha_i > 1/k$ indicates selection for a prey type and $\alpha_i < 1/k$ indicates selection against a prey type.

Feeding preference may result from active prey choice by the predator or from a variety of other factors that may affect the rate of encounter between predator and prey. We can best understand the role of behaviour in fish diet selection by breaking down the act of predation into its component parts (Fig. 11.1). The predation sequence

illustrated in Fig. 11.1 can be modelled using an extension of Holling's disc equation (Holling 1959a,b) to include attack probabilities and multiple prey types. In this model, the predator's feeding rate (net energy gained per foraging time, E/T) is expressed as:

$$E/T = \frac{\sum_{i=1}^{n} \lambda_i N_i E_i P_i(\mathrm{a})P_i(\mathrm{s}) - C_s}{1 + \sum_{i=1}^{n} \lambda_i N_i P_i(\mathrm{a})P_i(\mathrm{s})H_i} \qquad (11.2)$$

where the net energy value of prey type i, $E_i = A_i m b_i - C_h H_i$, A_i is the assimilable fraction of the energy content of prey type i, b_i is the mass of prey type i, m is a conversion constant for prey mass to energy, C_h is the energy costs of handling prey, H_i is handling time of prey type i, C_s is the energy cost of searching, λ_i is the average per-capita encounter rate with prey of type i, N_i is the average density of prey type i, $P_i(\mathrm{a})$ is the probability that an encountered prey of type i is attacked, and $P_i(\mathrm{s})$ is the probability that an attacked prey of type i is successfully consumed. Feeding rate is equal to the total amount of assimilable food that can be collected by a fish during one unit of search time, minus the energy cost of foraging, divided by the total foraging time that results from one unit of search time (Osenberg and Mittelbach 1989; Mittelbach and Osenberg 1994).

Preference (positive or negative) for a given prey type may result from factors that influence the rate at which a prey type is encountered (λ_i) or that influence the probability that an encountered prey will be consumed ($P_i(\mathrm{a})$ and $P_i(\mathrm{s})$). For example, larger prey are visible at further distances (Werner and Hall 1974; Confer and Blades 1975; Vinyard and O'Brien 1976) and prey that are more active are more easily seen by a searching fish (Ware 1973). Any factor that affects the rate of encounter between predator and prey may result in a predator showing a positive or a negative preference for a prey type. It is important to note, however, that while differential prey encounter may lead to selective foraging, meaning that there is a difference between the abundance of prey types in the fish's diet and the abundance of prey types in the
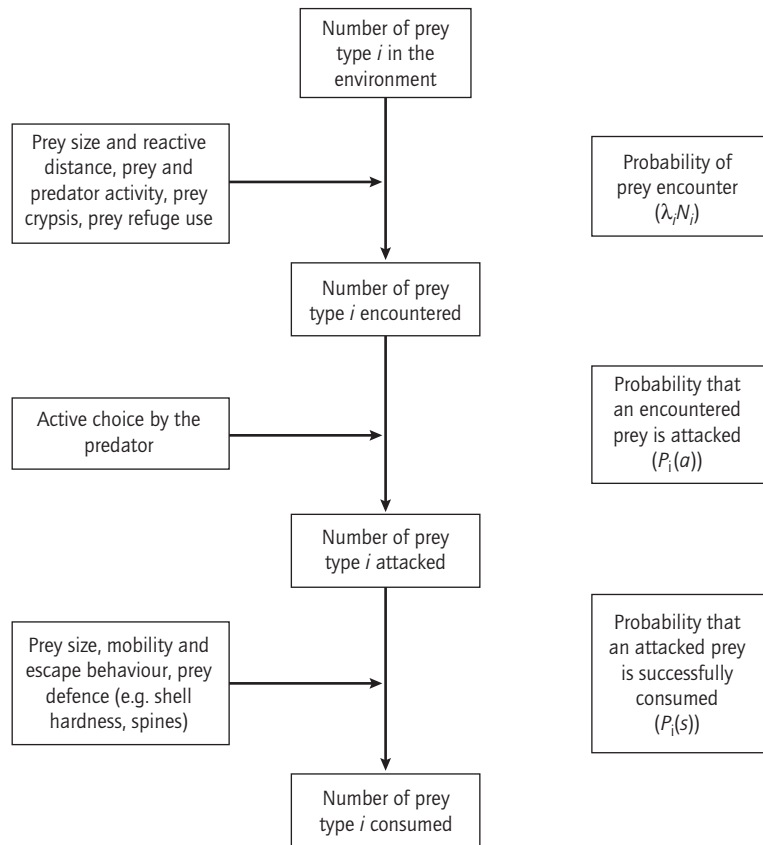
Fig. 11.1 Stages in the predation process. The right-hand column lists the components of a multi-species Holling functional response model (i.e. equation 11.2) that determine the probability that a given prey type (i) will be consumed. Listed to the left are attributes of predator and prey that influence these components. (Source: modified from Sih 1993.)

environment, this mechanism does not involve active predator choice.

Predator behaviour may enter into diet selection through a predator's choice of which prey items to pursue ($P_i(a)$) and the probability that a pursuit will result in successful capture ($P_i(s)$). When prey are small relative to the predator, capture success generally will be high. For example, adult planktivores have very high capture success when feeding on zooplankton. However, even for adult planktivores, some types of zooplankton such as copepods are sufficiently evasive that fish must use alternative capture techniques (Vinyard 1980). Fish that feed on hard-bodied prey like molluscs routinely encounter prey that differ in capture success, brought about by a variable probability of successfully crushing a shell (Wainwright 1987; Osenberg and Mittelbach

1989; Huckins 1997). The same problem is faced by piscivorous fish. Christensen (1996) and Sih and Christensen (2001) argue that piscivore diets are strongly influenced by the differential capture success of prey and that this is a major reason why piscivores generally prefer smaller prey than would be expected based on maximizing their energy intake per handling time (see Juanes 1994; Juanes et al., Chapter 12, this volume).

11.2.2 Diet selection and optimal foraging

Much of the theoretical development of foraging models has revolved around the question of predator choice: when should a predator choose to pursue a prey item that it has encountered? Ecologists and evolutionary biologists have used

optimization criteria to address this question of predator choice, arguing that natural selection should result in predator behaviours that maximize their rate of energy gain, which is a component of fitness. Charnov (1976) developed one of the first optimal diets models, using an equation similar to equation 11.2 to predict a predator's diet. In Charnov's model, predators adjust their attack probabilities $(P_i(a))$ to maximize their total energy gain (E/T). Two basic predictions that arise from Charnov's model and from similar models developed by Schoener (1971), Pulliam (1974), Werner and Hall (1974) and others are:

1 predators should prefer prey that yield more energy per unit handling time;

2 as the abundance of higher value prey increases in the environment, lower value prey should be dropped from the diet and predators should become more selective (Stephens and Krebs 1986; Sih and Christensen 2001).

Fish were used in some of the first tests of optimal foraging theory (OFT) (Werner and Hall 1974; Kislalioglu and Gibson 1976; Mittelbach 1981), and a number of articles have reviewed the application of OFT to understanding fish diet selection and feeding behaviour (Werner and Mittelbach 1981; Townsend and Winfield 1985; Hart 1986, 1989). In addition, two general reviews of OFT by Stephen and Krebs (1986) and Sih and Christensen (2001) have evaluated the overall success of OFT in predicting predator diets, including those of fish. What can we conclude from these and other studies about the applicability of OFT to understanding diet choice in fish? As Sih and Christensen (2001) note, this is a bit like asking whether the glass is half full or half empty. In many ways, OFT has been successful. Fish do prefer to feed on prey that yield higher energetic returns. However, we now recognize that other factors besides handling time need to be considered in measuring the cost of feeding on a prey item. In particular, for evasive prey, we need to also include the probability of capture $(P_i(s))$ in calculating the expected energetic return from prey type i (Christensen 1996). Also, for some prey types, digestive time may need to be included in the total 'handling' time for a prey item, although current evidence suggests that including

digestive time may not change the relative rankings of prey types (Kaiser et al. 1992; Nilsson 2000). Some studies have shown that prey selection by a fish changes as the stomach of the fish fills. A review of this area can be found in Clark and Mangel (2000).

Fish have also been shown to follow the OFT prediction that diets should become more selective as the abundance of more profitable prey increases in the environment (Werner and Hall 1974), and in a few cases predicted diets based on OFT closely matched observed diets (Mittelbach 1981; Galis and de Jong 1988; Persson and Greenberg 1990). However, in most cases, fish consumed some prey outside the optimal diet. The reviews by Stephen and Krebs (1986) and Sih and Christensen (2001) list 18 studies that tested the predictions of OFT with fish. In only a few of these studies (<20%) was there a good quantitative fit between predicted and observed diets. Given the simplicity of most optimal diet models, and the fact that these models do not incorporate many important components of feeding behaviour such as prey detection and recognition, prey capture success, predator learning and memory, it is not surprising that a quantitative fit between theory and observation is missing. However, most (>80%) of the fish studies reviewed by Stephen and Krebs (1986) and Sih and Christensen (2001) found at least qualitative agreement between predicted and observed patterns of diet selection. Further, the usefulness of OFT may extend beyond the study of feeding behaviour, as OFT provides one of the few means of predicting how the attack probabilities for a prey type $(P_i(a)$ in equation 11.2) should change in different environments. These attack probabilities are needed if we are to use a foraging model such as equation 11.2 to predict fish feeding rates under different environmental conditions.

11.3   FORAGING MODELS AND FISH GROWTH

Fish ecologists are often interested in understanding whether fish will grow better in one lake than in another or how a change in the prey resource

will affect fish growth rates. One approach to addressing this problem is to relate fish feeding rates to the abundance of prey in the environment (see also Jobling, Chapter 5, this volume). Foraging models provide a potential link between measures of prey abundance in the field and the expected energy intake of fish. Mittelbach and Osenberg (1994) reviewed four studies that used optimal foraging models to predict the growth or feeding rates of fish in the field. They found that in each case the predictions of the foraging models were well correlated with the performance of the fish. A simpler measure of prey abundance, the total biomass of prey available, was less successful at predicting fish growth rates. For example, total zooplankton biomass was unrelated to the growth of planktivorous bluegill sunfish (*Lepomis macrochirus*) in Michigan lakes (Fig. 11.2a), whereas the predicted feeding rate, calculated using equation 11.2 and the available zooplankton size–density distribution, was well correlated with bluegill growth (Fig. 11.2b). Hart and Connellan (1984) also showed that prey profitability, expressed as energy gained per handling time, had a significant effect on pike (*Esox lucius*) growth rates in the laboratory.

Mittelbach and Osenberg (1994) showed theoretically that available prey biomass will not be a good predictor of fish feeding rates or growth rates, except under fairly restrictive circumstances. Therefore, we will generally need to use some type of foraging model in order to translate prey availabilities into expected energy gains to the fish. However, Mittelbach and Osenberg (1994) also found that 'optimality' *per se* was often not a critical factor in predicting fish foraging gains. Rather, it was the effect of prey size on encounter rates and handling times that had the largest impact on predicting fish feeding rates (see also Osenberg and Mittelbach 1989; Persson 1990). Thus, the value of using optimal foraging models such as equation 11.2 to translate prey abundances into potential feeding rates may derive more from specifying the critical components of the foraging process, such as encounter rates, than from accurately predicting optimal diets.
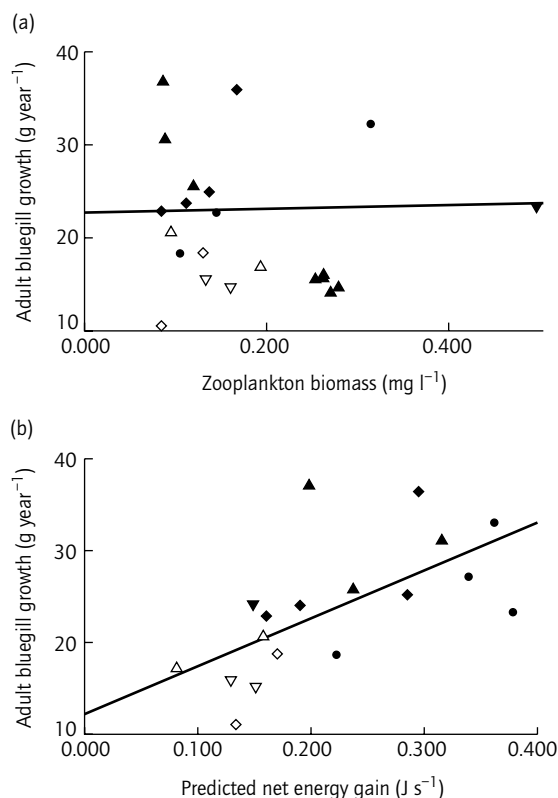
Fig. 11.2 (a) Average growth of adult bluegill as a function of the total biomass of zooplankton (dry mass, cladocerans only) available in seven Michigan lakes. Each point represents a specific lake/year combination, with each lake represented by a different symbol. (b) Adult bluegill growth as a function of the predicted net energy gain calculated using equation 11.2 and the size–density distribution of zooplankton available in these same lakes. (Source: modified from Mittelbach and Osenberg 1994; reproduced by permission of the University of South Carolina Press.)

11.4 FEEDING RATE AND GROUP SIZE

Fish feeding rates may also be affected by group size. For example, it is often assumed that fish in shoals suffer a decrease in individual feeding rates due to competition (Pitcher 1986). This assumption may well be true for fish in pelagic habitats (Eggers 1976). However, in structurally complex

habitats foraging in a group may actually increase individual fish feeding rates. For example, Pitcher et al. (1982) demonstrated that goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*) located artificial food clumps in the laboratory more rapidly when group size increased. However, Pitcher et al. (1982) did not measure the effect of group size on individual feeding rates, which is the critical parameter. Mittelbach (1984) showed that individual feeding rates of juvenile bluegill hunting for benthic amphipods first increased with group size and then decreased. In these experiments, foraging rates increased with group size because individual fish occasionally 'flushed' prey that they were unable to capture but were subsequently captured by other fish in the group. However, data on the effects of group size on individual feeding rates in complex environments are very limited. More empirical work is needed to determine if group size affects feeding rate and what direction this effect may take in different types of environments. If feeding rate decreases with group size, while protection from predators increases with group size, an optimal group size may result. However, such optimal group sizes are unlikely to be stable, as individual fish should tend to join a group rather than remain on their own (Clark and Mangel 1984; Pitcher 1986).

11.5 FORAGING AND HABITAT SELECTION

Ideal free distribution (IFD) theory has guided the study of habitat selection in fish and other foragers since its inception some 30 years ago (Fretwell and Lucas 1970; Fretwell 1972; see also Brown 1969; Orians 1969; Parker 1970). IFD theory is based on the optimal foraging principle that animals should select habitats that maximize their fitness, which is equated with feeding rate in the simplest IFD models, and on the assumption that feeding rates are density dependent. Here I examine the foraging behaviours of fish in light of IFD theory and general principles of optimal habitat selection. The literature on this topic is vast and my review only skims the surface of this conceptually rich subject.

11.5.1 Ideal free distribution

In the simplest version of the IFD, food is supplied to a foraging habitat or patch at a fixed rate, where it is consumed immediately. If predators are 'free' to select among patches, have perfect or 'ideal' knowledge of the rates of resource supply and do not differ in their competitive abilities, then we expect the number of predators in a patch to be proportional to the total food input to that patch. This is called the 'input-matching rule'. A number of experimental studies have tested the input-matching prediction, including studies by Milinski (1979, 1984) with sticklebacks (*Gasterosteus aculeatus*), Godin and Keenleyside (1984) with cichlids (*Aequidens curviceps*) and Abrahams (1989) with guppies (*Poecilia reticulata*). These studies and others (see Parker and Sutherland 1986; Tregenza 1995 for reviews) show that the number of fish foraging in a patch is often proportional to the rate of resource input, supporting the input-matching prediction of IFD. However, the further prediction of IFD theory, that the feeding rates of individual foragers should be equal in all patches, is rarely true (Parker and Sutherland 1986; Hugie and Grand 1998; Tregenza and Thompson 1998). A number of factors can lead to unequal feeding rates among individuals, including unequal competitive abilities. Simple IFD models have been modified to include the impact of unequal competitors (e.g. Parker and Sutherland 1986; Sutherland and Parker 1992), and in these models it is the sum of the competitive units that is predicted to match the input of resources to a patch. This is called the input-matching of competitive units. However, different combinations of numbers and types of competitors may satisfy this prediction. A recent study by Hugie and Grand (1998) suggests that even when foragers differ in their competitive abilities, the expected distribution of foragers predicted by IFD models with unequal competitors will tend to match the predictions of simple IFD models. Hugie and Grand (1998) review a number of studies with fish that support their hypothesis.

Classical IFD models assume a continuous input of resources into a patch and immediate

consumption of resources by the foragers. These models differ from 'standing-stock' IFD models, where food availability in a habitat is characterized by the density of the resource standing stock (Kacelnik et al. 1992; van der Meer and Ens 1997; Weber 1998). Natural environments are more closely mimicked by standing-stock models, where a predator's feeding rate within a habitat is determined by the standing stock of its prey. This, of course, is also the assumption of classical predator–prey models (Taylor 1984). We can use a foraging model such as equation 11.2 to predict predator feeding rates from prey standing stock, although in most cases a simpler version of Holling's disc equation is used. For example, Mittelbach (1981) and Werner et al. (1983a) used a variation of equation 11.2 to predict the potential feeding rates of bluegill sunfish feeding in the open water, the vegetation and on the bare bottom of Michigan ponds and lakes. They found that large bluegill, which were not threatened by predators, foraged mostly in the habitat with the highest predicted energy gain. Thus, the fish behaved according to OFT.

The foraging model used by Mittelbach (1981) and Werner et al. (1983a) assumes that there is no interference between predators and that feeding rates are a function of prey density. In this case, all fish should feed initially in the habitat that provides the highest foraging return. However, we expect relative habitat profitabilities to change as prey are depleted within a habitat, causing fish to switch habitats. In the studies of Mittelbach (1981) and Werner et al. (1983a), habitat profitabilities did change through time and large bluegill were able to track these changes, switching habitats to feed where there was the highest predicted energy gain. Theoretically, if foragers are of equal competitive ability, this system should settle into an equilibrium where the distribution of foragers among habitats results in each habitat yielding the same feeding rate (Lessells 1995; Oksanen et al. 1995). Habitats that have higher prey productivity will have higher forager densities. However, equilibrium is unlikely in a strongly seasonal environment such as in the bluegill study, where predator and prey dynamics vary in response to changing environmental conditions. In a more constant environment, equilibrium may occur. Power's (1984) classic study of armoured catfish (Loricaridae) feeding on periphyton (attached algae) in a Panamanian stream may be one such case. In Power's (1984) study, algal productivities differed among stream pools due to differences in shading. The density of armoured catfish was directly proportional to the percentage of open canopy over the stream. However, algal standing crops and Loricaridae growth rates, and estimates of their feeding rates, were similar in both sunny and dark pools. Power's (1984) results therefore match the predictions of ideal free habitat selection based on consumer–resource dynamics (Lessells 1995; Oksanen et al. 1995).

A number of studies have considered how interference amongst predators may affect predicted habitat distributions in standing-stock IFD models (e.g. Sutherland and Parker 1985, 1992; Parker and Sutherland 1986; Ruxton et al. 1992; Lessells 1995; Moody and Houston 1995; Stillman et al. 1997; van der Meer and Ens 1997). In these models, predator intake rate is assumed to decrease with increasing predator density as the result of interference. Predicted habitat distributions in these models are sensitive to the way in which interference is incorporated into the predator's functional response (Stillman et al. 1997; Weber 1998). However, the results of Free et al. (1977), Lessells (1995) and Oksanen et al. (1995) suggest that patterns of habitat use derived from models of ideal free habitat selection and consumer–resource dynamics may hold true unless interference is quite strong. For example, the armoured catfish studied by Power (1984) are known to exhibit feeding interference, yet their habitat distribution closely matched the predictions of IFD theory.

11.5.2 Incorporating costs of habitat use

Abiotic costs

IFD theory assumes that predators pay no cost in choosing habitats, hence the epithet 'free'. However, in nature costs are real. For example, Tyler and Gilliam (1995) considered the abiotic cost of

stream fishes that hold a position and that feed on prey that drift by. They argued that while faster-flowing sites may deliver prey at a higher rate, these sites may be more costly in terms of energy expended in holding a position and in terms of a reduced probability of successfully capturing faster-drifting prey. Both of these costs have been shown to be important in the choice of habitats by stream fishes (Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993). Tyler and Gilliam (1995) incorporated these costs into an IFD model and compared the predicted distributions of stream fishes under the IFD with costs to that of the simple IFD, using blacknose dace (*Rhinicthys atratulus*) in a laboratory stream. They found that the IFD incorporating costs did a better job of predicting the fishes' habitat use than did simple IFD theory.

Predation risk

The natural world is a dangerous place for predator and prey alike (see Krause et al., Chapter 13, this volume). Risk of injury or death is another potential cost of habitat choice. Fish and other organisms have been shown to respond to predation risk in choosing habitats. For example, Mittelbach (1981) and Werner et al. (1983a) found that large bluegills, which were relatively immune to predators, foraged in the habitats that yielded the highest energy gain. However, smaller bluegill, which were vulnerable to predation by largemouth bass (*Micropterus salmoides*), were more limited in their habitat use. Small bluegills fed in the protection of the littoral zone vegetation, even though the open-water habitat yielded a higher feeding rate and better growth (Werner et al. 1983b; see also Werner and Hall 1988). Thus, small bluegill appeared to trade-higher energy gain for a lowered predation risk. These and other studies (Milinski and Heller 1978) prompted theoreticians and empiricists to investigate the balance between foraging gain and predation risk, focusing on two main questions: (i) what was the optimal habitat choice that would maximize fitness and (ii) how did fish and other foragers respond to predation risk and

energy gain, and was their response consistent with maximizing fitness?

The difficulty in developing a theory of optimal habitat choice that incorporates both predation risk and foraging return is that these factors are expressed in very different units, predation risk as the probability of death per unit time and foraging return as energy gained per unit time. Abrahams and Dill (1989) approached this problem by using a fish's behaviour to evaluate how much of an increase in energy gain is required to get a fish to accept a given increase in mortality risk. Abrahams and Dill (1989) used IFD theory to quantify the energetic equivalence of predation risk for guppies feeding in two laboratory habitats. In their experiment, food was delivered at different rates in the two habitats, and they found that in the absence of predators guppies distributed themselves between habitats as predicted by the input-matching rule of IFD theory. Adding a fish predator to one of the habitats caused some of the guppies to shift to feeding in the safer habitat. The difference in per-capita feeding rates between the safe and dangerous habitats therefore provided a measure of the energetic equivalence of predation risk. This assumed that an individual's predation risk does not change with group size (Moody et al. 1996). In a second experiment, Abrahams and Dill (1989) increased feeding rates in the risky habitat by the amount predicted to offset the influence of predation risk. They found that the additional food resulted in a similar number of guppies using both the risky and safe habitats; female guppies, however, fit the predicted response better than males. Grand and Dill (1996) adopted this same approach to examine the use of cover by stream-dwelling coho salmon (*Oncorhynchus kisutch*). In nature, cover provides the salmon with protection from predators but may also result in reduced food availability. Grand and Dill (1996) used IFD theory to quantify the energetic equivalence of cover to the fish and then calculated how much additional food would have to be added to a risky patch in order to make it of equal value to a safe patch. When they added this additional amount of food, the fish returned to the distribution they had before the risk became

evident. Thus, the experiments of Abrahams and Dill (1989) and Grand and Dill (1996) show that fish can balance energy gain and predation risk in choosing habitats and that IFD theory provides a means of empirically equating these two factors.

The above studies provide an example of an empirical approach to equating energy gain and predation risk in determining habitat choice. However, in order to predict habitat use a priori, predation risk and foraging gain must be modelled in a common currency associated with individual fitness. Gilliam (1982) developed the first of these models, using the methods of optimal control theory. Stephens and Krebs (1986) provide a description of the theory and see also Werner and Gilliam (1984). Gilliam (1982) found that in the simplest case, where fish are of pre-reproductive size, population size is constant and mortality rate within a habitat is constant, then the habitat choice that maximizes a fish's fitness is selection of the habitat that minimizes the ratio of mortality rate (μ) to growth rate (g). That is, select the habitat which provides a unit of growth at the lowest mortality cost. This result was quickly labelled the 'μ/g rule' or Gilliam's rule and it had a profound effect on the development of subsequent theory of habitat selection incorporating predation risk and foraging gain. In particular, Ludwig and Rowe (1990) and Rowe and Ludwig (1991) incorporated time constraints into the predictions of optimal habitat choice, and Houston et al. (1993) developed a set of general models that incorporate the models of Gilliam (1982), Ludwig and Rowe (1990) and others as special cases. Mangel and Clark (1986, 1988) and Clark and Mangel (2000) show how questions of optimal habitat choice can be approached using the methods of dynamic programming, and Houston and McNamara (1999) summarize much of the theoretical development and predictions of state-dependent models with regard to optimal habitat choice under predation risk.

Do fish select habitats so as to optimally balance foraging gain and predation risk using the 'minimize μ/g rule' or some variant thereof? Clearly, a large number of studies show that both predation risk and foraging gain may influence the habitat use of fishes, and in the past 15 years several hundred papers have been published on this topic (see reviews in Dill 1987; Lima and Dill 1990; Lima 1998a,b). While many of these studies show that fish respond to the foraging gain/predation risk trade-off in an adaptive manner, few studies have actually tested specific models of optimal habitat choice in fish. Gilliam and Fraser (1987) tested a modification of the μ/g rule in the habitat choice of juvenile creek chubs (*Semotilus atromaculatus*). They showed that when fish have the choice between feeding in two or more habitats that differ in energy gain and predation risk, and when the fish may also use a refuge that contains no food and therefore has no predation risk, the μ/g rule collapses to the simpler rule, 'when foraging, minimize the ratio of mortality rate to gross foraging rate (f)'. Gilliam and Fraser (1987) tested the 'minimize μ/f' prediction by offering juvenile creek chubs a choice between two foraging areas that differed in experimentally manipulated resource densities and mortality risk from adult creek chubs. They found that the creek chubs choice of foraging habitats agreed well with the theoretical predictions (Fig. 11.3). In this study, the optimal habitat choice boiled down to a rather simple rule of thumb: prefer habitat A over habitat B if $\mu_A/f_A < \mu_B/f_B$, or, rearranging, prefer habitat A if $\mu_A/\mu_B < f_A/f_B$. Thus, foragers need only evaluate the relative mortality risks in two habitats compared with the relative feeding rates in order to make the correct habitat choice.

The natural world is of course much more complicated than the simple experimental environment in which Gilliam and Fraser (1987) tested their creek chubs. In particular, one of the realities of nature is that the predation risk within a habitat may vary through time (Sih et al. 2000). For example, an individual's risk within a habitat may decline when more foragers enter the habitat (a dilution of risk) due to increased vigilance by the group, predator satiation or predator confusion (Milinski and Heller 1978). A number of researchers have considered how changes in predation risk with group size may impact habitat choice within the context of IFD theory (e.g. McNamara and Houston 1990; Moody et al. 1996);
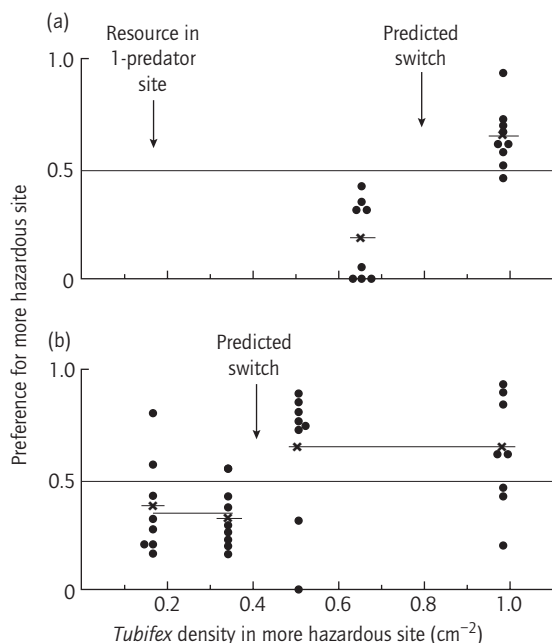
Fig. 11.3 Predicted and observed habitat selection by juvenile creek chubs: (a) habitat preference in experiments where habitats contained either one or three predators; (b) habitat preference in experiments with habitats containing one or two predators. The x-axis shows the density of resources (*Tubifex* worms) in the habitat with the higher mortality risk; the y-axis shows the observed habitat use (measured as preference for the riskier habitat). The vertical arrows labelled 'Predicted switch' indicate the density of resources in the riskier habitat, where the fish are predicted to switch from feeding in the safer habitat to feeding in the riskier habitat. Points represent the results of individual feeding trials. Crosses represent treatment means; horizontal bars represent pooled means for orthogonal contrasts. (Source: modified from Gilliam and Fraser 1987; reproduced by permission of the Ecological Society of America.)

Grand and Dill (1999) recently modelled this case for foragers of equal and unequal competitive ability. In general, these models predict that the dilution of risk with group size results in habitat distributions that differ from the IFD input-matching rule. Specific predictions, however, depend on the relative risk of using alternative habitats, the strength of risk dilution and the rela-

tive difference in competitive abilities among foragers (Moody et al. 1996; Grand and Dill 1999).

The more empirical aspects of predation are discussed by Juanes et al. (Chapter 12, this volume) and of prey avoidance of risk through refuge by Krause et al. (Chapter 13, this volume).

11.5.3 Habitat choice in a three-trophic-level system

A forager's risk of mortality within a habitat may also change due to the movement of their own predators between habitats. In a three-trophic-level system, predators at the top trophic level and foragers at the middle trophic level are both free to select between habitats that differ in resources at the bottom trophic level. In this situation, habitat choice by the predators and foragers can be modelled as a spatial game. Hugie and Dill (1994) modelled the situation where there are two habitats that differ in their inherent riskiness, independently of predator densities, and that differ in the rate of resource production. Foragers and predators are free to select between habitats and forager feeding rates follow the assumption of IFD theory, with resource production within a habitat being divided equally among foragers. Predator feeding rates are based on their functional response to prey density, which also determines the prey's mortality rate, and predators, being at the top trophic level, are assumed to have a constant mortality rate among habitats. Both predator and prey are assumed to choose habitats so as to maximize their net reproductive rate (R_0), which is an appropriate measure of fitness only when population size is constant over time (Stearns 1992; see Hutchings, Chaper 7, this volume for alternative fitness measures). Maximizing R_0 is the same fitness criterion used by Gilliam (1982), and Hugie and Dill's (1994) criterion of optimal habitat choice by both predator and prey is equivalent to Gilliam and Fraser's criterion of minimizing μ/f.

Hugie and Dill (1994) found that when habitats differ in their inherent riskiness, independently of predator density, foragers should prefer the less risky habitat, and the ratio of forager densities in the two habitats should be the inverse of the ratio

No interference

(a)

(b)

Interference

(c)

(d)
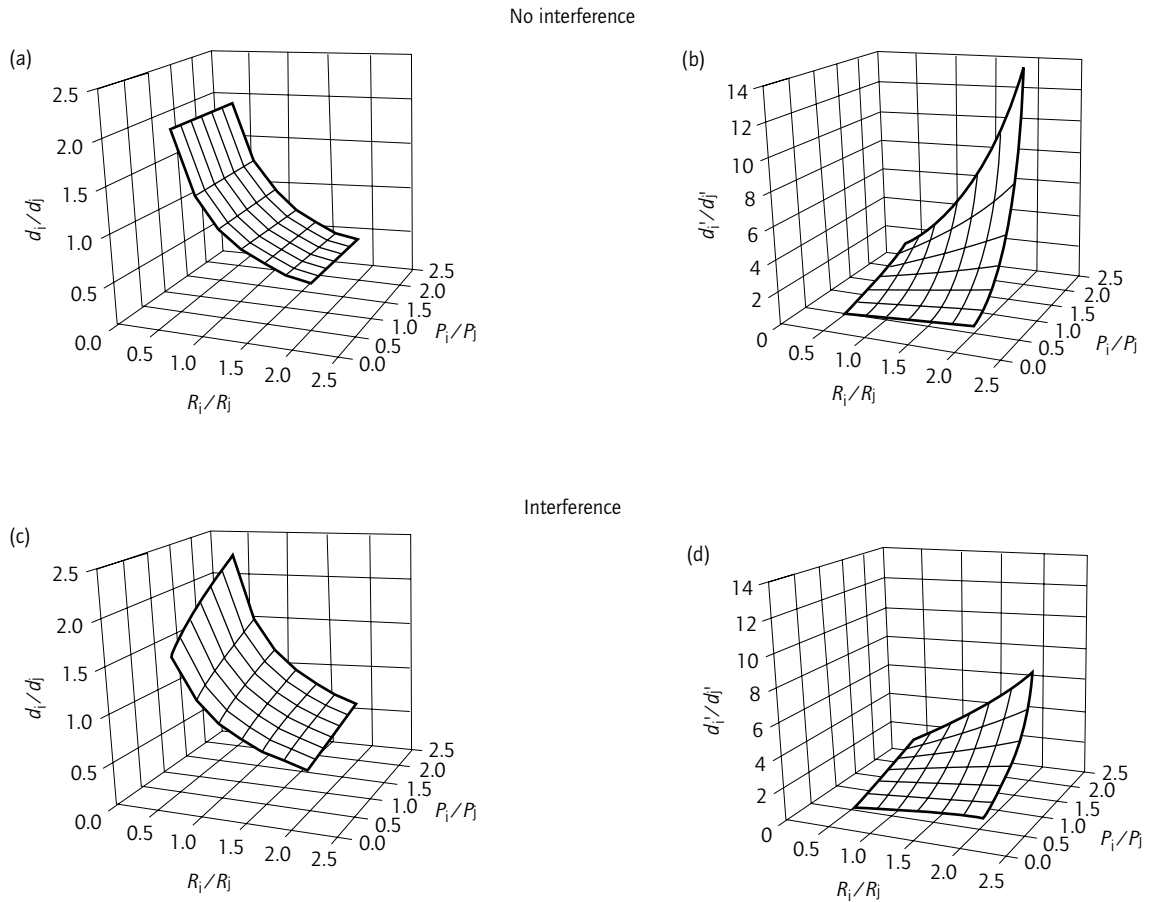
Fig. 11.4 Results of the habitat selection game between predator and prey. Habitats i and j differ in inherent riskiness (R) and productivity of the prey's food resource (P). All panels show the ratio of prey (d_i/d_j) and predator (d_i'/d_j') densities as a function of the ratios of habitat riskiness (R_i/R_j) and resource productivity (P_i/P_j). (a,b) Results for the basic model (no interference between predators); (c,d) results when predators interfere with each other's foraging ability. Note that in (a) and (b), predator density responds to differences in habitat productivities but prey density does not. In (c) and (d), both predator and prey densities respond to habitat productivities. (Source: modified from Hugie and Dill 1994.)

of the habitat risks (Fig. 11.4a). For example, if one habitat is twice as risky as another, it should have half the density of prey. There is of course considerable empirical support for the prediction that fish and other foragers should prefer the inherently less risky habitat (see reviews in Lima and Dill 1990; Lima 1998a,b). The more surprising prediction of Hugie and Dill's (1994) model is that habitat productivity should have no effect on the distribution

of foragers (Fig. 11.4a). Predator distributions, however, are dependent on both relative habitat riskiness and relative habitat productivity, and more predators will be found in the more productive habitats (Fig. 11.4b).

The results of Hugie and Dill's (1994) behavioural game between predator and prey closely parallel the predictions of ecological food web theory (Hairston et al. 1960; Oksanen et al. 1981)

based on trophic-level responses to changes in environmental productivity. In simple food-chain models with three trophic levels, the biomasses of the top and bottom trophic levels are predicted to respond positively to an increase in the productivity of the environment, whereas the biomass of the middle trophic level remains constant (Oksanen et al. 1981). In these models, changes in biomass among trophic levels are due to numerical responses brought about through births and deaths and not to movement of individuals between habitats of differing productivity (but see Wootton and Power 1993). The results of Hugie and Dill's (1994) analysis show that the same pattern of response to an increase in productivity within a habitat (i.e. an increase in the abundance of the top trophic level and no change in the abundance of the middle trophic level) can result from behavioural decisions of predators and foragers, with no change in global population size by the consumers. Wootton and Power (1993) suggest the same result, although their theoretical development of a behavioural model is limited to a short appendix to their paper. Hugie and Dill (1994) also note that if predators exhibit interference, then the abundance of both predators and foragers will depend on habitat productivity (Fig. 11.4c,d), which again is analogous to the findings of food-chain population models with interference among the top carnivores (Wollkind 1976; Mittelbach et al. 1988).

Hugie and Dill (1994) conclude their paper with the statement that 'Perhaps the single most important new insight arising from our modeling of habitat selection as a game is the prediction that prey distributions may not respond to experimental changes in food abundance, whenever their predators are free to respond in a dynamic way'. I would suggest that an equally interesting and exciting result is that behavioural models and population dynamic models predict the same pattern of trophic-level response to environmental productivity, albeit for different reasons. Schwinning and Rosenzweig (1990) examined a model system in which all three trophic levels were free to choose among habitats based on IFD criteria. They found that in general the system oscillated through time, with individuals shifting back and forth between habitats such that the three trophic levels could not achieve a simultaneous IFD. Schwinning and Rosenzweig (1990) present some of the factors that might stabilize such oscillations.

Adaptive responses by fish to predation risk and foraging gain may also lead to cascading effects in aquatic food webs. A number of studies have shown that a change in the abundance of piscivorous fish can have effects that cascade down the food chain to lower trophic levels, although these may be buffered by redundancy in marine food webs (see Polunin and Pinnegar, Chapter 14 and Persson, Chapter 15, this volume; and Kaiser and Jennings, Chapter 16, Volume 2). Such top-down effects are typically assumed to be transmitted by direct consumption of lower trophic levels by higher trophic levels. However, behavioural responses by fish and other foragers may produce the same type of trophic cascade, if an increase in the abundance of a higher trophic level causes foragers at the next lower trophic level to reduce feeding activity, shift habitats or spend more time in a refuge (e.g. Turner and Mittelbach 1990; Brabrand and Faafeng 1993).

11.6   CONCLUSIONS

In this chapter, I have used models of adaptive behaviour to provide a framework for understanding the foraging behaviour of fish. IFD theory, OFT and 'μ/g rules' all attempt to predict an animal's foraging behaviour based on the premise that energy acquisition is central to the fitness of an organism. The power of the optimality approach is that it provides a mechanism to predict, a priori, how a fish chooses its diet or selects its habitat in a given environment. These predictions can then be compared to the forager's observed behaviour in the laboratory or in the field. It is at this point, where model predictions are compared with empirical data, that a major bone of contention arises concerning the use of optimality models. Observed diets or patterns of habitat selection never precisely match the predictions of theory (see reviews by Stephens and Krebs 1986; Sih and Christensen 2001). To some, this implies that we should reject the theory and move on (e.g. Pierce and Ollason 1987). To others, qualitative agreement between

theory and data suggests that the general approach is valid and that a closer look at the mismatch between theory and data may provide a means to develop better models (e.g. Krebs and McCleery 1984; Stephens and Krebs 1986). While much has been written on this debate and other issues concerning the use of optimality models in biology, the topic remains contentious (Perry and Pianka 1997; Sih and Christensen 2001).

It is clear that quantitative studies measuring energy gain and mortality risk, or other costs of foraging, have provided a powerful framework for understanding the foraging behaviours of fish. No doubt, future studies of foraging theory will continue to wrestle with questions of how fish and other animals may evaluate potential energy gain, predation risk and other foraging costs in the 'real world' where foragers are less than 'ideal' in their knowledge and where behavioural choices are never 'free'. However, while the continued development and testing of foraging theory is important, I suggest that the opportunity to use foraging models as tools to study the population and community ecology of fishes is equally valuable. Incorporating adaptive foraging behaviour into predator–prey models can provide new insights into the predator functional response and predator–prey dynamics (e.g. Abrams 1990, 1991). Optimal foraging models may also provide a link between measures of prey abundance in the field and the predicted feeding rates of fish (Persson 1990; Mittelbach and Osenberg 1994). Finally, habitat selection behaviour provides an alternative mechanism for generating important population- and community-level phenomena in aquatic ecosystems, such as cascading effects and trophic-level responses to productivity.

ACKNOWLEDGEMENTS

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12 Feeding Ecology of Piscivorous Fishes

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12.1 INTRODUCTION

Fish exhibit tremendous diversity in feeding habits and the morphologies associated with feeding. A recent book (Gerking 1994) and various other overviews of fish feeding exist (Wootton 1990; Hobson 1991; Hart 1993). However, most of these tend to be general reviews of theory or focus on smaller non-piscivorous fishes. Our intent here is to review the feeding ecology of piscivorous fish, a subject which to our knowledge has never previously been reviewed. We focus on teleost fish, and on species and sizes that consume juvenile and adult prey and do not consider those that feed primarily on larvae or fish eggs.

12.1.1 Why piscivorous fish?

Piscivorous fish are broadly distributed phylogenetically and geographically, occur in most habitats and generally occupy the top of most aquatic trophic webs. Piscivorous fish also generally achieve the largest body size within fish communities, are represented by some of the largest species (many elasmobranchs, tunas, billfishes) and have potentially large impacts on their communities through predation. Finally, many piscivorous fishes, because of their ubiquity and large body size are among the most valuable harvestable species in many of the world's fisheries. In some cases, they compete with humans for commercially important resource species (V. Christensen 1996; Buckel et al. 1999a). Piscivorous fish as a

group, however, are difficult to categorize and describe, which perhaps explains why no reviews of their ecology exist.

12.2 ADAPTATIONS FOR PISCIVORY

12.2.1 What is a piscivore?

We define piscivorous fish as carnivorous fish that consume primarily fish prey. Most fish species are opportunistic and flexible in their feeding habits (Dill 1983) and no species consumes only fish prey; however many do ingest fish as the main prey item. Fish that eat other fish are second in proportion to those feeding on benthic invertebrates and are present in a variety of freshwater, estuarine and marine systems. They are equally common in tropical and temperate ecosystems. Keast (1985) examined the piscivore feeding guild of small lakes and streams and categorized piscivorous fish into primary and secondary piscivores. Primary or 'specialized' piscivores shift to piscivory within the first few months of life, whereas secondary piscivores only become fish-eaters later in life. Keast further suggests that secondary piscivores switch to fish as a way to maintain energetic efficiency as they grow. This can only be achieved by eating progressively larger prey and, at a certain point, fish are the only prey available. Furthermore, secondary piscivores are not structurally adapted for piscivory other than acquiring a large mouth as they age.

12.2.2 *What are the adaptations for piscivory?*

Feeding behaviours and morphological adaptations

When observed in detail it becomes clear that piscivore feeding behaviour is complex and flexible in dealing with different prey types. Behaviours can generally be grouped into the following categories, which are also associated with particular morphological adaptations.

Luring Luring is a sit-and-wait behaviour where prey are attracted by a 'lure', which consists of a stalk topped by a device that resembles a source of food; the lure is a modification of the first dorsal spine (Gerking 1994). Luring is typical of the anglerfish (order Lophiiformes). In addition, among the frogfish various morphological features allow the predator to blend into the rocky environments in which they live as a form of camouflage. Anglerfish have a considerable gape and ingest prey sizes that are large compared to other piscivores.

Stalking Stalking is the unobtrusive pursuit of prey before the attack occurs. This strategy is common to trumpetfish (Aulostomidae), longnose gar (Lepisosteidae) and needlefish (Belonidae). These species have similar morphologies, long slender bodies with a long snout and sharp teeth.

Chasing Large piscivores are able to chase and 'swim-down' prey. This strategy is best represented by the billfish (Xiphiidae and Istiophoridae) and some tuna (Scombridae) and yellowtail or pompano (Carangidae). These fish must be able to attain high cruising and accelerating speeds. Their bodies can be described as thunniform or carangiform, where thrust is maximized by a lunate tail with a high aspect ratio, a narrow caudal peduncle that minimizes sideways thrust and a large anterior body depth that minimizes recoil of the head end. These same features, along with a relatively rigid and streamlined body, also minimize drag (see Brix, Chapter 4, this volume). Chasers can be either lungers, such as the pike (*Esox* spp.), where attacks are started at close range from an S-shaped position,

strikes occur at high speed and missed prey are rarely pursued, or they can be pursuers such as trout (*Salmo trutta*), where attacks start from a C-shaped position, strikes occur at low speeds from a short distance and missed prey are chased.

Ambush This strategy is used by species that attack from seclusion, although an element of chasing may also occur. Examples are morays (Muraenidae), pike (Esocidae) and summer flounder (Pleuronectidae). Few morphological similarities exist in species that use this behaviour other than the ability to use camouflage and high-speed attacks. However, distinct patterns of kinematic, pressure, electromyographic and behavioural profiles of prey capture are exhibited by ambushers and pursuers.

Other A variety of other rarer feeding habits each with their own specialized morphologies, particularly in the dentition, include forms of parasitism such as blood-sucking in lampreys (Petromyzontidae) and catfishes (Trichomycteridae and Cetopsidae), scale-eating in many cichlids and characoids, and fin and eye-biting (Gerking 1994).

A novel feeding behaviour common to planktivores has recently been observed for a few species of piscivores (Sazima 1998). Ram suspension (or filter) feeding is defined as swimming through the water with the mouth wide open and opercles flared as a way of filtering small prey items out of the water column without directing attacks towards individual prey. This may be a mechanism used by piscivores feeding on relatively small prey in high concentrations (B. Hanrahan and F. Juanes, personal observation).

Most piscivores ingest their prey whole. A few species are able to tear off and ingest pieces and good examples are piranhas (*Serrasalmus* spp.) and African tiger fish (*Hydrocyon vittatus*). The most detailed analysis of partial prey eating has been performed for bluefish (*Pomatomus saltatrix*) (Juanes and Conover 1994a; Scharf et al. 1997). Juvenile bluefish switch from taking prey whole to partial prey consumption when the prey to predator size ratio is about 0.35 independent of

prey type (Scharf et al. 1997). This ability allows bluefish to attack much larger prey sizes than can predators of similar size and is likely to be a function of specialized musculature and dentition. Bluefish are also unique in that they ingest prey tail-first, whereas most other piscivores that have been examined eat prey head-first. Tail-first ingestion may be a result of pursuing prey rather than ambushing it, or a way to reduce prey mobility thereby increasing prey vulnerability, as has been observed in piranhas.

Schooling in predators

Schooling by prey is generally thought of as an adaptation for evading, confusing and reducing the efficiency of predators (Pitcher and Parrish 1993). Schooling also has hydrodynamic and foraging functions. Little empirical work has been done on whether schooling by predators enhances predation efficiency in piscivores. Field studies have shown that, in general, group attacks tend to result in higher capture success rates (Pitcher and Parrish 1993). Eklöv (1992) has shown that the foraging efficiency, measured as growth rate, varies between a group-foraging, actively searching piscivore (Eurasian perch, *Perca fluviatilis*) and a solitary-foraging, stalking piscivore (pike, *Esox lucius*). Under similar conditions, grouped perch grew more than single perch or grouped pike. In contrast, solitary pike grew better than solitary perch or grouped pike. Schooling in piscivores may have foraging costs and benefits. Prey encounter rates may be maximized but the probability of losing a prey item to kleptoparasitism is also greater when predators attack in groups (Juanes and Conover 1994a). There has been anecdotal information collected that suggests that some piscivorous fish hunt cooperatively (Pitcher and Parrish 1993), although potential mechanisms have not been quantified under controlled conditions.

Active piscivorous pelagic fishes are characterized by a range of length to maximum depth ratios (the fineness ratio), which ranges from 4.0 to 6.5 and which maximizes feeding efficiency and minimizes drag (Blake 1983). Bluefish, a primary piscivore that switches to fish prey at about 40 mm total length, has a fineness ratio between 3.5 and 5.0 (Juanes et al. 1994). Interestingly, offshore invertebrate-feeding juveniles (<40 mm) are already morphologically specialized for piscivory, suggesting a trade-off between feeding efficiency and future diet. A result of this trade-off may be to accelerate the onset of piscivory.

Life history

Onset of piscivory Most piscivorous fish undergo ontogenetic shifts in diet (Werner and Gilliam 1984; Keast 1985; Winemiller 1989). These shifts generally progress from consumption of zooplankton to consumption of benthic macrofauna or prey fish, with a concomitant increase in mean prey size as predators grow. There is much variation in the timing of the shift to piscivory among primary and secondary piscivores (Mittelbach and Persson 1998; Mittelbach, Chapter 11, this volume). A few species of scombrids apparently forgo the zooplanktivorous stage and start eating fishes at first feeding, whereas others shift early in the larval period (Tanaka et al. 1996). The shift to piscivory invariably results in an increase in predator growth rate (Buijse and Houthuijzen 1992; Juanes and Conover 1994b; Olson 1996). Among the scombrids studied by Tanaka et al. (1996), there was a direct correlation between the age at the onset of piscivory and early growth, with those species shifting to piscivory at first feeding capable of reaching 100 mm during the first month of life.

Within fish cohorts, the largest individuals are often able to switch to piscivory while the smallest are delayed and experience reduced growth. This effect leads to the often-observed bimodality in size distribution of juvenile piscivores (Adams and DeAngelis 1987; Frankiewicz et al. 1996). Because survivorship is generally size-selective in fish (Sogard 1997), bimodality can result in increased mortality of individuals in the smaller size mode (Olson 1996).

What allows species to shift to piscivory? The timing of the onset of piscivory depends on predator morphology, predator and prey phenologies, prey abundance and abiotic factors. Clearly predators

have to be larger than their prey in order to be able to ingest them. Large body size and large mouth gapes are therefore generally considered an important constraint on prey use, particularly piscivory (Werner 1977; Wainwright and Richard 1995; Mittelbach and Persson 1998). Biomechanical features such as jaw mechanics and tooth development have also been implicated (Jenkins et al. 1984; Wainwright and Richard 1995). Among piscivorous scombrids, ontogenetic development of the digestive system (Tanaka et al. 1996) and development of the visual system (Margulies 1997) have been correlated with the onset of piscivory. Walleye (*Stizostedion vitreum*) generally shift to piscivory between 30 and 60 mm in length but are able to ingest larvae when they are as small as 10 mm; the earlier onset of piscivory may be related to the abundance of prey in appropriate size ranges (Mathias and Li 1982). However, because the switch to piscivory is most often preceded by an invertebrate-feeding stage, piscivores must ensure rapid growth during that phase so that when fish prey are available the feeding shift can occur. If growth is slowed during the invertebrate-feeding stage, the piscivore size advantage over its fish prey is reduced leading to delays in the shift to piscivory (Olson 1996). Environmental factors such as low temperatures early in the growing season can also reduce growth and delay piscivory (Buijse and Houthuijzen 1992; Olson 1996).

Is acceleration of the onset of piscivory adaptive?
Because of the dramatic increase in growth rate following the shift to piscivory and because size-selective mortality is so prevalent among juvenile fishes (Sogard 1997), natural selection should favour life-history strategies in piscivores that minimize the length of the zooplanktivorous phase. One such strategy to attain an acceleration of the onset of piscivory would be to match the timing and location of spawning with the availability of fish prey. Freshwater primary piscivores have evolved the ability to spawn earlier than other fishes, thereby attaining sufficient size to allow them to consume juvenile fish spawned later in the same year. This pattern has been observed in largemouth bass (*Micropterus salmoides*), pike

and walleye (Forney 1971; Keast 1985). Among marine fish it is much more difficult to examine the timing of predator and prey spawning. However, bluefish appear to have evolved a life-history strategy whereby they are spawned at approximately the same temperature as their future prey but at a more southern latitude. This divergence allows bluefish to attain the size advantage required when they shift to piscivory after being advected to higher latitude estuaries where their prey are abundant.

In a recent review of the freshwater fish literature, Mittelbach and Persson (1998) showed that those species born larger and with larger mouth gapes become piscivorous at younger ages and smaller sizes, although they did not find a relationship between spawning temperature, used as an indicator of timing, and size at the shift to piscivory or size at age 1. However, species that accelerated the onset of piscivory by shifting early were larger at age 1 and continued to be larger through later ages.

A potential cost of early onset of piscivory is reduced growth and survival if habitat conditions dictate prey abundance. Furthermore, because most piscivores are strongly size-selective (Juanes 1994), if availability of appropriately sized fish prey is delayed, growth may be reduced (Buckel et al. 1998).

Resource polymorphisms

Adaptive trophic specialization can in some cases lead to the evolution of resource polymorphisms, where trophically and morphologically specialized morphs can coexist and ultimately speciation can occur. Among fishes various examples of trophic polymorphisms include piscivorous morphs. For example, in Arctic charr (*Salvelinus alpinus*), four trophic morphs are often recognized. The four morphs have differing life-history strategies, morphologies and behaviours that are genetically based (Skulason et al. 1993). Using life-history theory, Mangel (1996) has shown that the evolution of a large piscivorous morph in trout ('ferox' trout) can occur if the growth rates of the different asymptotic morph sizes differ and if

there is size-dependent mortality. Other aspects of alternative life-history evolution caused by competitive reproductive behaviour are reviewed by Hutchings (Chapter 7, this volume).

12.3 COMPONENTS OF PREDATION

12.3.1 *Search, encounter, pursuit, capture, handling*

For a prey fish to be included in the diet of a predator, it has to be located, pursued, captured, manipulated or handled, and finally digested (Mittelbach, Chapter 11, this volume). Each of these steps must be performed successfully by the predator in order for the predation process to be complete. Therefore, prey have several opportunities to avoid being eaten during the course of the interaction. The first of these is to not be detected. Predators have evolved various modes of searching for prey. At the same time, prey have evolved an assortment of behaviours to reduce their chances of being detected by potential predators (Krause et al., Chapter 13, this volume). The probability of any one prey being encountered will then be determined by the morphological and behavioural characteristics of both predator and prey.

Most predators that consume motile prey, such as fish, utilize one of two basic search/encounter modes: ambush or sit-and-wait tactics and cruising tactics as described earlier. The types and sizes of prey eaten by a predator are often associated with the foraging tactics employed. For example, Greene (1986) showed that invertebrate predators that employed ambush tactics consumed larger prey relative to cruising predators. He further demonstrated that prey encounters for ambush predators were strongly dependent on prey swimming speeds, whereas variation in prey activity had no discernible effect on encounter rates for cruising predators. Among fish, ambush predators have also been shown to take larger prey relative to more actively searching predators. The inclusion of larger prey items in the diets of ambush predators is thought to be a function of their dependence

on prey activity producing encounters and the positive relationship that exists between body size, prey movement and detectability.

The estimation of encounter rates between fish predators and prey remains an elusive problem in fish ecology. Specifically, for piscivorous fishes, the mobility of potential prey means that behaviours and movement patterns of both predator and prey will ultimately affect rates of encounter. Due to the variable nature of the plethora of environmental parameters that can influence the distribution of animals in space and time, encounter rates *in situ* are virtually impossible to measure with any certainty. Laboratory tanks used for piscivores and their prey are generally too small to yield any realistic estimates of encounter rate, as all prey are usually within the visual field of a given predator. Therefore, encounter probabilities are often estimated using mathematical models that incorporate average swimming velocities of predator and prey as well as a predator detection radius (Gerritsen and Strickler 1977). Although theoretical models can be quite elegant, they remain burdened with many assumptions that often cannot be tested. Because no predation can occur without an encounter first, much future research will be devoted to better understanding the factors that contribute to variable rates of encounter.

Once prey are encountered, predators must be sufficiently capable of capturing prey for it to be eaten. Piscivorous fishes generally have lower capture probabilities compared with planktivores. Usually about half of piscivore attacks on average are successful compared with 70–80% for planktivorous fishes. Capture success in piscivores has also been shown to be directly related to relative body sizes of prey and predator, and generally declines linearly as the prey size to predator size ratio increases (Fig. 12.1). Similar size-based capture success functions have been observed for several piscivore species representing different life stages (Miller et al. 1988; Juanes and Conover 1994a). Differences in prey type have also been shown to influence predator capture success, as prey escape proficiencies vary among species (Wahl and Stein 1988; Scharf et al. 1998). The strong dependence of piscivore capture success on prey size and type
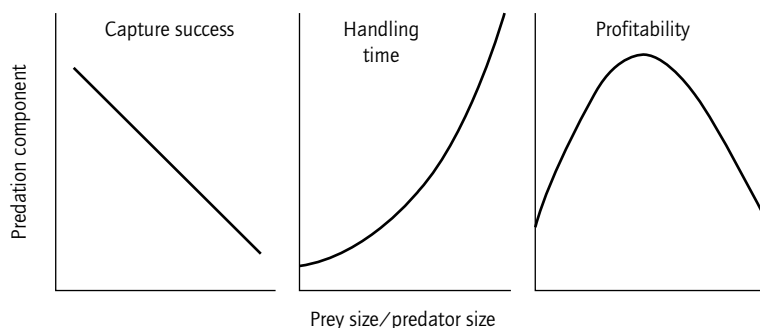
Fig. 12.1 General empirical relationships between predation components and relative prey size for piscivores.

indicates that it plays an important role in determining relative vulnerabilities to predation for different prey.

Similar to capture success, handling time in piscivorous fishes is affected by both prey size and type. Because larger prey sizes often need to be manipulated before swallowing, increasing prey size typically causes an exponential increase in handling time (Fig. 12.1). The rate of increase in handling time has been shown to be unique for specific prey types (Hoyle and Keast 1987; Scharf et al. 1998). Handling time has historically been a critical parameter to estimate, as it has frequently been used to represent the primary energetic cost of feeding in theoretical foraging models attempting to predict predator diet (Mittelbach, Chapter 11, this volume). Although foraging models have demonstrated some success in predicting diets of planktivorous fishes, past models for piscivores have often failed (Sih and Christensen 2001). More recent models that incorporate differential capture probabilities based on prey size and type have proven more successful in predicting piscivore diets (Rice et al. 1993). The combination of size-dependent encounter rates, capture probabilities, energy content and handling times can be used to construct profitability functions for specific prey types. For piscivores, these functions are typically dome-shaped curves that peak at intermediate ratios of prey size to predator size (Fig. 12.1). However, most often encounter rates cannot be estimated with confidence and curves are constructed using only capture success and handling time functions. The specific relation, for each prey type, between encounter probability and prey size will determine whether the profitability peak is shifted toward smaller or larger relative prey sizes. Accurate profitability functions that incorporate a broad range of prey and predator sizes can be extremely valuable for predicting piscivore diets.

12.3.2 Functional and numerical responses

Predatory response to variations in prey density can be grouped into two categories. The functional response refers to the number of prey eaten per predator per unit time as a function of prey density. Changes in number of predators in response to variations in prey density describes the numerical response.

Functional responses

There are several different forms of functional response. A subset of these have been classified as the type I, II and III models (Holling 1965). The type I response occurs when the number of prey eaten per predator per unit time increases linearly with increasing prey density (Fig. 12.2a). The proportion of prey density consumed stays constant and this response is also called density-independent predation (Fig. 12.2d). Most vertebrates have a type II or III functional response (Hassell 1978). The type II response is represented by a negatively accelerating curve (Fig. 12.2b); therefore, the proportion of prey density consumed decreases with increasing
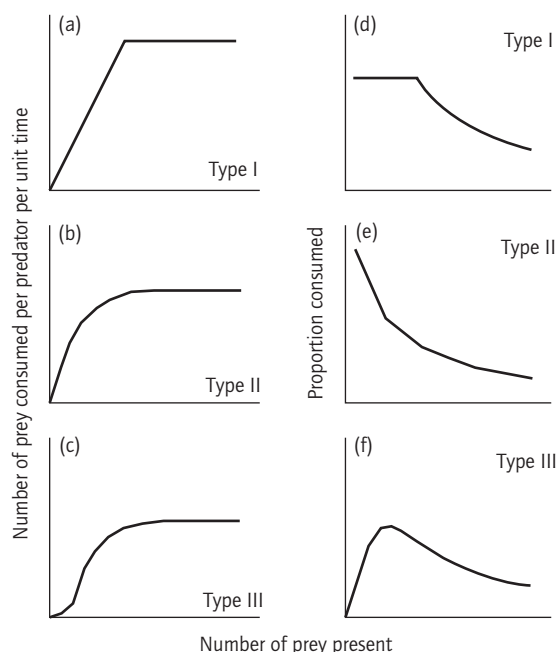
Fig. 12.2 (a–c) Shapes of hypothetical functional responses: (a) type I, (b) type II and (c) type III. (d–f) Proportion of prey consumed or percentage mortality corresponding to the functional responses: (d) type I, (e) type II and (f) type III.

prey density and is referred to as negative density-dependent predation. Under this regime the risk of being preyed upon is high at low prey densities but decreases with increasing prey density (Fig. 12.2e). Positive density-dependent predation can result when a predator feeds with a type III functional response. The shape of this function is sigmoidal (Fig. 12.2c); when the proportion of prey density consumed is plotted the slope is initially positive, meaning that the risk of being preyed upon is small at low prey densities but increases up to a certain point as prey density increases (Fig. 12.2f). Predation components such as attack rate and handling time (Section 12.3.1) can be estimated from these functions (Holling 1965; Hassell 1978).

In general, piscivorous fishes have a type II functional response. For example, type II responses were found in Arctic charr preying on migrating sockeye salmon (*Oncorhynchus nerka*) smolts

(Ruggerone and Rogers 1983) and southern flounder (*Paralichthys lethostigma*) preying on spot (*Leiostomus xanthurus*) (Wright et al. 1993). Lake trout (*Salvelinus nemaycush*) were capable of high predation rates at low prey fish densities, suggesting a type II response (Eby et al. 1995). Petersen and DeAngelis (1992) found that type II and III models gave similar fits to field data of northern squawfish (*Ptychocheilus oregonensis*) feeding on juvenile salmonids.

Although the type III functional response has not been observed with regularity, it has been proposed as a potential mechanism in regulating population abundance (see Section 12.6). Several factors can lead to a type III functional response, such as predator learning, prey refuge and the presence of alternative prey (Holling 1965). The presence and accessibility of a prey refuge has been hypothesized to be a factor leading to positive density-dependent mortality in some piscivore–prey systems (Bailey 1994; Hixon and Carr 1997). Alternative prey can lead to a type III functional response through switching behaviour (Murdoch and Oaten 1975). Prey switching occurs when the prey type with the highest relative abundance is included disproportionately more in the predator's diet than would be expected from random feeding (see Section 12.4.1 for an example).

Functional responses are critical parts of the multispecies virtual population analysis (MSVPA) method of modelling fish populations (Shepherd and Pope, Chapter 7, Volume 2). MSVPA differs from single-species virtual population analysis (SSVPA) in that interspecific and intraspecific predation are included to estimate levels of natural mortality, which in SSVPA is assumed constant. Generally, MSVPA has assumed a type II functional response, which may be reasonable for predators that do not depend on a small number of prey species, as in temperate systems, but may not be adequate for predators that do depend on few prey species, as in boreal systems. Inclusion of a type III response can have important effects on forecasts based on MSVPA, including producing more than one solution to MSVPA equations (Magnússon 1995; see also Shepherd and Pope, Chapter 7, Volume 2).

Numerical responses

Predator numbers can respond rapidly to increasing prey density, as when predators aggregate on prey fish, or can respond slowly, such as increased reproductive success (Peterman and Gatto 1978). We know little about numerical responses in piscivorous fish. This is surprising given its potential importance in regulating population levels; the lack of data stems from the logistical difficulties of measuring such a response. Whenever a predator increases in density in response to increasing prey fish density, the total predation rate response can differ from the predator's functional response. A sigmoidal response (type III) may more typically describe a piscivore's total response; the total response is a function of both the functional and numerical response (Bailey 1994).

12.4 PREY TYPE AND SIZE SELECTIVITY

Selective predation can be defined as the consumption of prey in different proportions than those available in the predator's surrounding habitat (Chesson 1978; Mittelbach, Chapter 11, this volume). This is in contrast to random feeding, where predators feed indiscriminately on prey in accordance with their relative availability. Predators that feed in a random manner with respect to relative prey abundance levels are usually referred to as opportunistic feeders because they adjust their feeding habits rapidly to match variation in the local prey field. Predators that consume a narrow range of prey types or sizes regardless of changes in the prey field are thought of as specialists and represent the most extreme case of selective predation. Most predators fall somewhere along a continuum between opportunists and specialists.

12.4.1 Observed patterns

Numerous instances of prey type and size selection by piscivorous fishes have been reported in both freshwater and marine communities. For example, Wahl and Stein (1988) used laboratory experiments and large-scale field manipulations to determine patterns of prey selection in several freshwater predators, including muskellunge (*Esox masquinongy*), tiger muskellunge, and northern pike. Results demonstrated that each of the predators consistently selected for shad prey as opposed to Centrarchid prey. The authors concluded that behavioural and morphological differences between prey types resulted in differential vulnerability to predation and the observed patterns of selection. Research on the feeding habits of piscivorous bluefish in marine waters off the northern Atlantic coast of the USA have also revealed evidence for selective predation on specific prey types. Buckel et al. (1999b) demonstrated that, during early summer in shallow estuarine habitats, juvenile bluefish consumed young-of-the-year striped bass (*Morone saxatilis*) in greater proportions than a random sampling of the prey environment, and that this positive selection was directly related to striped bass abundance. In other words, they showed prey switching behaviour as referred to in Section 12.3. During southerly autumn migrations in continental shelf waters, juvenile bluefish have also shown the propensity for selecting specific prey types, particularly bay anchovy (*Anchoa mitchilli*) (Buckel et al. 1999c). Selection for specific prey sizes may be even more prevalent than prey type selection among piscivorous fishes. A recent review of 32 laboratory and field studies concluded that selection for small prey from available size distributions was a common phenomenon for both freshwater and marine piscivores (Juanes 1994). This study also revealed that most piscivorous fishes consumed prey smaller than the optimal prey sizes predicted by energy maximization models, independent of both predator and prey type as well as predator size (Mittelbach, Chapter 11, this volume).

12.4.2 Behavioural mechanisms of selective feeding

Selective feeding can result from both morphological constraints of predators and behavioural interactions between piscivores and their prey. Predator gape size ultimately limits the sizes of prey in-

gested and can also affect the types of prey consumed. However, recent studies indicate that behavioural capabilities of both predator and prey can regulate the sizes and types of prey eaten before morphological constraints become important. In a well-designed series of laboratory experiments, B. Christensen (1996) evaluated the effects of prey antipredator behaviours on the sizes of roach (*Rutilus rutilus*) consumed by piscivorous Eurasian perch. Feeding experiments were conducted at two different spatial scales, determined by tank volumes, to control the level of antipredator behaviour expressed by the prey. In smaller arenas that limited prey escape ability, the author found that perch were able to consume large roach approaching gape limitations. In larger arenas, where prey antipredator behaviours were not suppressed, the maximum size of roach consumed by perch was significantly smaller. The author concluded that the sizes of prey eaten were largely dependent upon relative predator and prey mobility (Mittelbach, Chapter 11, this volume). Juanes (1994) hypothesized that common patterns of selection for small-sized prey by piscivorous fishes were the result of size-dependent vulnerabilities of prey to predator capture, rather than predator preferences. He proposed that many examples of selective feeding in fishes were actually passive selective processes rather than active predator choice, with attack rates being relatively equal among different prey sizes but smaller prey being consumed more frequently due to ease of capture (see also Hart and Hamrin 1990). Prey behaviour can also influence the rate of attack among different prey types available to a predator. For example, laboratory experiments demonstrated higher attack rates by goby (*Gobiusculus flavescens*) predators on herring (*Clupea harengus*) larvae compared with cod (*Gadus morhua*) larvae, with attack proportions being strongly related to differential levels of prey activity between the species (Utne-Palm 2000). Predictions of prey selection from most traditional foraging models assume that optimal choices are mainly the result of behavioural decisions by predators (Stephens and Krebs 1986). For piscivorous fish predators, the behavioural and foraging capabilities of both predator and prey can clearly alter attack and capture rates of predators and contribute significantly to the observed patterns of selective feeding.

12.5 PREDATOR-SIZE AND PREY-SIZE RELATIONSHIPS

Because they are the top predators in many aquatic systems, knowledge of the sizes of prey included in the diets of piscivorous fishes is essential in order to identify their potential impact on prey survival and their role in structuring populations at lower trophic levels. This is particularly important for the ecosystem approach to fisheries management, where knowledge of interactions is critical (Pauly and Christensen, Chapter 10, Volume 2). Further discussion of how size-dependent processes structure communities can be found in Persson, Chapter 15, this volume. From a behavioural standpoint, relative body sizes of prey and predator can have significant effects on predator feeding success. Detection and capture of prey by piscivores are enhanced with increasing size for several reasons, including increased sustained and burst swimming speeds and better visual acuity (Webb 1976). The escape proficiency of prey also varies with ontogeny as reaction distances increase and swimming abilities are improved with size (Brix, Chapter 4, this volume). Morphological characteristics that influence piscivore–prey interactions, such as predator gape size and robustness of prey morphological defences (e.g. spines), also scale with ontogeny. Therefore, identifying patterns of prey size use by piscivorous fishes can provide important clues as to the mechanisms that shape piscivore diets and the effects of predation by piscivorous fishes on community structure.

12.5.1 *General patterns and hypotheses*

For piscivorous fishes, the sizes of prey consumed generally increase with predator size. In addition, the range of prey sizes eaten typically increases in larger predators, as maximum prey size often increases rapidly while minimum prey size may
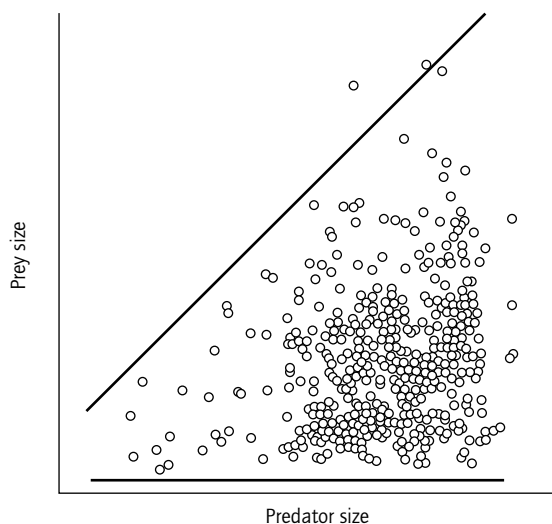
Fig. 12.3 Hypothetical predator size–prey size relationship for a piscivore, illustrating typically observed changes in minimum and maximum prey sizes consumed with increasing predator size.

change only slightly over a broad range of predator sizes (Fig. 12.3). For example, Mittelbach and Persson (1998) demonstrated increasing mean and maximum prey sizes as body size increased for 12 species of freshwater piscivores. The authors further noted that for many of the piscivores they examined, minimum prey size remained fairly constant with increasing predator body size. Scharf et al. (2000) revealed similar predator size–prey size patterns for a group of 18 marine piscivores in continental shelf waters off the Atlantic coast of the USA. Expanding prey-size ranges that retain small prey in the diet of larger piscivores means that prey sizes consumed by smaller predators can be a subset of the prey sizes consumed by larger predators, which may result in a competitive disadvantage for smaller predators (Wilson 1975). However, when the range of prey sizes eaten is examined as a ratio of predator size rather than on an absolute scale, ontogenetic changes are more subtle. For example, Pearre (1986) studied a large group of predators that included 43 species of larvae, juveniles and some small adult fishes in an effort to detect general trends in prey-size distri-

butions eaten by fish predators of varying body sizes. Based on ratio-scale analyses, he concluded that the range of prey sizes eaten did not change significantly with increasing body size for most predators and that older larger predators should not compete with smaller ones.

Although predator size–prey size relationships for piscivorous fishes are often reported, potential mechanisms that lead to the commonly observed pattern of increasing maximum prey sizes coupled with stationary minimum prey sizes are generally lacking. Scharf et al. (2000) noted that the continued inclusion of small prey in the diets of larger predators contrasts with predictions of optimal foraging models for particulate feeders, which indicate that the largest prey available should be consumed preferentially to maximize net energetic return. The authors hypothesized that the combination of high relative abundance and high capture probability for small prey relative to large prey may lead to consistently high vulnerability to predation for small prey fishes as already discussed. Because predator handling times also increase rapidly with prey size, they suggested that the retention of small prey in the diet may reflect profitable foraging decisions by predators because search, capture and handling costs remain low.

12.5.2   What determines maximum prey size?

Maximum prey sizes eaten by piscivores can be limited by several factors. Of foremost importance are morphological limitations imposed by predator gape size and throat width. Most piscivorous fishes swallow prey head first after manipulating prey so that the largest body depth is positioned laterally in the mouth (Reimchen 1991). A strong relationship between prey body depth and predator gape width has been detected for several piscivorous fishes (e.g. Hambright et al. 1991). General mouth shape and structure can also affect the types and sizes of prey that can be ingested. For example, Keast and Webb (1966) demonstrated strong relationships between mouth morphology and the feeding ecology of several freshwater fishes. The effects of piscivore gape limitations on

maximum prey sizes eaten can also impact prey populations. Persson et al. (1996) examined the potential community-level effects of predator gape limitation in a field study of predation in European lakes. Prey fishes in four lakes were exposed to two predators with different gape sizes and their populations monitored. Results indicated that prey exposed to the smaller-gaped predator reached a size refuge sooner, were more abundant and had slower growth rates due to intraspecific competition compared with prey exposed to the larger-gaped predator. The effects of piscivore gape size were also observed at lower trophic levels, indicating the potential importance of predator gape sizes on community dynamics (Persson, Chapter 15, this volume).

Other factors may restrict maximum prey sizes eaten by fish predators before morphological limitations imposed by gape size become important. The behavioural tactics used by predators to search for, encounter and attack prey can affect prey sizes consumed. For example, Gaughan and Potter (1997) compared the diets and mouth sizes of five estuarine species of larval fish and concluded that mouth width had only a small influence on prey sizes eaten and that disparate feeding patterns among larvae were likely due to behavioural differences. Behavioural capabilities of both predator and prey can also contribute considerably to the sizes of prey eaten. The ability of prey to evade predators is related to body size, with larger prey being more efficient at avoiding predator strikes. Therefore, maximum prey sizes eaten by piscivorous fishes can often be considerably smaller than gape sizes (Juanes and Conover 1995; B. Christensen 1996).

12.6 POPULATION REGULATION

Shepherd and Cushing (1990) stated that

> there is some basis for the belief that fish populations are regulated in some way. In fact, the evidence is twofold: first, that they do not explode when subjected only to low

(natural) levels of mortality: secondly, that they do not collapse at all quickly, when subjected to high levels of mortality.

One of the more well accepted mechanisms put forward to explain population regulation in fish is density-dependent mortality in larval and juvenile stages through interspecific predation or cannibalism (see Section 12.6.2; Myers, Chapter 6, this volume; Shepherd and Pope, Chapter 8, Volume 2).

Density-dependent mortality can lead to the maintenance of population stability (Murdoch and Oaten 1975; Hassell 1978). Field studies provide evidence for density-dependent mortality in marine fishes (Myers and Cadigan 1993; Forrester 1995; Hixon and Carr 1997). Several of these investigations provide evidence that piscivorous fishes are the dominant cause of density-dependent mortality. However, identifying the mechanism that generates density-dependent predation mortality has been elusive (Bailey 1994). Potential mechanisms leading to density-dependent predation mortality as a result of predator behaviour are described in Section 12.3.2. Density-dependent prey responses can also influence mortality rates. For example, competition for food at high density may lead to reduced growth rates, with prey being vulnerable to gape-limited piscivores for longer periods.

12.6.1 Population and community effects

Piscivorous fishes are known to have a dramatic influence on population- and community-level dynamics (Persson, Chapter 15, this volume). The impacts of piscivores can extend down several trophic levels (Zaret and Paine 1973). In freshwater systems, the trophic cascade model describes zooplanktivore, zooplankton, and phytoplankton abundance under high and low levels of piscivore abundance (see Carpenter et al. 1985; Persson, Chapter 15, this volume; Kaiser and Jennings, Chapter 16, Volume 2). When piscivore abundance levels are high, density of zooplanktivorous fish is reduced, which leads to increased zooplankton

(herbivore) and reduced phytoplankton abundance levels. Opposite abundance levels to those described above are observed during periods of low piscivore density. Hambright (1994) describes how the vulnerability of zooplanktivores to piscivory determines the magnitude of zooplanktivory and thus its effect on lower trophic levels. Piscivorous fish can influence the life-history strategy of their prey. Reznick et al. (1990) showed that under separate piscivore regimes (low vs. high predation), guppies (*Poecilia reticulata*) evolved different life-history parameters such as age at maturity, reproductive effort, brood size and size of offspring (Hutchings, Chapter 7, this volume).

Cannibalism is interesting because of its potential role in regulating population levels through its contribution to natural mortality; however, evidence for density-dependent cannibalism in non-captive fishes has not been discovered (Smith and Reay 1991). Henderson and Corps (1997) found that bass (*Dicentrarchus labrax*) year-class strength had a 3-year periodicity, which they believed to result from cannibalism within the nursery.

Animal abundance levels are known to exhibit periodicity as a result of predator–prey or host–parasite cycles. In a predator–prey cycle, increases in predator abundance are concurrent with declines in prey population levels; subsequent periods of low prey abundance can lead to predator declines and prey release. We are aware of only one example of a predator–prey cycle for a piscivorous fish. Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasi*) populations in Hecate Strait, British Columbia have patterns of abundance that are suggestive of such a cycle (Walters et al. 1986). The lack of evidence for a piscivore–prey cycle may result from the flexible feeding behaviour of piscivores, allowing them to remain at stable population levels when one of their prey populations is at low abundance.

Piscivores can have indirect non-lethal effects on prey fishes. These include all of the behavioural responses made by prey when confronted with a piscivore. These behavioural responses can lead to differences in community structure. The dominant indirect effect on prey fishes in a northern bog in the USA after northern pike were introduced was emigration; this led to a rapid decline in prey fish abundance and a change in community structure (He and Kitchell 1990).

12.7   METHODS OF STUDYING PREDATION IN THE FIELD

There are several methods used to determine the effects of piscivorous fish on prey populations and communities. A direct approach is to make comparisons between treatments where piscivores are present or absent. These treatments may be natural or artificial. Modelling has been used successfully to determine the influence of predators on prey populations (Mittelbach, Chapter 11 and Persson, Chapter 15, this volume). Studies that estimate predation mortality and compare this to total prey mortality make up another group of studies. Estimates of consumption rate along with knowledge of diet composition, prey sizes and predator abundance are used to estimate predation mortality. Detailed descriptions of stomach content analysis and methods to estimate consumption rates are described by Jobling (Chapter 5, this volume).

Tethers (usually monofilament fishing line) are used to hold prey fish in place; the fate of the prey fish allows one to assess relative predation intensity in both space and time. Danilowicz and Sale (1999) used tethering of French grunt (*Haemulon flavolineatum*) to determine when, over a diel cycle, predation intensity was highest. They found that the risk of being eaten was lowest during diurnal periods and highest during dusk and nocturnal periods. Age-0 rainbow trout (*Salmo gairdneri*) were tethered in British Columbia lakes to determine the spatial and temporal patterns of piscivory; it was concluded that the risk of predation varied greatly over both space and time (Post et al. 1998). Clearly, tethering experiments, as with other predator–prey studies, would need to conform to the animal ethics regulations of the countries and institutions involved.

Filming has been used to both identify predators and gain insight into the intensity of piscivory.

Carr and Hixon (1995) used filming of small patch reefs to aid in identifying pelagic piscivores and for measuring their visitation rates to experimental reefs.

12.8   IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Fishing alters the age and size structure of populations as older and larger fish are often removed first, and eventually the fishery is supported by the small newly recruited individuals. In many ecosystems, large piscivorous species were the initial targets of fishing. After the fishing down of these populations, the fisheries shifted to smaller species at lower trophic levels (Pauly and Christensen, Chapter 10, Volume 2). Although most marine landings are of small planktivores, it is fishing and the removal of large species at high trophic levels that affects ecosystem structure and functioning, leading to 'top-down' control (Carpenter et al. 1985; Hixon and Carr 1997; (Kaiser and Jennings, Chapter 16, Volume 2). For example, on Georges Bank, the decline in ground-fish stocks has led to a dramatic increase in forage fish such as herring and mackerel and a replacement of gadid and flounder species by small elasmobranchs (Fogarty and Murawski 1998). As more and more stocks become overexploited, fewer top predators will dominate oceanic food webs and both direct and indirect community effects will be prevalent. Predator removals can also be a deliberate form of fisheries management, whereby decreases in predation pressure are predicted to result. However this strategy does not always proceed as predicted (V. Christensen 1996; Kaiser and Jennings, Chapter 16 and Cowx, Chapter 17, Volume 2).

The opposite problem, with similar results, occurs when predators are deliberately or inadvertently added to ecosystems (Cowx, Chapter 17, Volume 2). The effects of piscivore introduction has been documented in temperate, boreal and tropical lakes (Zaret and Paine 1973; Mills et al. 1994; Vander Zanden et al. 1999). The most dramatic recent example has been the introduction of the Nile perch (*Lates nilotica*) to Lake Victoria, the world's largest tropical lake by surface area. The main effect of the predator introduction, similar to that observed in most systems where it has occurred, has been an accelerated decline of the diverse endemic cichlid fauna of the lake and the recent extinction of at least 200 species (Seehausen et al. 1997). However, the Nile perch introduction has also resulted in a fourfold increase in fishery yield and a doubling of fishery-related employment (Pitcher and Hart 1995; Kitchell et al. 1997).

Piscivore stocking, particularly in freshwater systems, has also been used as a way to improve water quality in eutrophic lakes and reservoirs. This process, termed 'biomanipulation', works through trophic cascading and has been quite successful in improving water quality of culturally eutrophic lakes and reservoirs (Drenner and Hambright 1999), although it can also have a variety of unexpected negative impacts.

Marine reserves have been effective in restoring and protecting many reef fishes (Polunin, Chapter 14, Volume 2) and they appear to be a promising tool for marine ecosystem sustainability (National Research Council 1999). However, reserves, if not planned carefully enough, can have negative impacts because of potential effects of physical factors combined with increased protection of piscivorous fishes. For example, in a small reserve in Barbados, size and abundance of piscivores were greater within the reserve than on adjacent reefs, but recruitment of grunts (Haemulidae) was lower because of predation pressure and oceanographic patterns of larval supply (Tupper and Juanes 1999).

12.9   CONCLUSIONS

Piscivores are a diverse group of fish that show distinct behaviours and specialized morphologies. The timing of the onset of piscivory is critical to many species and may have led to adaptive strategies that accelerate the shift to piscivory. The predation process can be better understood by examining the components of predation, and the

predatory response to changes in prey density can be estimated by generating numerical and functional responses. Piscivorous fish exhibit general patterns of prey type and size selectivity driven by attack behaviours and prey-specific behavioural responses by the prey. Predatory fish can have large impacts on prey communities in all habitats where they occur and are thus common targets for conservation and management, as they are often the first species to be affected by harvesting; however, they can also have both positive and detrimental effects when deliberately or inadvertently added to ecosystems.

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13   Fish as Prey

J. KRAUSE, E.M.A. HENSOR AND
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13.1   INTRODUCTION

Most fish experience some degree of predation risk throughout their lives. There are numerous strategies that reduce this risk. Predation has such an immediate effect on fitness that it is a powerful selective force, and different species from different environments have reached a variety of solutions to reduce predation risk (Helfman et al. 1997). Although evasion of predators is important, fish cannot hide indefinitely. They must also do some or all of feeding, courting, mating, spawning and defending territories against competitors, all of which are activities important to an individual's fitness. Therefore fish must accept some degree of predation risk, but can minimize the danger by efficiently detecting and reducing their vulnerability to predators (Godin 1997; Smith 1997).

One of the most important tasks of prey is to correctly identify what does and does not pose a potential predation threat. Not all large species are necessarily dangerous and there should be a high selection pressure on being able to recognize predators. Karplus and Algom (1981) showed that prey are indeed capable of distinguishing between the facial features of predatory and non-predatory reef fish species. Once a predator has been identified, it is important for fish to obtain information on whether an attack is likely to take place or not. This will depend largely on whether the predator is hungry or satiated. It has been suggested that one of the important functions of predator inspection behaviour by prey might be to find out whether or not predators are hungry (Dugatkin and Godin 1992). Licht (1989) has shown that guppies, *Poecilia reticulata*, are indeed capable of making this distinction.

On encountering a predator, a fish can either freeze or flee (Fig. 13.1), and split-second decisions made by a prey fish can greatly affect its chances of survival. These decisions must be based on a number of factors, such as distance to the nearest cover, the physical condition of the fish, the potential efficacy of crypsis, which depends on light levels and substratum type, or degree of protection from spines and other morphological predator deterrents. Fish with well-developed defences may be more likely to opt for immobility, relying on those defences to protect them if they are detected and attacked. Fish with fewer morphological antipredator adaptations might be more likely to flee from danger. In reality, however, fish may need to combine a number of strategies to achieve the optimal escape mechanism.

In this chapter we highlight the various methods that prey fish employ to reduce their vulnerability to predators. We focus on those areas of prey defences that have not received much attention lately in terms of books and reviews but which have been the subject of substantial recent research. Therefore we touch lightly on morphological defences, such as crypsis, body armour and alarm substance, and refer to recent detailed treatments of these topics, whereas recent investigations of the size and composition of free-ranging
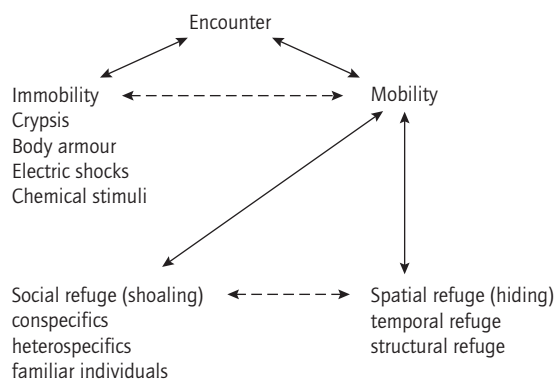
Fig. 13.1 Summary of the various strategies fish employ to reduce the risk of predation following an encounter with a predator.

shoals and experimental work on refuge use are given more space.

13.2   IMMOBILITY

Immobility only works as an antipredator behaviour if a fish is well camouflaged, has some morphological adaptation to make it unpalatable or can be confident the predator's senses are too poor to detect it when still. Aspects of prey fish morphology that play a part in predator avoidance and deterrence include crypsis, body armour, changes in body shape, electric shocks and the production of distasteful substances or toxins. Spines, chromatophores, electrophores and extra body mass are all costly to produce at the outset but can later benefit the fish in energetic terms, in addition to the antipredator benefits conferred. If the fish is sufficiently well protected to afford immobility in the face of predation risk, it saves the energy that more vulnerable fish expend in fleeing from the predator and seeking shelter. Remaining in open water has the added advantage of allowing the fish better access to information about the whereabouts of the predator and enabling judgements about when it is safe to resume normal activity.

13.2.1   Avoiding identification as prey

Crypsis allows prey to avoid detection by the predator if it blends in with the background. This is a strategy found in many transparent fish larvae, counter-shaded pelagic fish and flatfish (Helfman et al. 1997; Smith 1997). Crypsis also works if it mimics objects that are detected by the predator but not perceived as prey (Endler 1986). It usually works best if the prey is immobile because most predator species are very sensitive to movements and often select their prey on this basis (Krause and Godin 1995). In some cases such as the leaf-fish, *Monociorrhus polyacanthus*, slow movements resembling that of a drifting leaf are compatible with crypsis (Breder 1946; Randall and Randall 1960; Randall & Emery 1971). However, even if slow movement remains possible, behaviours such as foraging, mating and territorial defence remain largely incompatible with crypsis .

Batesian mimicry is where a species mimics another species that is distasteful or dangerous to the predator and is another strategy used by fishes to escape being identified as palatable. This is thought to occur in a number of fish species. The venomous blenny, *Meiacanthus atrodorsalis*, is apparently mimicked by non-venomous heterospecifics (Losey 1972), and a cardinalfish (Apogonidae) resembles a venomous scorpionfish (Scorpaenidae) (Seigel and Adamson 1983). Another attack deterrent is the production of eyespots that mimic the large eyes of predatory species (Winemiller 1990). One of the most striking examples of this kind of mimicry is the moray eel, *Gymnothorax meleagris*, which is mimicked by *Calloplesiops altivelis* that displays a conspicuous eyespot when faced with a potential predator (McCosker 1977). The occurrence of Batesian mimicry in the fish world is well supported but so far little direct evidence exists for Müllerian mimicry, in which toxic or distasteful species have coevolved the same bright warning colours to advertise their unpalatability to mutual benefit. The latter is relatively common in insects (Ritland 1995). This could be an interesting area for further research. It is especially worth bearing in

mind that some forms of mimicry in fish might not be readily apparent to humans, because it is based on a sense other than vision.

13.2.2   Avoiding subjugation after capture

Once a fish has been captured by a predator there is still a chance of escape. A number of morphological and behavioural adaptations have evolved to effect this. Several so-called mechanical methods (*sensu* Endler 1991) can potentially prevent the predator from swallowing its prey. In many populations of three-spine sticklebacks, *Gasterosteus aculeatus*, fish have evolved long dorsal and ventral spines and bony plates (Reimchen 1994) that make it difficult for many predatory species to swallow them (Hoogland et al. 1957). Similar adaptations can be found in porcupinefish and pufferfish, which inflate their bodies and erect spines (Brainerd 1994; Wainwright et al. 1995). Reimchen (1994) pointed out that prey species often have multiple predators and therefore have to adapt to a multitude of different selection pressures, resulting in morphological diversity. Some populations of three-spine sticklebacks show a high degree of diversity in adult body size. Larger body size reduces predation risk from gape-limited predators, whereas small adult size allows earlier reproduction at the cost of higher predation (for further discussion of the timing of reproduction and mortality, see Hutchings, Chapter 7, this volume). The coexistence of such different life-history strategies depends on whether there is a fitness equilibrium for a mixed evolutionarily stable strategy (Parker 1984). Furthermore, there is good evidence that traits such as spine length and number of lateral plates are under strong selection pressure by predators. Moodie (1972), for instance, showed that the spine length of sticklebacks that were consumed by cutthroat trout, *Oncorhynchus clarki*, were proportionately shorter than those in the general population.

A particularly interesting form of inducible morphological defence has been reported in crucian carp, *Carassius carassius* (Brönmark and Miner 1992). In response to the presence of pike, *Esox lucius*, crucian carp are capable of substantially increasing their body depth within a period of several weeks. Deeper bodies increase handling time for gape-limited pike and increase the chances of escape for prey (Nilsson et al. 1995). The increase in body depth has also been shown to be reversible and thus seems to represent an adaptation to short-term invasions of crucian carp habitat by pike.

Many fish species are known to release an alarm substance from specialized club cells when their skin is torn during handling by a predator (Smith 1997). On release, this substance can trigger a strong alarm response in conspecifics and heterospecifics. Observation of this phenomenon has led to speculation that the primary function of this substance may be to provide a warning signal. However, there would only be a benefit to the sender if individuals within shoals were closely related to each other. The first observation on alarm substance was made by von Frisch (1941) on minnows, *Phoxinus phoxinus*, for which no evidence of close relatedness between shoal members has been found (Naish et al. 1993). It has been demonstrated in a number of species, such as three-spine stickleback, that individuals are capable of discriminating between sibs and non-sibs. However, evidence from the field for preferential association with kin is scarce (Ferguson and Noakes 1981; Poyard et al. 1999; see Krause et al. 2000 for a review). Most of the studies on alarm substance have been conducted in the laboratory and evidence of its effectiveness in the field is weak. Recent experiments showed that minnows failed to respond to alarm substance under field conditions, or showed only a very weak response, suggesting that the responses of fish to alarm substance may be highly context-dependent (Magurran et al. 1996; Irving and Magurran 1997). A study by Mathis et al. (1995) demonstrated that predators are actually attracted by alarm substance and has led to the idea that the function of the substance is to attract additional predators, which will interfere and thus increase the prey's chances of escape. The processes leading to the evolution of alarm substance in fish could thus be analogous to those

underlying distress calls in birds and mammals. Further research is needed.

13.3 MOBILITY

13.3.1 *Grouping*

Group size

Shoaling has been shown to provide effective protection from a number of predator species (Neill and Cullen 1974; Major 1978; Landeau and Terborgh 1986; Krause and Godin 1995). Neill and Cullen (1974) exposed prey to four species of predators: two fish predators (perch, *Perca fluviatilis*, and pike) and two cephalopod species (squid, *Loligo vulgaris*, and cuttlefish, *Sepia officinalis*). In the experiments with fish predators, juvenile bleak (*Alburnus alburnus*), dace (*Leuciscus leuciscus*) and minnow, and cyprinodontids (*Poecilia reticulata*) were used as prey. For the cephalopod predators, atherinids (*Atherina* spp.) and mullets (*Mugil* spp.) were used. The experiments demonstrated that prey per-capita predation risk decreased dramatically with increasing group size in each case. There are a number of group size-related effects besides simple dilution that are thought to be responsible for this decrease in risk. The presence of multiple moving targets can confuse predators, making it difficult to target one individual (Neill and Cullen 1974; Milinski 1977; Krakauer 1995). This reduces the chances of an attack being initiated as well as actual capture success if an attack is made. Another important factor that makes life in groups safer is the presence of multiple watchful individuals, making it harder for predators to approach undetected and stage surprise attacks (Magurran et al. 1985).

Despite the fact that predator hunting success decreases, in some situations larger groups are preferentially attacked compared with smaller ones (Krause and Godin 1995). However, the preference for larger groups is not strong enough to override the above antipredator benefits of grouping so that per-capita risk still declines with group size. The fact that predators prefer larger groups could be linked to the fact that larger groups are more conspicuous. In fact, predator preference is related specifically to the activity level of groups and not merely their size. Krause and Godin (1995) manipulated shoal activity in guppies, *P. reticulata*, by using water of different temperatures to change the activity level of fish and showed that blue acara cichlids, *Aequidens pulcher*, the predator, preferred the most active groups irrespective of group size. Turner and Pitcher (1986) illustrated the important role of prey conspicuousness by showing that individuals are safer in groups than alone, provided that the probability of detection and subsequent attack by predators does not increase over-proportionately with increasing group size. Predators can take at most one individual in an attack, a phenomenon that has been termed the 'encounter-dilution effect' (see Pitcher and Parrish 1993 for details).

Interestingly, grouping does not always protect prey from predators. In a study of shoals of creek chub, *Semotilus atromaculatus*, attacked by rock bass, *Ambloplites rupestris*, Krause et al. (1998a) found no effect of group size on per-capita predation risk if predators managed to surprise prey groups. This was attributed to the fact that surprise attacks may at least partially circumvent antipredator strategies by prey. It is possible, for instance, that the confusion effect is weakened if predators are not detected prior to an attack. Perhaps because their large gape allows them to consume entire shoals at once, several species of cetacean predators are also known to be unaffected by prey group size and in some cases they even take advantage of grouped prey (Nottestad 1999). The sonar that many large aquatic predators use to find their food may require shoals to be above a certain size in order to be detected. However, shoaling is a common strategy among prey fish targeted by such predators. This has to be seen in the context of an environment that has multiple predators, which makes it impossible for prey to simultaneously adopt optimal strategies against each type of predator. The assumption here is that cetaceans are not the major predators of such species and account for only a small proportion of the overall

mortality rate due to predation, whilst other more important predators select for large group sizes.

Group composition

There is general consensus that the presence of predators in the environment is one of the main causes for the evolution of grouping in prey and an important determinant of prey group size (Pulliam and Caraco 1984; Godin 1986, 1997; Magurran 1990; Pitcher and Parrish 1993; Helfman et al. 1997). However, predators also have more subtle influences on the grouping strategy of prey. Some predator species suffer from the confusion effect of grouping prey and one way of reducing this problem is to focus on prey that differ phenotypically from the rest of the group (Landeau and Terborgh 1986; Theodorakis 1989). The phenomenon whereby predators single out such prey individuals is called the oddity effect. It is typical of predators that attack mobile grouping prey, whereas predators that feed on stationary prey usually develop a prey search image based on the phenotype of the most common prey type (Beukema 1968). Thus there are two frequency-dependent types of predation: one that is positively frequency-dependent, where the predator prefers the common prey type, and another which is negatively frequency-dependent, where the predator prefers the odd prey type. These two types of predation select for different grouping tendencies in prey. If predators prefer odd prey, then we should expect phenotype matching to be selected for. Indeed the latter has been demonstrated in a number of studies: in laboratory experiments individual banded killifish, *Fundulus diaphanus*, preferred to shoal with conspecifics over heterospecifics, and three-spine stickleback and two-spotted goby, *Gobiusculus flavescens*, preferred to shoal with size-matched over unmatched individuals; these fish were also found to be assorted by species and body length in the field (Ranta et al. 1992; Krause 1994; Krause and Godin 1994; Krause et al. 1996; Peuhkuri et al. 1997; Svensson et al. 2000).

The preference of predators for phenotypically odd prey could potentially lead to the evolution of mimicry. A less abundant species *A* could gain a benefit from grouping with a highly abundant species *B* by being better protected against predators in larger groups. However, for this benefit to be fully realized, individuals of species *A* would have to resemble individuals of species *B*. Otherwise they would appear as phenotypically odd and the advantage of joining a larger group might be outweighed by being odd in the group. In populations where a certain overlap of phenotypic characteristics between different species already exists, a preference of predators for odd prey could thus become the driving force behind the evolution of mimicry rings that could potentially involve a large number of different species (Ehrlich and Ehrlich 1973). The above-mentioned group-size effect would also benefit the mimicked species *B*, thus guaranteeing the stability of such mimicry rings. A first example of this form of mimicry has been described by Dafni and Diamant (1984) who found a system in which a solitary fish species mimics a shoaling species to gain protection from grouping. However, there may be circumstances where the mimicked species *B* does not benefit from the mimicry, perhaps because predators are less able to learn an aposematic signal. The importance of mimicry to fish is a promising area of research.

The common phenotype is only preferred by predators that are unconstrained by the confusion effect. This should lead to the evolution of polymorphic prey groups because any prey phenotype that dominates the group numerically will be selected against. Also, predators encountering a diversity of different escape strategies will find it more difficult to learn how to most effectively combat any one of them.

Group geometry

So far the assumption has been that an individual outside a group is subject to a high predation risk and that all individuals within a group have the same lower predation risk. The latter assumption, however, is rather unlikely. Hamilton (1971), in his ground-breaking study on the geometry of selfish herds, predicted that individuals on the edge of a group have a higher risk of predation than centrally positioned ones. This prediction was

based on the assumption that the predator always attacks the nearest prey within range. Hamilton's theory of marginal predation is well supported by evidence from stationary animal groups (Krause 1994) but there is controversy over whether it can be applied to mobile fish shoals (Parrish 1989; Krause 1993; Bumann et al. 1997; Krause et al. 1998a). Most studies to date have only provided indirect evidence for or against Hamilton's theory by measuring the number of attacks directed at certain shoal positions (Parrish 1989) or by looking at positioning behaviour of fish (McKaye and Oliver 1980; Krause 1993). Some of the studies that recorded actual mortalities employed vague definitions of shoal positions or did not correct for the fact that numbers of individuals in the centre and periphery of a group might have been different (Parrish et al. 1989). In a more recent study, Bumann et al. (1997) extended Hamilton's model to mobile groups and stationary as well as mobile predators, making predictions about the distribution of predation risks within fish shoals. The results from the model indicate that in addition to the positive risk gradient from the centre to the periphery, as predicted by Hamilton's model for stationary groups, there is another positive risk gradient from the relatively more safe rear to the relatively less safe front part of groups. This prediction was tested using a shoal of 13 creek chub as prey and rock bass as a predator. Chub in the front half of the shoal were attacked and captured significantly more often than ones in the rear, and the lead fish was the one with the highest predation risk in the shoal (Krause et al. 1998a). The existence of risk gradients within fish shoals is likely to influence individual positioning behaviour and thus may have consequences for overall group shape and structure. If the risk is higher for front positions, we may expect that the inter-individual distances between fish will be lower there as a means of risk reduction (*sensu* Hamilton 1971). We might also expect that fish in middle and rear positions 'hide' behind frontal fish and thus give the shoal an elongated structure (Bumann et al. 1997). There is an indication from detailed three-dimensional measurements of roach shoals that both the predictions for higher fish densities

in the front part of shoals and an elongated overall shape were met (Bumann et al. 1997).

13.3.2 Refuge use

Spatial and temporal refugia

The most familiar form of spatial refuge is structural, for example a crevice under a rock or a patch of weed. In pelagic zones, however, there may not be fixed visible refuges. The water column may be divided into areas of different depths or temperatures, which still offer shelter to prey. For example, sufficient depth offers protection from predators that use vision to locate prey. Many fish-eating birds are restricted to the top few metres of the water. Streams can contain shallow fast-moving riffles and deeper slow-moving pools, each having their own distinct characteristics with respect to predation risk (Bremset and Berg 1999).

Bremset and Berg (1999) observed juvenile trout, *Salmo trutta*, and Atlantic salmon, *S. salar*, of different size classes and found that smaller juveniles stationed themselves closer to the river bank, nearer the bottom than larger juveniles. Food availability was higher in the open water; however the predation risk also increased with distance from the river bank. Thus young-of-the-year salmonids were excluded from the upper part of the water column, in part by competition from larger more dominant conspecifics and partly by a need to reduce the risk of predation and/or cannibalism by older conspecifics. In this case, the smaller fish restricted their movements to the river bank and bottom only of the river as a whole, and therefore could be considered to have been using these areas as a spatial refuge.

Prey can reduce their predation risk by being active when predators are absent or the likelihood of successful attack is reduced. The cycles of emergence seen in the periodical cicada (*Magicicada* spp.) are thought to play a part in predator avoidance (Itô 1998), as are the diurnal patterns of invertebrate drift found in some freshwater systems (McIntosh and Peckarsky 1996; Huhta et al. 1999). Behavioural periodicity related to predation risk has also been demonstrated in some fish species.

Table 13.1 Costs and benefits of refuge use.

Costs	Benefits
Lost opportunity	*Safety from*
Feeding (Dill and Fraser 1997)	Immediate predation (Milinski 1993; Sogard and Olla 1993; Smith
Courting (Perrin 1995)	1997)
Mating (Perrin 1995)	Predation when vulnerable (e.g. when spawning/brooding/newly
Uncertainty	hatched) (Sogard 1997; Rodewald and Foster 1998)
Food availability (Sih 1992, 1997; Dill and Fraser 1997)	*Metabolic effects*
Predator presence (Sih 1992; Eklöv and Persson 1996)	Reduced energy expenditure when food supply poor (Dill and Fraser
Social effects within refuge	1997)
Increased competition for space, position, information and food	*Protection from*
(Pallini et al. 1998)	Damaging environmental conditions, e.g. currents, extreme
Social effects outside refuge	temperatures (Brown 1999)
Reduced defence of territory (Sargent 1985), food (Humphries et al.	*Reduced stress*
1999) and mates (Sargent 1985)	

For example, Naud and Magnan (1988) studied evening offshore migrations by northern redbelly dace, *Phoxinus eos*, and concluded that during the day the fish were forced to form shoals near physical structures to reduce their risk of predation by brook charr, *Salvelinus fontinalis*, thus forgoing the opportunity to feed in the more productive limnetic habitat. Some marine fish larvae have been shown to start their drift up into the water column when the prevailing currents ensure food is plentiful in the surface waters and predation by macrozooplankton is at a minimum (Frank and Leggett 1985). A seasonal switch from diurnal to nocturnal foraging at low temperatures has been observed in juvenile Atlantic salmon (Fraser et al. 1993; Fraser and Metcalfe 1997; Metcalfe et al. 1999) and minnows (Greenwood and Metcalfe 1998). Metcalfe et al. (1999) concluded that by increasing their nocturnal activity relative to their diurnal activity, the salmon experienced reduced predation pressure from visual hunters, at a time when their nutritional requirements were low enough to allow reduced diurnal foraging.

Refuge trade-offs

Trade-offs, particularly between foraging and predation risk, are reviewed by Mittelbach in Chapter 11, this volume. We therefore provide only a cursory review of costs of refuge use here. The extent to which an individual benefits from the reduced predation risk will vary according to the losses it incurs while in hiding. Juvenile fish, often comparatively more at risk of predation than larger conspecifics (Sogard 1997; Krause et al. 1998b), may trade off reduced feeding opportunity for increased protection from predators by remaining in safer but less productive areas (Bremset and Berg 1999). Conversely, individuals in poorer condition or with higher nutritional requirements, perhaps as a result of parasitism, may be prepared to take more risks in order to maximize their food intake (Giles 1983; Milinski 1990, 1993). Growing large enough to become invulnerable to some types of predator can also be seen as entering a partial refuge. The various costs and benefits of refuge use, any of which a fish may have to balance during hiding, are shown in Table 13.1.

The costs of refuge use

Lost opportunity The opportunities to feed, court or mate while in hiding may be greatly reduced (Sih 1992). In the case of spatial refugia, food availability and the chances of interaction with conspecifics are potentially lower (Mittelbach,

Chapter 11, this volume). Fish that seek temporal refuge, by avoiding activity during risky periods, may be missing the best times for feeding or mating. For example, Fraser and Metcalfe (1997) concluded that the feeding efficiency of juvenile Atlantic salmon was significantly impaired by low light levels during their switch to nocturnal feeding in winter. This was not compensated for by winter drift abundance being slightly higher by night than by day. They concluded that many individuals accepted the minimum intake required for survival, in return for a significantly lower risk of predation by predominantly diurnal avian predators.

The extent of the opportunity lost depends on the nature of the resource. Food availability in aquatic environments is seldom constant: a fish relying on a patchy food resource may be forced to take advantage of a plentiful supply whenever it arises, as the arrival of the next meal cannot be predicted. Dill and Fraser (1997) demonstrated that polychaete worms, *Serpula vermicularis*, emerged sooner after a fright stimulus when the concentration of food present at the time of hiding was greater. They concluded that the worms were tracking short-term fluctuations in local food availability and were modifying their hiding duration accordingly. Since food availability outside the refuge can vary greatly, the costs incurred by remaining in hiding also change over time. If there is no food available, an individual can save energy by remaining in the refuge.

A fish that is better able to track fluctuations in its food resource will operate closer to the optima for refuging and foraging and will thus improve its fitness. However, the accuracy with which fish can assess the external conditions may be impaired, because remaining in the refuge restricts the amount of information available. This leads to the problem of uncertainty.

Uncertainty   The condition of the fish, such as its nutritional or reproductive status, will have a bearing on the amount of time it can spend in hiding before it must feed or commence other activities. For example, a hungry fish may be prepared to leave hiding sooner (Krause et al. 1998b, 1999). By depriving sticklebacks of food over a 2-day period, and then refeeding them again over 2 days, Krause et al. (1999) demonstrated an inverse relationship between percentage weight lost and hiding duration. Hungrier fish seemed to accept a higher predation risk in return for increased foraging opportunity.

By assessing the conditions outside the refuge, fish can weigh up the advantages of remaining inside. Information about food availability or predator presence gleaned from within the refuge will form the basis of a decision to leave. However, fish are not omniscient (Sih 1992). Underestimating the availability, or overestimating the quality, of food may lead to increased searching or handling time, thereby increasing the risk of detection by a predator (Sih 1992). Given the choice between death, the immediate cost of underestimating the predation risk, and lost feeding opportunity, which comes from overestimating the predation risk, a few animals will sometimes stay in hiding much longer than actually necessary to avoid the predator (Sih 1997).

Social effects within the refuge   Fish that seek shelter together experience different social costs. Whilst hiding in a spatial refuge they may have to compete for resources inside, which are in any case likely to be limited. Information about the conditions outside the refuge affects survival and can be considered a resource, in which case the spatial position of a fish within a refuge may affect its fitness. A fish closer to the boundary with the wider habitat will be in a better position to assess the conditions outside the refuge than one further back, although this position may leave it marginally more at risk of being spotted by a predator. Observation of the fate of individuals entering or leaving the refuge can enable estimation of the local predation risk. Allied to this, there may be antipredatory benefits in leaving the refuge in a group. However, fish may experience increased competition if many individuals emerge together at a particular time of day.

Social effects outside the refuge   By seeking shelter, a fish may be unable to defend its territory, food sources or mates from competitors. The costs

of this depend largely on whether its competitors are equally at risk from predation and how many competitors are in the vicinity. Competitors may employ similar refuge strategies, and could also be in hiding, or they may have their own territory to defend. When a fish is forced away from guarding a food resource, its potential loss in favour of its competitors depends on their feeding rate and how far they have to venture from their own territory. In some situations, a vacated territory can be quickly won back on return from refuge, although this will not be universally true. Some systems show a strong 'owner's advantage', where it is easier to hold on to a territory than it is to usurp another. Such effects can also affect third parties. If a territory holder finds that its neighbour has taken refuge and been replaced by another, then it is likely to experience a higher rate of aggression from the new neighbour than previously from the familiar 'dear enemy'.

There are also reproductive costs to a fish in hiding. The male three-spine stickleback must spend considerable time and effort tending his nest if his eggs are to hatch successfully. He must defend the nest from raids by conspecifics and must fan the eggs to prevent them from dying through lack of oxygen (Wootton 1976). He cannot spend too much time away from the nest engaged in antipredator behaviour, resting or feeding (Blouw 1996).

The benefits of refuge use

Safety from predation   One would expect individuals that experience higher predation risk to seek refuge more often or for longer periods of time. For instance, Rodewald and Foster (1998) found that gravid three-spined sticklebacks remained in closer proximity to refuge than non-gravid females in lakes harbouring predatory fish. This difference in behaviour was not observed in lakes where predatory fish were absent. Carrying eggs makes the female stickleback's body distended, and she suffers a reduction in agility and stamina as a result (Rodewald and Foster 1998). This reduction in escape ability was concluded to be the most likely explanation for the gravid females remaining closer to refuge.
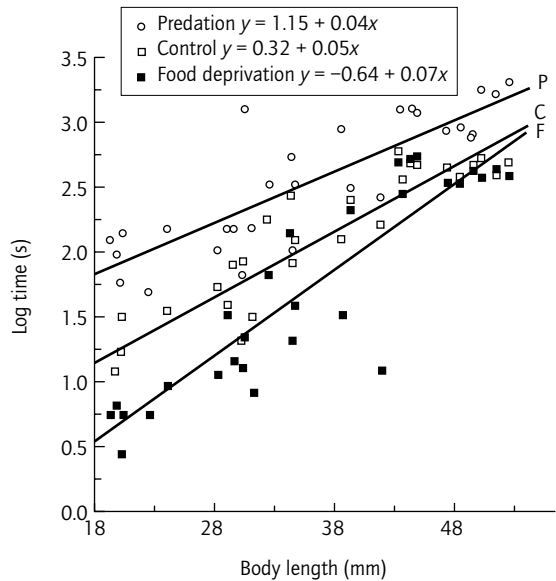
Fig. 13.2   Experiment by Krause et al. (1998b). Individual sticklebacks ($n = 30$) of different body size were released and took shelter under a polystyrene float. The behaviour was observed under three different treatments: control (C), simulated predator attack (P) and food deprivation of 2 days (F). The time of emergence showed a significant increase with body size in all three treatments (control, $r^2 = 0.84$, $P < 0.001$; predation, $r^2 = 0.71$, $P < 0.001$; deprivation, $r^2 = 0.83$, $P < 0.001$).

Juvenile fish are generally, although not always, at higher risk of predation (Sogard 1997). However, it does not always follow that a higher risk of predation will lead to longer hiding times. Small juvenile fish have a high relative metabolic rate and are therefore more at risk from starvation than larger fish. In fact, Krause et al. (1998b) observed that large fish emerged later from a refuge and returned to the refuge sooner than small fish. They concluded that the risk of starvation decreased more sharply than the risk of predation as the fish increased in length (Fig. 13.2). Therefore, larger fish could better afford the lost feeding costs of remaining in hiding than smaller conspecifics, which were forced to leave refuge in search of food. The large number of factors affecting refuge use makes it hard to predict how long a particular

individual is likely to remain in hiding. Krause et al. (1999) showed that emergence times in *G. aculeatus*, although greatly variable between each fish, were highly consistent for individual fish between different days of testing. This was likely to have been due to individual differences in weight changes over the 2-day period of food deprivation. Further examples of how refuges are used and how use changes with age, giving an ontogenetic niche shift, are given by Mittelbach (Chapter 11, this volume).

Protection from adverse conditions   Spatial and temporal refugia also provide protection from strong currents, extreme temperatures and other potentially damaging environmental conditions. The temporal refuge sought by juvenile Atlantic salmon at low temperatures, when they restrict their diurnal foraging, is one example. The usual method of attack avoidance that salmon employ is by a burst acceleration towards cover. However, because both reaction time and acceleration rate are temperature dependent, at low temperatures the ability of the fish to escape is severely impaired, leaving them at much higher risk from endothermic predators (Fraser et al. 1993; Fraser and Metcalfe 1997; Metcalfe et al. 1999). Brown (1999) noted that cutthroat trout in Dutch Creek, Alberta formed aggregations during the winter months and that the majority then remained sedentary until temperatures increased again. However, some fish were forced to move to warmer stretches of the river when anchor ice began to form in the water column. Anchor ice develops from the bottom of a pool upwards and can choke it to the extent that the water flow is directed down a few high-velocity channels, in which the fish find it hard to maintain position (Brown 1999). They must then seek refuge in warmer water.

Reduced stress   Stress in fish can be caused by many factors, including poor water quality and attack by predators. It is deleterious to fish health on a number of levels: it can increase respiration rate and heart beat, which leads to energetic losses, and can leave them more susceptible to disease (Helfman et al. 1997). While in hiding fish benefit from a reduction in stress levels. They do not have to be as vigilant for predators as they are outside, unless assessing the predation risk before leaving the refuge.

13.4   CONCLUSIONS

Fish have evolved a wide range of behavioural and morphological adaptations to reduce their susceptibility to predators. However, the intrinsic problems faced by prey fish are similar in all cases. Generally, an individual must assess the relative profitability of an antipredator strategy in terms of the associated costs and benefits with regards to factors such as predation risk, access to information, lost opportunities and energy expenditure. In this chapter we have described how individuals can remain immobile, relying on not being identified or on being able to escape after capture or by forming groups or taking refuge, and so reduce their costs of encounters with predators. Relatively little information currently exists on how individuals select one particular strategy from a whole set of available ones, how repeatable such choices are and on the thresholds at which dynamic strategy changes might take place. For instance, is there a group size at which grouping becomes the preferred antipredator strategy over refuge use? Grouping might not be as safe as refuging but it allows for continued foraging. The trade-off between predation risk and foraging benefits should also depend on the nutritional state of the individual, making grouping particularly attractive to hungry fish.

Survival depends on swift and accurate decision-making by prey during encounters with predators and little is presently known on potential constraints regarding the speed of information processing and strategy choice in this context. This could be an interesting field for further experimental work and theoretical studies.

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Part 4
Fish in Ecosystems

14 Trophic Ecology and the Structure of Marine Food Webs

NICHOLAS V.C. POLUNIN AND J.K. PINNEGAR

14.1 INTRODUCTION

A corollary of the sustainable use of marine resources is that these resources are not exploited in isolation and a broad perspective is therefore desirable. The exploitation of any resource inevitably has wider implications (Christensen et al. 1996), and one of the most frequently expressed concerns about intensive fishing is that it will lead to imbalances in ecosystem function that have ramifications for community structure overall (Walters and Holling 1990; Jennings and Kaiser 1998; Pauly and Christensen, Chapter 10 and Kaiser and Jennings, Chapter 16, Volume 2). The changes involved need not always be 'negative'; for example, it is thought that removal of large predators will sometimes increase the abundance and productivity of prey organisms and these may benefit fisheries (Jennings and Kaiser 1998; Pauly et al. 1998a). However in other cases, the removal of predators by fishing has resulted in increases in the abundance of organisms such as sea urchins, which at high densities often have detrimental effects on communities as a whole (review in Pinnegar et al. 2000). There is an emerging consensus among fisheries scientists and managers of aquatic resources that conventional single-species analyses ought to be replaced by approaches that explicitly account for ecological interactions, and especially those of a trophic nature (Walters et al. 1997; Pauly and Christensen, Chapter 10, Volume 2). However, there is little consensus concerning the analytical and conceptual tools that should be used as a basis

for such research or management (Botsford et al. 1997).

One major scientific context for understanding interactions among organisms is that of the ecosystem, and 'ecosystem management' has become a useful focal point among those probing the scientific bases for a holistic and sustainable approach in the use of natural resources (Haeuber and Franklin 1996). However, delving into the structure and workings of ecosystems soon reveals the piecemeal and fragmentary nature of the information available (McCann et al. 1998), yet such enquiry is essential if the science of management is to develop and is to address more appropriately the purpose of sustaining the supply of environmental goods, i.e. the fish and services such as waste removal, in coastal waters.

An important class of interactions which occurs within ecosystems is that involving fluxes of nutrients and energy, the study of which is generally referred to as trophodynamics. Food chains and webs specifically aim to describe the trophic relationships amongst organisms in a community and are a major focus of trophodynamic studies. An appealing feature of trophic fluxes is that they can be quantified in common currencies, such as units of energy, mass or carbon. They link many of the components of ecosystems and have long been viewed by some as the cornerstone of ecosystem ecology (Odum 1968). Such concepts apparently underpin the notion that each human action, however specialized and local, inevitably has wider consequences, and these may at times include sur-

Open ocean   **Coastal zone**   **Upwelling**
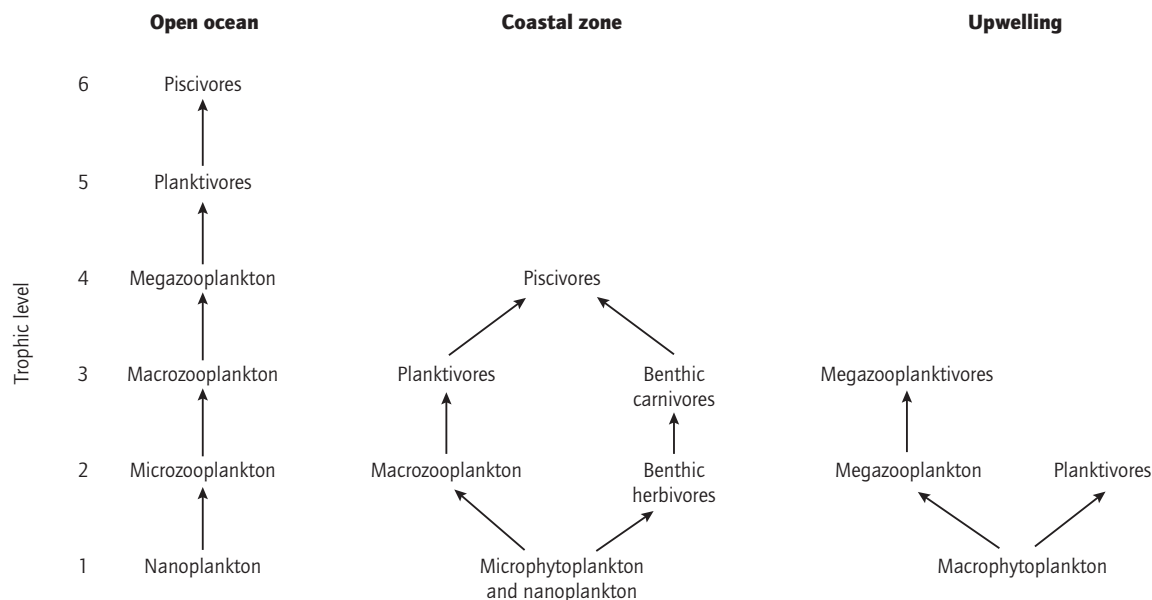
Fig. 14.1   Food chains postulated by Ryther to characterize the three marine provinces that he identified as a basis for estimating global marine fish productivity; the arrows indicate fluxes of organic carbon to consumers. (Source: after Ryther 1969.)

prises and failures that influence the sustainability of the activities involved. Yet great uncertainties result from inferring secondary effects within ecosystems from trophodynamic linkages alone, and Menge (1992, 1997) has provided a detailed picture of the relative strengths of direct and indirect interactions within particular marine systems based on small-scale experiments.

The aim of the present chapter is to explore the origins and possible implications of the uncertainty in trophic interactions and to consider how information on indirect effects of exploitation and management might be derived at scales appropriate to an analysis of the possible effects of fishing or the consequences of creating marine protected areas (discussed explicitly by Polunin in Chapter 14, Volume 2). The specific objectives of the chapter are to (i) consider limitations of the use of food chains to predict processes such as fish production, (ii) assess current understanding of food webs and what this is based on, (iii) assess variations in interaction strength in food webs and implications of

this and (iv) evaluate the roles of fish in food webs and consequences of changes in their abundance as a result of management controls or exploitation. Aspects of individual trophic behaviour are analysed in Chapter 11–13 of this volume. The application of an ecosystem perspective to fisheries management is presented by Pauly and Christensen in Chapter 10, Volume 2.

14.2   FOOD CHAINS AND FOOD WEBS

As with much other information on ecological communities, there are two possible extremes in arranging feeding relationships on the basis of the available data. One of these extremes is to combine species into groups that are trophically similar (Fig. 14.1), while the other is to represent all relationships that exist among species in a complex reticulated system (Fig. 14.2). The first of these, the food chain, may be used because data are in short
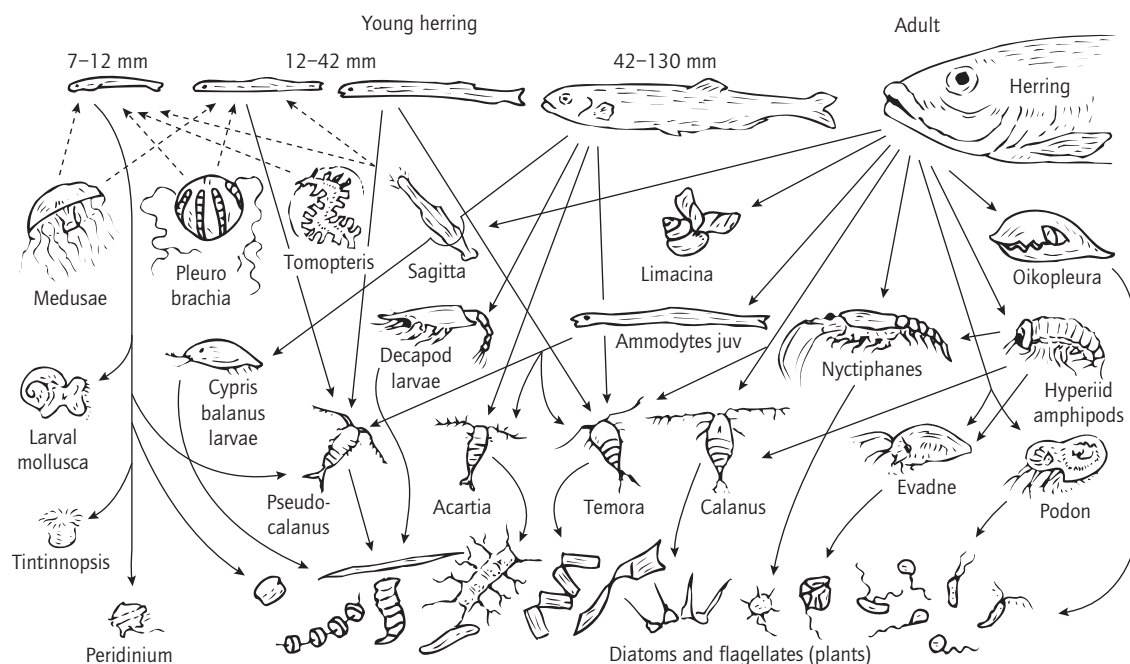
Fig. 14.2   Representation of the planktonic food web supporting the Atlantic herring, *Clupea harengus*, and including predators of the larvae (broken arrows); arrows indicate feeding by predators on prey organisms. (Source: from Hardy 1959. Reproduced by permission.)

supply and separate relationships between species cannot reliably be depicted, or it might be that the data do exist but by aggregation the dominant interactions are highlighted. The second extreme, the food web, supposes that detailed information is available and that meaningful patterns and properties can be gleaned from such a complex arrangement. While the first approach predates the second, it has nevertheless persisted in various forms (Ulanowicz 1995; Jennings et al. 2001, 2002) and the purpose here is to consider the range of possible approaches, beginning with their historical development and reviewing their relative strengths and weaknesses.

14.2.1   Food chains

Food chains owe much to the early work of Elton (1927) and Lindeman (1942). Typically they rely upon the aggregation of functionally similar species into groups or trophic levels arranged in a linear chain, between which fluxes and transfer efficiencies can be traced. The apparent simplicity and elegance of the food-chain concept and the ability to quantitatively compare systems in terms of two variables, namely trophic level (an integer) and the efficiency of food-chain transfer (expressed as a fraction), has proved overwhelmingly attractive to many ecologists (studies reviewed in Cushing 1975).

Ryther (1969) used simple food-chain theory to predict marine fishery productivity of the world's oceans. To do this he divided the oceans into three 'provinces', the open ocean, the coastal zone and upwelling areas. These provinces vary substantially in primary productivity and, in addition, the size of the most prevalent primary producers also differs significantly. It was supposed that the larger the plant cells at the base of the food chain, as often found in nutrient-rich areas, the smaller the number of trophic levels needed to convert this organic matter into a form useful for fishery exploitation.

Table 14.1 Ryther's (1969) estimates of global marine fish productivity based on food-chain characterization of production and assuming the existence of distinct 'provinces' of contrasting productivity, together with correct knowledge of their areas, net primary productivities, numbers of trophic levels and mean food-chain efficiencies.

Province	Area (10^6 km^2)	Mean net primary productivity (g m^{-2} year^{-1})	Total net primary productivity (10^9 tonnes year^{-1})	Trophic levels	Efficiency (%)	Fish productivity (fresh 10^6 tonnes year^{-1})
Open ocean	326	50	16.3	5	10	0.1
Coastal zone	36	100	3.6	3	15	120
Upwelling areas	0.36	300	0.1	1.5	20	120

For example, the nanoplankton predominant in open oceans cannot be captured directly by most crustacean zooplankters such as copepods, requiring additional trophic levels consisting of intermediate-sized microzooplankton, such as protozoans and larval nauplii of microcrustaceans, that are then consumed by copepods, and so on (Fig. 14.1). Ryther (1969) further supposed that the least productive oceanic regions had the lowest efficiencies of carbon transfer along food chains. Where food is less available animals must perform more work to hunt, locate and capture prey, and thus less of the food consumed is converted to production.

Combining efficiency estimates with the number of trophic levels, Ryther (1969) was able to contrast the high fish productivity of upwelling regions, which form only 0.1% of oceanic waters, with the extremely low fish productivity of the open ocean systems, which make up 90% of oceanic waters (Table 14.1). Overall fish productivity of the world was estimated to be approximately 240 million tonnes annually (Table 14.1). Assuming that only half or so of this productivity might be available sustainably as yield, Ryther (1969) tentatively suggested a potential total marine fishery harvest of 100 million tonnes annually. Similar annual estimates (102–142 million tonnes) were obtained by Gulland (1970) using more extensive primary productivity and transfer efficiency data, and these can be considered close to the current world catch as estimated from recorded landings (FAO 1995). The most important consequence of this early practical use of food-chain studies was the discovery that fish resources in the world's oceans are potentially limited and

that they were likely to be fully exploited within the next decade or so (Cushing 1975). More recently Pauly and Christensen (1995) calculated the primary productivity required to sustain global fisheries catches, on the basis of a mean energy transfer efficiency between trophic levels of 10%, based on 48 Ecopath models of aquatic ecosystems (Pauly and Christensen, Chapter 10, Volume 2) and fractional estimates of trophic level as opposed to the discrete integers used by Ryther (1969). It was estimated that around 8% of global aquatic primary production was required to support annual world catches of 94 million tonnes plus 27 million tonnes of discarded bycatch; in shelf and freshwater systems as much as 24–35% may be required. Estimating transfer efficiencies between trophic levels was previously a matter of much conjecture and usually pertained to single-species populations (Slobodkin 1961). The values obtained by Pauly and Christensen (1995), though unsurprising in terms of their mean (Morowitz 1991), differed radically from Ryther's (1969) guesses at the mean transfer efficiencies of different provinces (Pauly et al. 2000).

The weaknesses of the approach adopted by Ryther (1969) and subsequent authors, and the food-chain approach generally, are many (Alverson et al. 1970; Lasker 1988); for example, predictions of the levels of biomass yield for different regions of the world ocean are open to disagreement. Nevertheless, with analyses of the critical state of world fisheries becoming ever more abundant, the shortcomings of Ryther's study provide a number of points to discuss. General issues highlighted by Ryther's (1969) analysis include the following.

1 Feeding relationships among organisms in ecosystems are more appropriately represented as food webs rather than food chains, since many species, including those targeted by fisheries, feed at more than one trophic level (Polis and Strong 1996).

2 The food-chain concept implies that size and/or productivity of consumer populations are driven by primary productivity (i.e. 'bottom-up'), although other processes in food webs such as predation may also be very influential.

3 Ecological efficiencies will vary among types of organisms and among developmental stages within species (e.g. Pimm 1988). Thus aggregate efficiencies for trophic levels are likely to be unrealistic.

4 Materials egested or not used by the organisms in food chains are not necessarily lost from the ecosystems involved; for example, detritus may be used by detritivores, with important implications for fish productivity (Polis and Strong 1996). Indeed, much of the dissolved and particulate organic matter released by marine consumers is now thought to return to the food web via the 'microbial loop' (Azam et al. 1983), which largely consists of bacteria, heterotrophic flagellates and microzooplankton (detritus recycling is also given prominence by Pauly and Christensen in Chapter 10, Volume 2).

5 Ryther (1969) predicted that oceanic upwelling areas would have shorter food chains than the oligotrophic open oceans (Fig. 14.1). Energy is cumulatively lost through processes such as defecation and excretion as a food chain is ascended and thus a high-level carnivore should require a substantial home range in order to sustain it. Sites with high primary productivities should exhibit longer food chains than those with low productivities, since more energy is available for transfer upwards to support predators at increasing trophic levels (Pimm 1982).

It is not clear how ecologically appropriate it was to divide up the world's oceans into the three 'provinces' of Ryther (1969) or the five of Pauly and Christensen (1995). Longhurst et al. (1995) proposed a system for dividing up the ocean into biologically coherent zones using primary produc-tivity data from the NASA Coastal Zone Colour Scanner (CZCS) and 21 872 chlorophyll depth pro-files measured in the ocean. This system, which is reviewed in detail in Longhurst (1998), consists of four primary 'domains', namely polar, wester-lies (temperate), trade-winds (tropical) and coastal, and these are themselves partitioned into 57 sec-ondary biogeochemical provinces. These range in size from the Red Sea and Persian Gulf province (0.56 million km^2) to the South Pacific Subtropical Gyre (37.29 million km^2), and in productivity from the North Pacific Tropical Gyre (59 g m^{-2} $year^{-1}$) to the Northeast Atlantic Continental Shelf (730 g m^{-2} $year^{-1}$). The total estimated annual primary productivity of the global oceans was 45–50×10^9 tonnes, which is more than double that estimated by Ryther (1969) (Table 14.1) and sig-nificantly greater than the value of Pauly and Christensen (1995) (43.9×10^9 tonnes).

14.2.2 Food webs

Food webs are representations of the feeding rela-tionships within whole communities of organ-isms based principally on data obtained through dietary analysis (Fig. 14.2). Such analyses typically involve gut contents data, and a wealth of different methods have been developed for use in studies of fish (Hyslop 1980; Jobling, Chapter 5, this volume). From the North Sea, in particular, stomach con-tents data have been extensively collected (Daan 1989) for use in the construction of multispecies fisheries models (Magnusson 1995; Shepherd and Pope, Chapter 7, Volume 2). However, gut content analyses have a number of limitations (Deb 1997); for example, they tend to provide mere snapshots of diets at particular points in time and space. Moreover, the durations of the snapshots vary amongst species, given variations in gut turnover (Jobling, Chapter 5, this volume), and neglect certain types of dietary materials, such as gelatinous plankton and detritus, that may never-theless be very important. The significance of this point is emphasized by Righton et al. (2001) who show that feeding behaviour of cod (*Gadus morhua*) varies temporally in the North Sea and Irish Sea. Organisms at the base of food webs

tend to be particularly poorly characterized (Hall and Raffaelli 1993) and excessive lumping together of species may greatly affect the apparent properties of food webs (Goldwasser and Roughgarden 1997). Gut contents therefore offer a poor basis for elucidating the detailed interactions which must exist (Paine 1988). Immunological assays of gut contents may be useful in such circumstances to supplement visual data on diets (van der Veer et al. 1998), although in general most links in food webs remain unsuccessfully identified (Cohen and Newman 1988).

There are additional tools available for elucidating food-web structure. A principal method involves the use of stable isotopes, in particular those of carbon and nitrogen (Pinnegar and Polunin 2000). Carbon and nitrogen each exist in two stable isotopic forms (^{12}C and ^{13}C, ^{14}N and ^{15}N) that differ in atomic mass. The least abundant isotopes (^{13}C and ^{15}N) contain one more neutron and are thus one atomic mass unit heavier than the most abundant isotopes (^{12}C and ^{14}N). Chemical fractionation occurs because a chemical bond that involves a heavier isotope has a lower vibrational frequency and is therefore stronger than an equivalent bond involving the lighter isotope. Thus the probability of a bond breaking is greater for compounds containing ^{14}N or ^{12}C than for those containing ^{15}N or ^{13}C. When an animal consumes its food, the unreacted substrate (i.e. faeces) becomes enriched in the heavier isotope compared with the reacted product, which is absorbed into the body. However, the processes of catabolism, transamination and deamination and the resulting excretion of products such as carbon dioxide, ammonia or urea during respiration or assimilation result in the animal tending to become enriched rather than depleted in the heavier isotope with respect to their food. The ^{15}N concentration in tissues of consumers is typically enriched by ~3‰ δ units relative to those of their prey (Minagawa and Wada 1984), whilst tissues are enriched in ^{13}C by only ~1‰ as trophic level increases (DeNiro and Epstein 1978).

When major component organisms of a community are analysed, the resulting data can constitute a form of 'fingerprint' of the food web because primary materials such as higher plants, benthic algae and phytoplankton tend to differ in the relative abundance of carbon stable isotopes (Harrigan et al. 1989), while the nitrogen stable isotope data are good indicators of trophic level (Vander Zanden et al. 1997; Kline and Pauly 1998). Such fingerprints are likely to show a number of characteristics in common. For example, when two widely separated coral reef sites in the South Pacific (Fig. 14.3) are compared, piscivorous fishes exhibit the highest values of the nitrogen stable isotope index $\delta^{15}N$, meaning that they are enriched in the isotope ^{15}N, benthic algae exhibit a higher $\delta^{13}C$ index, which means they are enriched in the isotope ^{13}C compared with planktonic materials, and planktivorous and herbivorous fish have mean $\delta^{15}N$ values greater than the plankton and algae they consume (Fig. 14.3). In addition to this, piscivores typically exhibit somewhat intermediate $\delta^{13}C$ values between benthic-algal and planktonic sources (Fig. 14.3), suggesting that both sources may ultimately contribute to production of these fishes. Many of the similarities between the Pacific reef sites are also evinced in the isotopic profiles of Caribbean coral reefs (Fig. 14.4a) and Mediterranean temperate rocky reefs (Fig. 14.4b). Thus similar isotopic patterns can be discerned in the food webs of widely separated systems, highlighting the fact that these data reflect repeatable and meaningful features of the food webs concerned.

Other uses for stable isotopes include the elucidation of migration patterns (Hobson 1999), since organisms moving between isotopically distinct food webs can carry with them information on the location of previous feeding. Such an approach has proven particularly useful to track inshore versus offshore and marine versus freshwater movements in anadromous fishes (Hesslein et al. 1991). Stable isotopes of nitrogen and carbon can reveal ontogenetic dietary changes in both fish (Lindsay et al. 1998) and invertebrates (Hentschel 1998) and have been used to examine whether such changes occur earlier or later under differing fishing regimes (Persson and Hansson 1999). Several studies, notably those of Wainright et al. (1993) and Thompson et al. (1995), have used stable isotope
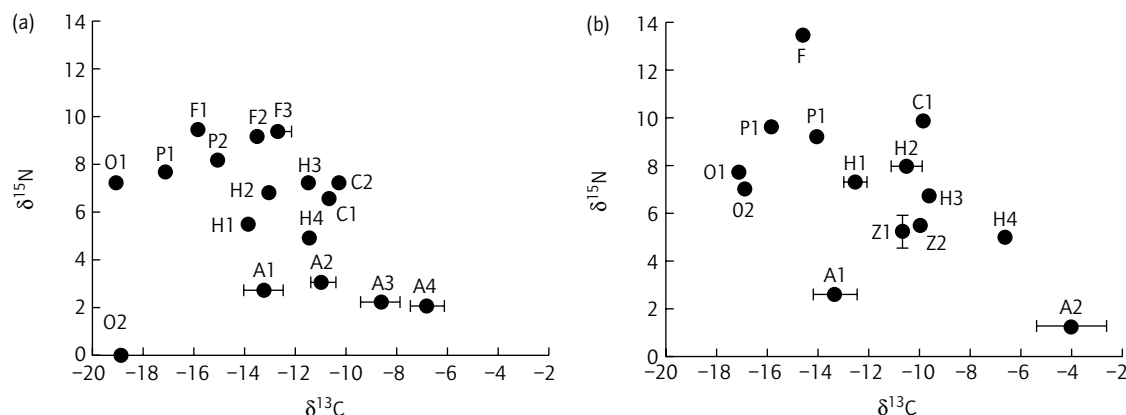
Fig. 14.3 Comparison of the isotopic 'fingerprints' of two shallow coral reef food webs, 3000 km apart in the South Pacific, based on the natural abundance data (mean ± SE, where visible) of carbon (δ^{13}C) and nitrogen (δ^{15}N). (a) Northwestern outer margin of the Great Astrolabe Reef, Dravuni, Fiji. Algae: A1, algal turf in territories of the fish *Plectroglyphidodon lacrymatus*; A2, calcareous encrusting algae; A3, algal turf in territories of the fish *Acanthurus lineatus*; A4, algal turf in territories of the fish *Stegastes nigricans*. Coral-feeding fishes: C1, *Chaetodon trifasciatus*; C2, *Chaetodon baronessa*. Piscivorous fishes: F1, *Aphareus furca*; F2, *Plectropomus leopardus*; F3, *P. laevis*. Planktonic materials: O1, POM >53 µm collected in March; O2, POM >53 µm collected in September. Plankton-feeding fishes: P1, *Pseudanthias pascalus*; P2, *Caesio caerulaureus*. (b) Barrier reef at Tiahura, Moorea, French Polynesia. Algae: A1, algal turf in territories of the fish *Stegastes nigricans*; A2, calcareous encrusting algae. Coral-feeding fish: C1, *Chaetodon trifasciatus*. Piscivorous fish: F, *Cephalopholis argus*. Herbivorous fishes: H1, *Acanthurus nigrofuscus*; H2, *Stegastes nigricans*; H3, *Ctenochaetus striatus*; H4, *Chlorurus sordidus*. Planktonic materials: O1, POM >53 µm collected during the day; O2, POM >53 µm collected at night. Plankton-feeding fishes: P1, *Heteroconger* sp.; P2, *Myripristis violaceus*. Reef-building corals: Z1, *Acropora* sp.; Z2, *Porites* sp. (Source: N.V.C. Polunin, unpublished data.)

compositions in archival tissues of predatory fish and seabirds to look for long-term changes in the trophic structure of North Atlantic food webs, and have tentatively related such changes to changing patterns of exploitation over the past 50–100 years.

It is becoming progressively less expensive to measure stable isotopes in biological tissues, and technological advances are making the method increasingly available to ecologists. A major advantage of these data over conventional dietary analyses is that the tissues that are sampled turn over relatively slowly and stable isotope compositions therefore reflect the diet of the animal over substantial periods of time. In the case of most late juvenile and adult fishes, the time-scale concerned will be of a year or more (Hesslein et al. 1993), but will tend to be shorter for very young fishes (Doucett et al. 1996) and other organisms in which

tissue turnover is more rapid. Monteiro et al. (1991) focused on muscle lipids because they sought to highlight relatively short-term dietary histories of anchovies. On the other hand, removal of lipid is likely to reduce the variability of isotope data (Pinnegar and Polunin 1999).

Gut contents and stable isotope data each have their own relative merits (Table 14.2). The uses of gut contents data are reviewed by Jobling in Chapter 5, this volume. These data have strengths in resolving individual trophic linkages, but the extent of these is limited to those parts of the diet that are readily identified and quantified. Stable isotope data can be especially useful for assessing the relative importance of major pathways (Doucett et al. 1996), whether two species feed similarly or dissimilarly, and for indicating the component of the diet that is actually assimilated and not simply
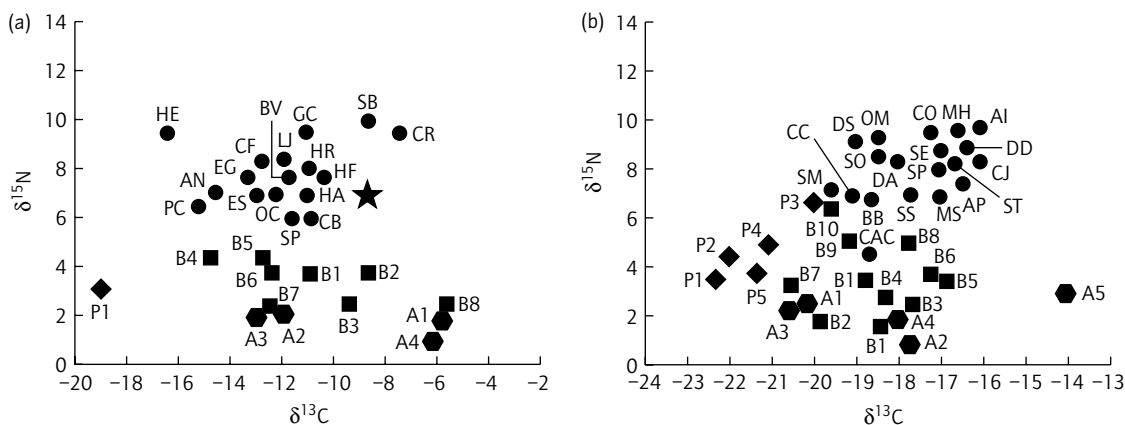
Fig. 14.4 Isotopic 'fingerprints' of (a) Caribbean coral reef and (b) Mediterranean rocky littoral community (Revellata Peninsula, Corsica). Plants are represented by hexagons, benthic invertebrates by squares, pelagic invertebrates by diamonds and fishes by circles. (a) Caribbean. Algae and seagrasses: A1, *Batophera* sp.; A2, *Halimeda* sp.; A3, *Syringodium filiforme*; A4, *Thalassia testudinum*. Invertebrates: B1, *Bittium varium*; B2, *Chiton squamosus*; B3, *Diadema antillarium*; B4, *Grapsus* sp.; B5, *Panulirus argus*; B6, Serpulidae; B7, *Strombus gigas*; B8, *Tripneustes esculentus*; P1, plankton. Fishes: AN, *Aetobatus narinari*; BV, *Balistes vetula*; CB, *Calamus bajonado*; CF, *Cephalopholis fulva*; CR, *Carangoides ruber*; EG, *Epinephelus guttatus*; ES, *Epinephelus striatus*; GC, *Ginglymostoma cirratum*; HA, *Haemulon album*; HE, *Hemiramphus* sp.; HF, *Haemulon flavolineatum*; HR, *Holocentrus rufus*; LJ, *Lutjanus jocu*; OC, *Ocyurus chrysurus*; PC, *Priacanthus cruentatus*; SB, *Sphyraena barracuda*; SP, *Sparisoma* sp.; Star, green turtle *Chelonia mydas*. (Source: data from Keegan and DeNiro 1988.) (b) Mediterranean. Algae and seagrasses: A1, *Cystoseira balearica*; A2, *Cladophora prolifera*; A3, *Halopteris scoparia*; A4, *Dictyota dichotoma*; A5, *Posidonia oceanica*. Benthic invertebrates: B1, *Paracentrotus lividus*; B2, *Sphaerechinus granularis*; B3, *Haliotis lamellosa*; B4, *Cerithium vulgatum*; B5, *Bittium reticulatum*; B6, *Eunice harassi*; B7, mixed benthic amphipods; B8, *Leptomysis livingula*; B9, *Pagurus chevreuxii*; B10, *Lysmata seticaudata*; B11, *Xantho poressa*. Pelagic invertebrates: P1, zooplankton >200 μm; P2, *Anchylomera blossevillei*; P3, *Siriella* spp.; P4, *Pelagia noctiluca*; P5, *Chelophyes appendiculata*. Fishes: AI, *Apogon imberbis*; AP, *Atherina presbyter*; BB, *Boops boops*; CC, adult *Chromis chromis*; CCj, juvenile *Chromis chromis*; CJ, *Coris julis*; CO, *Conger conger*; DA, *Diplodus annularis*; DD, juvenile *Dentex dentex*; DS, *Diplodus sargus*; MH, *Muraena helena*; MS, *Mullus surmuletus*; OM, *Oblada melanura*; SE, *Serranus scriba*; SM, *Spicara maena*; SO, *Symphodus ocellatus*; ST, *Symphodus tinca*; SP, *Scorpaena porcus*. (Source: data from Pinnegar and Polunin 2000.)

that which is ingested. In addition, stable isotope analysis has proven useful for measuring trophic level (Minagawa and Wada 1984) and for discerning spatial variations in nutrition (Jennings et al. 1997). There are also constraints to the use of stable isotopes and their interpretation (Table 14.2); one such constraint, relevant to the elucidation of food webs, involves the phenomenon known as 'isotopic routing' (Gannes et al. 1997). It would appear that the isotopes obtained in the diet of a particular consumer are not always evenly apportioned once ingested, such that the nitrogen and carbon derived from certain dietary components, such as animal proteins, may be routed to

different tissues or body processes compared with those derived from other sources, such as plant carbohydrates. The upshot of this is that tissues may not always reflect the isotopic composition of the bulk diet and might actually reflect the isotopic composition of an apparently minor dietary constituent. This phenomenon may be particularly apparent in herbivorous animals such as the parrotfish *Sparisoma* spp. (Fig. 14.4a) and the sparid *Sarpa salpa* (Fig. 14.4b), which exhibit $\delta^{15}N$ values higher than would be expected if they were feeding on plant material. Since it is more efficient to assimilate proteins and to catabolize carbohydrates, and because the plant material consumed

Table 14.2 Advantages and disadvantages of gut contents and stable isotope analyses for elucidating the trophic relationships of consumers.

Information	Gut contents	Stable isotopes
Resolution of principal trophic pathways in food webs	Can be good where individual sources are identifiable (e.g. indigestible hard parts)	Can be good if pathways well distinguished by δ^{13}C of the basal materials, poor if more than two pathways
Connectance (proportion of linkages that are realized)	Good but only for individual sources that are identifiable	Poor because only broad categories distinguishable as a rule
Measure of nutritional roles of different dietary items	Poor because diet, not actual absorption, quantified	Can be good because isotopes are in materials that have been assimilated
Measure of short-term differences in diet of large predators	Potentially good because data are only short term	Poor because tissue turnover slow
Measure of spatial differences in diet of large predators	Will be good where major items identifiable	Will be good where shifts occur in items with distinct δ^{13}C and/or in trophic level
Measure of trophic level	Often inaccurate because diet incompletely described	Can be accurate if basal materials identified, and change in δ^{15}N per trophic level validated

by herbivores largely consists of carbohydrates but is often supplemented with small amounts of proteinaceous animal materials (Robertson 1982), the contribution of plant sources in the diet of herbivorous fishes may be greatly underestimated by stable nitrogen isotope analyses.

Stable isotope data and conventional dietary data have thus together contributed to the elucidation of food-web structure (Pinnegar and Polunin 2000) and both methods have revealed features that would not otherwise have been detected using the other method.

A further indirect method that can yield useful information about a consumer's diet is the analysis of fatty acids (Iverson 1993). When triglycerides and other forms of lipid are ingested, they are broken down into free fatty acids and monoglycerides before the body can incorporate them. Ingested fatty acids that are not utilized for immediate energy requirements are generally stored without substantial modification in adipose tissue (Iverson et al. 1995). Chain elongation and insertion of double bonds may occur to some extent when fatty acids are incorporated into cell membrane structure (Hagen et al. 1995; Pond et al. 1997), and some biosynthesis can occur from other dietary components such as amino acids. Despite these potential

changes, differences in fatty acid composition are detectable in the tissues of animals that have fed on different diets. As is the case with stable isotopes, these differences reflect dietary integration over longer time periods (Sargent et al. 1988; Fraser et al. 1989). In laboratory diet-switch experiments, tissue fatty acid patterns may change significantly in only 3 weeks in adult cod to reflect the patterns found in the new food (Kirsch et al. 1998). Thus gut contents analysis indicates dietary patterns over short time periods of hours to days, stable isotopes can be used to elucidate patterns over longer time periods of months to years, and fatty acid analysis may reflect diet over periods of intermediate duration of weeks to months.

Because of their great variety, long-chain and polyunsaturated fatty acids would appear to be particularly suitable as trophic tracers in marine organisms. It has been demonstrated that specific fatty acids or combinations of them are associated with certain taxonomic classes of phytoplankton (Sargent 1976, 1978). Thus species of Chrysophyceae, Haptophyceae and Dinophyceae are characterized by the presence of C18:4 $(n-3)$ and C18:5 $(n-3)$ fatty acids, which are essentially absent from diatoms. Diatoms are typified by the fatty acids C16:4 and C20:5 $(n-3)$ as well as hav-

ing a higher ratio of C16:1 ($n − 7$) to C16:0 fatty acids than other phytoplankton classes, thus providing the potential for identifying the transfer of different sources of production through a number of trophic levels. Analysis of fatty acid profiles have been widely used to elucidate the diets of fish, marine mammals and seabirds (Iverson et al. 1997), to differentiate between marine and freshwater sources (Smith et al. 1996) and to highlight differences between geographically separated populations of the same species (Iverson et al. 1997; Logan et al. 2000). They have also been used to look for seasonal and ontogenetic patterns in the diet of fish and invertebrate species (Pedersen et al. 1999), and different species of marine fish, cephalopods and crustaceans vary markedly in their fatty acid profiles (Iverson et al. 1997; Raclot et al. 1998).

Complicated food-web diagrams such as that illustrated in Fig. 14.5a have become the most common way of visualizing the complex interactions that exist within communities. However, such depictions may have many shortcomings as a basis for predicting indirect impacts of human interventions or natural changes in the environment. Possible weaknesses include the following.

1 Diets vary temporally and spatially (Righton et al. 2001), yet most food-web studies assume steady-state conditions and data are derived from very short-term studies conducted at small spatial scales (Frid and Hall 1999). Composite food webs, where they exist, build upon data from many areas and points in time and may offer a promise of generality, but then beg questions of local accuracy (Paine 1988).

2 Many dietary items, such as dissolved organic matter, particulate detritus, gelatinous zooplankton, fish eggs and spat, are often poorly quantified. Thus certain pathways within systems, which may support a large part of fish production, will scarcely be described (Hall and Raffaelli 1993).

3 Particular organisms, notably bacteria, fungi, protozoans, nematodes and other small metazoans, typically tend to be greatly underrepresented and/or incorrectly assigned in food webs, yet may play important roles (Pimm 1982). Larger

consumers that are well represented may also be poorly characterized because of a paucity of dietary data for them (Cortés 1999).

4 As with food chains, food webs indicate trophic fluxes among organisms in the system, but feeding is only one of many types of interaction among organisms. Processes such as migration and recruitment may also be very influential in controlling population sizes (Jones 1991) and thus food-web structures.

In most cases the knowledge base of food webs is very thin (Goldwasser and Roughgarden 1997), but it is worth highlighting a few further characteristics of food webs before proceeding. Food webs vary greatly both spatially and temporally, at the top especially through fluctuations in processes such as recruitment and fishing, and at the bottom by means of variations in primary productivity including the effects of seasonality. In some cases, concomitant changes may occur across all trophic levels at large spatial scale and be linked to long-term climatic trends (Aebischer et al. 1990; Polovina et al. 1994). The boundaries of food webs may often be hard to define (Pimm et al. 1991; Pauly and Christensen, Chapter 10, Volume 2), given the extent of export and import of organic matter and of large-scale migrations of animals (Hesslein et al. 1991). Omnivory is often widespread and may reduce the potential for indirect effects such as trophic cascades and 'prey-release' (Kaiser and Jennings, Chapter 16, Volume 2). This is because predators in the community can feed opportunistically at more than one trophic level (Monteiro et al. 1991; Polis and Strong 1996).

In spite of evidence that certain trophic pathways may be relatively long and that there is a relationship between web size, or the level of aggregation, and mean food-chain length (Hall and Raffaelli 1993), individual trophic pathways within webs rarely consist of more than four trophic levels (Hall and Raffaelli 1993; Pauly et al. 1998b). Many factors may limit the length of food chains (Pimm 1982, 1991; Sterner et al. 1997). Amongst the most obvious is primary productivity, yet food chains in productive systems are not necessarily shorter than those in oligotrophic systems (Briand and Cohen 1987).
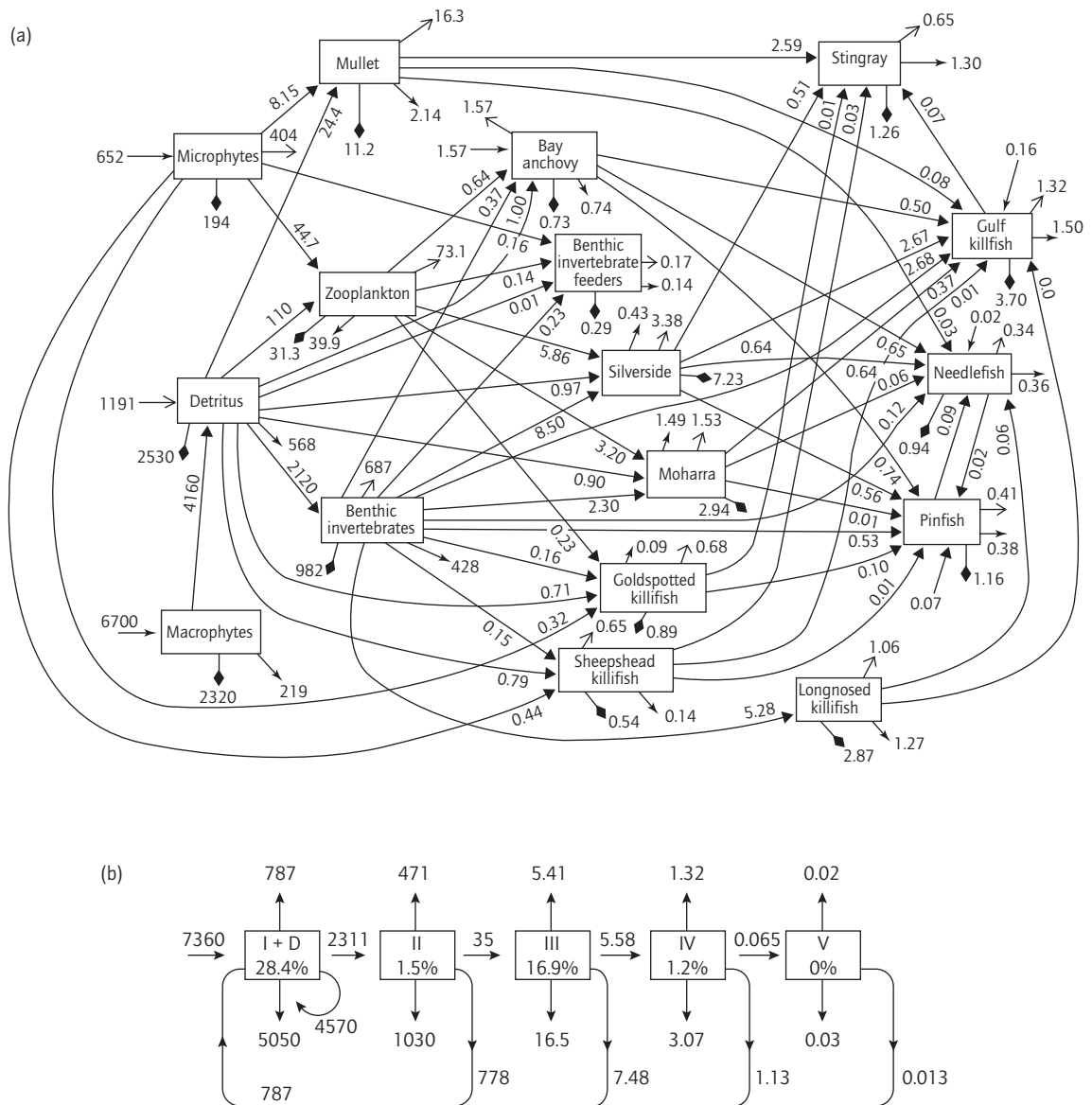
Fig. 14.5 Carbon flows (mg m^{-2} day^{-1}) among taxa of a marsh ecosystem, Crystal River Florida: (a) schematic food web; (b) aggregated chain of trophic transfers derived from (a). (a) Unfilled arrows ($\rightarrow$) depict returns to detritus; diamond-shaped arrows ($\rightarrow\!\!\blacklozenge$) represent respiration; sharp arrows ($\rightarrow$) depict import or export; triangular arrows ($\rightarrow$) represent trophic fluxes. (b) Flows out of the top of boxes represent export and flows out of the bottom represent respiration. Recycling of non-living material is through compartment D (detritus) and the percentages within the boxes represent annual trophic efficiencies. (Source: after Ulanowicz 1995.)

Ulanowicz (1995) has provided procedures for passing readily from complex food webs (Fig. 14.5a) to simple concatenated chains of trophic interactions (Fig. 14.5b). Such chains, Ulanowicz (1995) claimed, are useful because they provide an accurate but uncomplicated picture of the system's underlying trophodynamics, while making it possible to map arbitrarily complicated networks into a common topological format. The method involves the construction of a matrix of feeding coefficients and the allocation of the different dietary interactions, but not the consumer itself, into discrete trophic levels (*sensu* Ulanowicz 1986). Cycles within the system via detritus are treated separately (Ulanowicz 1995) and detritus is assigned to trophic level one. The food chain or 'Lindeman spine' that results from these procedures (Fig. 14.5b) is open to comparison with 'spines' from other systems and many marine and freshwater assemblages have been compared as a result (Pauly and Christensen, Chapter 10, Volume 2). Confidence in linear representations of food chains has been raised by strong positive correlations found between $\delta^{15}N$ and body size across whole trawl assemblages in the North Sea (Jennings et al. 2001, 2002). The relationship suggests that body size not taxonomy primarily drives predator–prey relations in the North Sea, but this needs to be tested at other locations.

If food webs constitute useful maps of ecological communities (Paine 1988), a major question concerns what they show and where they lead. The fact is that the existence of a feeding relationship between two organisms does not necessarily indicate that they interact strongly. Changes in one compartment need not lead to accompanying changes in the other (Paine 1980, 1992). A major reason for this is that predation is only one source of mortality (Kaiser and Jennings, Chapter 16, Volume 2). All biological populations fluctuate in abundance, and the degree of fluctuation may depend on an array of density-dependent and density-independent factors such as recruitment success, predation, pathogens and the consequences of environmental disturbance. An implication of this basic fact, combined with the reticulate nature of food webs, is that a signal initiated at a point within a food web, for example through disturbance of one of its components, can be expected to be rapidly attenuated with each trophic step (Strong 1992).

A way forward in understanding functional linkages among organisms, or groups of organisms, will be found only where empirical data on interaction strengths are available. The next step is therefore to consider how relevant information of this sort can be derived.

14.3   INTERACTION STRENGTH IN FOOD WEBS

The strength or importance of a trophic relationship cannot be assumed equivalent for all web members. A consumer will be a strong interactor if, in its absence, pronounced changes ensue. Removal of a weakly interacting species will yield no or slight change (Paine 1980).

Although the intent is often to identify large-scale characteristics that are of interest to environmental managers, most food-web data are derived from measurements and manipulations at spatial scales that are extremely small (Menge 1992, 1997; Menge et al. 1994; Wootton 1994). The large-scale implications of the small-scale observations remain essentially untested. Major indirect effects of perturbations characterized from small-scale studies, such as predator controls on prey abundance, trophic cascades and keystone predation, seem to be little known from empirical work at large spatial scales (Estes and Duggins 1995; Jennings and Kaiser 1998), whether in benthic systems (Pinnegar et al. 2000) or pelagic systems (Verity and Smetacek 1996).

Experimentation is the standard scientific approach to establishing the strength of connections between components in nature, such as the selective exclusion experiments of Paine (1992), but at large scales in the marine environment rigorous experimentation remains more or less impossible because of ethical, logistical and financial constraints. An alternative is to study the consequences of large-scale perturbations arising from management decisions (Walters' 1986 concept of

Fig. 14.6 Trophic cascades inferred for kelp beds in (a) California and (b) Alaska. Arrows indicate feeding on prey organisms; h, herbivory; p, predation. (Source: from Pinnegar et al. 2000; for primary sources see text.)
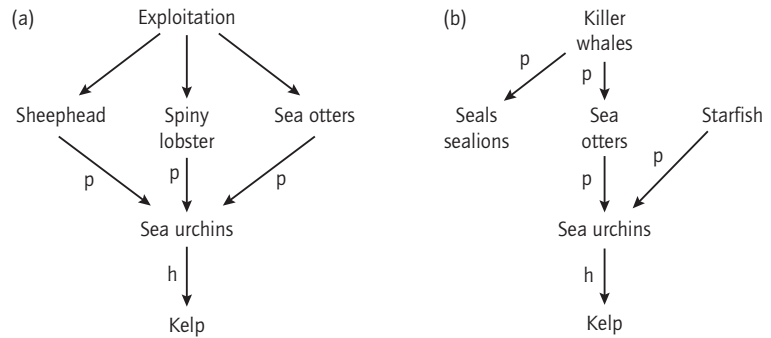
adaptive management) or developments such as those of fisheries or marine protected areas, or to look at responses following climatic events. Such large-scale work has identified a number of cases of interactions involving three or more trophic levels, nearly all of which are based on hard substrata, namely rock and coral reef (Pinnegar et al. 2000). Three case studies will be used here to characterize the dominant types of interaction that have been found in benthic systems.

Population explosions of the sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* have been known for 30 years to occur in the kelp forest of the California coast (North and Pearse 1969). The spiny lobster *Panulirus interruptus* (Tegner and Dayton 1981; Tegner and Levin 1983), sea otter *Enhydra lutris* (Lowry and Pearse 1973) and sheephead wrasse *Semicossyphus pulcher* (Cowen 1983) have all been implicated as biological agents controlling the sea urchins (Fig. 14.6a). Changes in abundance of the sea urchins in turn seem to affect abundance of macroalgae (Cowen et al. 1982). The evidence is that there are strong interactions among large predators, major herbivores and the structure of the macroalgal community. An implication of this is that exploitation of the otter, lobster or wrasse will have important consequences for the entire system (Juanes et al., Chapter 12, this volume; Kaiser and Jennings, Chapter 16, Volume 2).

In the Aleutian Islands of Alaska, islands with sea otters have fewer sea urchins (*Strongylocentrotus polyacanthus*) than those without (Estes and Palmisano 1974). The latter tend to have abundant macroalgal assemblages (Estes et al. 1978), although a starfish (*Pycnopodia helianthoides*) also plays a role in determining this structure (Duggins 1983). Where sea otters have increased in abundance, sea urchins have declined, in contrast to sites with unchanged sea otter populations where sea urchin numbers have remained relatively steady (Estes and Duggins 1995). In large areas of western Alaska, however, a recent decline in sea otter abundance has been attributed to predation by killer whales, predation which had not been observed before 1991 (Estes et al. 1998) (Fig. 14.6b). Since the sea otter is a major focus of conservation work, an implication is that, at least where it is not vulnerable to killer whales, protection of this animal will have consequences for the entire system, although the outcome is likely to be influenced spatially and temporally by the intensity of sea urchin recruitment (Reynolds et al., Chapter 15, Volume 2).

In the Caribbean, many coral reefs became overgrown with macroalgae in the early 1980s and have remained so ever since (Hughes 1994). Evidence from large-scale correlations in the Caribbean and also comparisons between protected and unprotected areas in Kenya suggest that intensive fishing has led to widespread increase in sea urchin densities (Hay 1984; McClanahan 1994) through the removal of urchin predators and also of competing herbivorous fishes (McClanahan and Shafir 1990) (Fig. 14.7). On shallow Caribbean reefs where sea urchins were abundant, a pathogen led to large-scale decimation of the urchins in 1982–3 and was the immediate cause of the macroalgal
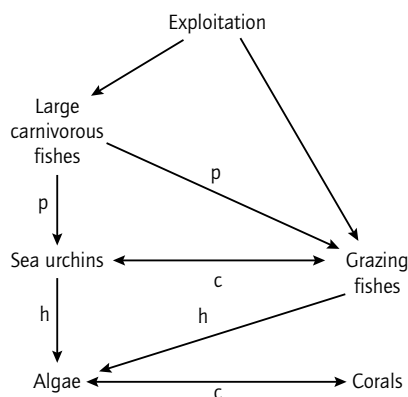
Fig. 14.7 Relationships among predators, grazers, macroalgae and corals inferred for reefs on the north coast of Jamaica and in Kenya. Arrows indicate feeding on prey organisms; h, herbivory; p, predation; c, competition. (Source: from Pinnegar et al. 2000; for primary sources see text.)

overgrowth (Lessios 1988; Hughes 1994), but in deeper areas correlative and experimental evidence points to grazing fishes being important controllers of macroalgae (Morrison 1988; Williams and Polunin 2001). The role of fish may be moderated by spatial escapes from herbivory following loss of coral cover through diseases, bleaching and cyclone impacts (Fig. 14.7). Thus, even where strong evidence for predation controls is deduced, other factors that are not explicit in food webs can prove important determinants of community structure and are likely to influence any future change of state in the system.

Leontief (1951) developed a method to assess the importance of direct and indirect interactions in the economy of the USA, using what has since been called the Leontief matrix. This approach was introduced to ecology by Hannon (1973) and Hannon and Joiris (1989). Using this method it becomes possible to assess the effect that changes in the biomass of a particular group will have on the biomass of other groups in the system. Ulanowicz and Puccia (1990) developed this approach and it is now widely utilized as a routine within the Ecopath modelling system (Pauly and Christensen, Chapter 10, Volume 2).

14.4 IMPLICATIONS OF FOOD WEBS AND TROPHODYNAMICS FOR FISH AND FISHERIES SCIENCE

There has been debate amongst ecologists over whether bottom-up forces, such as primary productivity and nutrient availability, or top-down forces, such as predators and consequently fishing, predominate in communities, and thus whether 'little things' (Wilson 1987) or 'big things' (Terborgh 1988) exert the most control over natural systems (Hunter and Price 1992; Persson, Chapter 15, this volume; Pauly and Christensen, Chapter 10, Volume 2).

The generally weak evidence for far-reaching effects such as trophic cascades has often been taken as a sign that most marine food webs are driven 'bottom-up' (Strong 1992) by carbon fluxes from primary producers (Ryther 1969), and this was partly because grazers appeared not to be limited by food supply in the pelagic zone and on reefs. Greater understanding, at least in the pelagic zone, has indicated that grazing is in fact more intense than previously thought (Verity and Smetacek 1996), while on reefs food limitation of grazers cannot be excluded because much of the primary production may be accounted for by export (Polunin and Klumpp 1992). Consequently, faced with such uncertainty, Hunter and Price (1992) offered the sensible advice that ecologists not ask 'Do resources or predators regulate this particular population?' but rather should try to assess what factors might moderate resource limitation and predation in the system, determining when and where each of these factors will predominate (Kaiser and Jennings, Chapter 16, Volume 2 discuss this issue with particular regard to the effects of fishing).

Ecological systems are extraordinarily complex and several models have been proposed that link the strength and dynamics of trophic interactions with the overall stability of communities (reviewed in Pimm 1991). Data on natural food webs have generally indicated that these are character-

ized by many weak interactions and only a few strong ones (Paine 1992). May (1973) showed that 'complex' ecological systems tend to be unstable. Since complexity will eventually cause a system to fall apart, with strong fluctuations in abundance and eventual loss of species, the view that held sway in the ecological literature for nearly two decades was that natural systems tend to be quite simple and dominated by strong interactions. However, McCann et al. (1998) have demonstrated that the multitude of weak links that exist in natural systems are important in promoting community persistence and stability by damping oscillations caused by strong interactions between consumers and resources and thus preventing the loss of species (Polis 1998). Consequently, strong interactions may not in fact be as dominant in natural systems as many originally assumed they were, since food webs dominated by strong interactions may be more prone to instability (McCann et al. 1998), and may thus be less persistent, than those containing many weak linkages. It thus becomes imperative to understand better the extent of strong and weak links in systems.

The reefs and other rocky habitats for which strong interactions seem most convincingly established are scarcely amenable to anything other than small-scale artisanal fisheries. On the other hand, the effects of industrial-scale fisheries are likely to be greater, yet understanding of such effects is in many respects more primitive (Kaiser and Jennings, Chapter 16, Volume 2). This seems to be because the large-scale fisheries have scarcely yet been amenable to the spatial comparisons that have yielded valuable data on the effects of small-scale fisheries (Jennings and Kaiser 1998). However, responses such as an increase in the biomass of cephalopods and particularly squid in intensively fished soft-bottom demersal systems do seem to be a worldwide phenomenon in response to fishing (Caddy 1983; Gulland and Garcia 1984; Pauly 1985, 1988; Pipitone et al. 2000).

Even though the evidence for top-down controls is not as strong and predictable as might be expected, the understanding of feeding and food webs can nevertheless be used as the basis for making several predictions as to the systemic effects of fish-

ing and, conversely, the protection of target species in marine protected areas (MPAs) (Polunin, Chapter 14, Volume 2). For example, it can be predicted that in MPAs the following conditions will prevail.

1 Trophic level of predators normally targeted by intensive fishing will tend to increase because their average size will tend to be greater and thus they will be able to feed on larger prey (Juanes et al., Chapter 12, this volume), and because large prey organisms, also targeted by fishing, will tend to be more abundant; thus fish of the same size will be able to feed more often at higher trophic levels.

2 The range of trophic levels at which such large predators will be able to feed, a form of omnivory, will tend to be greater (Diehl 1992) because the larger an animal, the greater the range of sizes of prey it can potentially eat.

3 Ontogenetic dietary changes, which many fishes exhibit, will occur later if they are size-related because there will be more competition for resources, leading to slow growth. The same size will be reached at greater mean age (Persson and Hansson 1999; Mittelbach, Chapter 11, this volume).

As yet, these ideas remain untested. However, it is generally assumed in many studies and indeed in most existing fisheries models that prey are consumed in direct proportion to their abundance in the environment and in relation to the fraction that they represent of the total available prey biomass. This is known in foraging theory as a type II functional response (Holling 1959; Juanes et al., Chapter 12, this volume). A type II functional response implies that consumption rate rises in proportion to prey density but then gradually decelerates until a plateau is reached. However, considerable temporal variation has been revealed in the diets of many predatory fish species (Greenstreet et al. 1998; Righton et al. 2001) and little is known of the actual relationships that exist between the diets of fish and the abundance of their prey at different temporal and spatial scales (Greenstreet et al. 1998). For example, predators might switch between different prey species when a particular prey is at low density. The upshot of such behaviour (termed a type III response) would be a sigmoidal relationship between the number of

prey consumed and prey density (Juanes et al., Chapter 12, this volume). The implication would be that many existing fisheries models, such as multispecies virtual population analysis (Shepherd and Pope, Chapter 7, Volume 2), greatly overestimate predation on species that are rare.

14.5   CONCLUSIONS

The science involved is far from perfect, but the demands for scientifically based management of the coastal zone are growing rapidly and have already long since surpassed the supply of information supported by conventional science. Many investigators feel themselves caught between the needs of the world and the discipline of the science. On the one hand, the principles of interactions among species within communities are beginning to be understood better and the methods have improved for elucidating them further. On the other hand, it is an understanding of what these principles mean in the functioning of systems at large scales that is noticeably lacking. For example, the word 'trophodynamics' used as a label for this field of scientific activity is not a good indicator; a relatively large amount is known about the trophic links but almost nothing is known of the dynamics. The data on which food webs are based indicate fluxes, yet these fluxes are very poorly quantified and aggregation of species-level data into trophic groups subsumes much detail, a great deal of which is important for the understanding of the functioning of whole systems (Pauly and Christensen, Chapter 10, Volume 2). Magnitudes of material fluxes are rarely known; where they are, they are not good predictors of the relative strength of interactions when comparing different trophic levels. For example, the fluxes at the bases of food webs that are large, say between primary producers and grazers, in absolute terms do not indicate stronger interactions than between top predators and their prey. Rather, the fluxes are more predictive of interaction strength within trophic levels and are especially predictive within trophic groups, where different fluxes, such as consumption rates by different predators, are most likely to indicate the impacts of particular predators. Thus, food webs map ecological communities (Paine 1988) in only a very restricted sense; nonetheless they are maps of complex systems about which there would otherwise be very little basis for understanding or prediction.

ACKNOWLEDGEMENTS

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15 Community Ecology of Freshwater Fishes

LENNART PERSSON

15.1 INTRODUCTION

Ecology has been defined as the scientific study of the interactions between organisms and their environments (Krebs 1972). A useful starting point to address questions about interactions among organisms in relation to environmental conditions is to study patterns in the distribution of species or functional groups over space and time. Changes over space in abundance relationships between fish species or groups of species have been observed along several environmental gradients, including temperature, light and productivity (Colby et al. 1972; Leach et al. 1977; Magnuson et al. 1979; Schlosser 1987; Persson et al. 1991, 1992). The purpose of this chapter is to discuss some of these patterns but also to provide a framework for a mechanistic understanding of the patterns observed. Because a fundamental characteristic of fish populations, as with populations of many other species, is that individuals differ substantially in size, such a treatment has to consider the implications of size structure for ecological interactions.

In the following, I first consider studies that have focused on large-scale patterns in the distributions of fish species, including between-continent comparisons often using multivariate techniques. This part shows that a number of basic environmental variables, such as temperature, light and productivity, have major influences on the distribution of species across environmental gradients. At the end of this section I deal with the ecological perfor-

mance of different species in relation to abiotic factors such as light and temperature. This treatment can largely be seen as a treatment of the fundamental ecological niche, *sensu* Hutchinson, of different species. The actual niche of a species will be constrained by ecological interactions with other species. Fish ecology has played a prominent role in the development of ecological theory regarding niche dynamics and ecological interactions in general (Nilsson 1963; Svärdson 1976; Werner and Hall 1977, 1979; Werner 1986; Persson 1988). The presence of size structure also means that interactions among fish populations are generally a result of a mixture of size-dependent competitive and predator–prey interactions (Werner 1986; Persson 1988; Mittelbach and Osenberg 1993; Persson et al. 1999; Juanes et al., Chapter 12, this volume).

Studies of distribution patterns across systems show that size-structured interactions are of major importance for large-scale community patterns (Persson et al. 1991, 1992; Mittelbach and Osenberg 1993; Olson et al. 1995). Changes in fish community structure also have consequences for other trophic components of aquatic food webs (Carpenter et al. 1987; Persson et al. 1992). I consider the effects of fish on lower trophic components, which include a number of pathways such as direct predation on zooplankton, effects of fish consumption on nutrient recycling in pelagic environments, and translocation of nutrients between habitats (Schindler et al. 1996; Vanni 1996).

In a final section I discuss how size structure in fish populations can be formally analysed using a

modelling approach termed 'physiologically structured population models' (De Roos 1997; Persson et al. 1998). This modelling approach is based on a two-state-level concept and explicitly links individual-level processes such as individual growth to population-level processes. I argue that this modelling approach may form a productive research agenda for increasing our understanding of the implications of size structure for the community dynamics of fish. Methods for obtaining population parameters from size distributions are given by Pitcher (Chapter 9, Volume 2).

15.2 COMMUNITY PATTERNS AND BASIC ECOLOGICAL PERFORMANCE

15.2.1 Large-scale community patterns

Many studies focusing on fish community structure have stressed the insular nature of many lakes and the similarities between lakes and islands (Rahel 1984). This is so particularly for the theory of island biogeography, which relates species diversity to two major processes: immigration and extinction rates (MacArthur and Wilson 1967). The focus of island biogeography theory has traditionally been on species–area relationships using the slope of the regression between species diversity and area to analyse community patterns. However, as noted by Magnuson et al. (1998), the slope of the species–area regression has a variety of possible interpretations with respect to the importance to species diversity of isolation and extinction. Area *per se* is also correlated with many isolation and extinction properties of lakes. For example, there is a negative relationship between lake area and the proportion of lakes without a connecting stream in small forest lakes (Magnuson et al. 1998).

To reduce the problem with interpretations and correlations, multivariate approaches have been advanced to separate the possible roles of immigration and extinction in comparative studies (Tonn et al. 1990; Magnuson et al. 1998). The most extensive comparative studies on community patterns

using multivariate techniques have been carried in North American (particularly Wisconsin), Finnish and Swedish lakes (Tonn et al. 1990, 1995; Magnuson et al. 1998). These studies mainly considered small, often forest, lakes and have suggested that extinction is more important than isolation, which influences immigration, in determining community structure (Tonn et al. 1995; Magnuson et al. 1998). This has been related to the fact that small forest lakes have a number of features that contribute to frequent (relative to immigration) extinctions, such as low pH, seasonally occurring low oxygen levels and piscivores. The degree of isolation was not unimportant but it played a lesser role in observed patterns in species richness and assembly type (species configuration). However, differences were found between continents. In Finnish lakes, assembly type was explained by isolation to a larger extent than by each of four extinction factors, which was not the case in Wisconsin lakes (Tonn et al. 1990).

Magnuson et al. (1998) suggested that the reason that extinction is more important than isolation in explaining species richness and assembly type in small lakes is because immigration rates are low, often varying between decades to millennia. In contrast, extinctions can occur at substantially shorter time-scales from months up to a few decades after invasions. Correspondingly, studies in North American lakes show that immigration rates are much higher in larger lakes than in smaller lakes, partly due to human influences. Thus, lake area determines the importance of extinction rates vs. immigration rates in explaining species diversity and assembly type.

In Wisconsin lakes, three major factors were isolated as being of prime importance for extinction rates: winter-kills due to low oxygen, low pH and predation by pike (*Esox lucius*) or largemouth bass (*Micropterus salmoides*) (Magnuson et al. 1998). The frequency of winter-kills is expected to depend on environmental factors like lake depth, productivity, latitude and altitude. The importance of pH in determining species richness has become increasingly clear as a result of the acidification of lakes and its amelioration by liming that aims at restoring fish communities

(e.g. Appelberg 1998). Sensitivity to low pH also differs between species: cyprinids and salmonid fishes are more sensitive than, for example, perch (*Perca fluviatilis*). Extinctions due to predation have been reported from North American lakes, where predators like northern pike, largemouth bass and yellow perch (*Perca flavescens*) may eliminate populations of small cyprinids. The extinction probability for sensitive prey fish populations after their invasion of Wisconsin lakes inhabited by piscivores was on the same range as the extinction probability due to winter-kills and pH (Magnuson et al. 1998). In contrast, in European lakes cyprinids are able to persist more readily with piscivorous predators because Eurasian cyprinids can grow to a size where they are no longer susceptible to predation (Tonn et al. 1990).

Other differences in processes affecting species richness and assembly type have also been found between continents and regions. As described above, extinction factors were more important than isolation factors for Wisconsin lakes in comparison with Finnish lakes (Magnuson et al. 1998). Furthermore, conductivity and lake depth were more important in Finnish lakes, whereas pH was more important in Wisconsin lakes. Swedish lakes differed from Finnish and North American lakes in that geographical factors were of outstanding importance for separating Swedish lakes, whereas abiotic factors and lake morphometry were more important in Finland and in two North American regions (Tonn et al. 1995).

Studies of species distributions of fish in streams show that headwater streams with low aquatic primary productivity generally have lower species richness and fish assemblages, characterized by fast-colonizing fish species subject to large fluctuations in local densities (Schlosser 1987). Studies of tropical systems suggest that these systems show the same pattern in changes in species richness with stream order as temperate systems, suggesting that similar mechanisms are operating in structuring fish communities in temperate and tropical systems (Winemiller and Leslie 1992) (Fig. 15.1). Complementing these studies, Winemiller (1992) found in a comparative interregional/intercontinental study an increase in species ecomor-
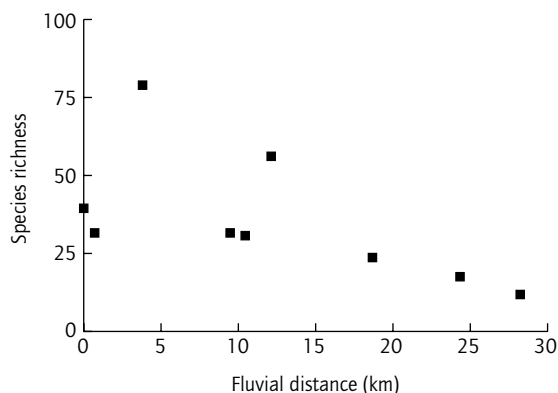
Fig. 15.1 Changes in species richness with fluvial distance from mouth in Rio Tortuguero, Costa Rica. (Source: data from Winemiller and Leslie 1992.)

phological diversification with decreasing latitude. This increase in morphological diversification in high-diversity tropical faunas was, based on ecomorphological measures, not associated with an increase in species packing. However, whether the greater species richness associated with greater niche diversification was a result of an expansion of the total range of food and habitat resources used or due to a finer subdivision of available resources could not be determined based on ecomorphological measures only.

15.2.2 Basic ecological performance

The performance of different fish species under different abiotic environmental conditions can, among other things, be related to the fact that physiological rates are directly influenced by factors such as temperature, light, salinity, pH and oxygen and that different species have different optima with respect to these factors (Power 1990; Brix, Chapter 4, this volume). In the following, I consider temperature and light in more detail with respect to the performance of different species.

For poikilotherms like fish, temperature is a major factor affecting overall ecological performance through its effect on energetics (Brett and Groves 1979). (Effects of temperature on rates of
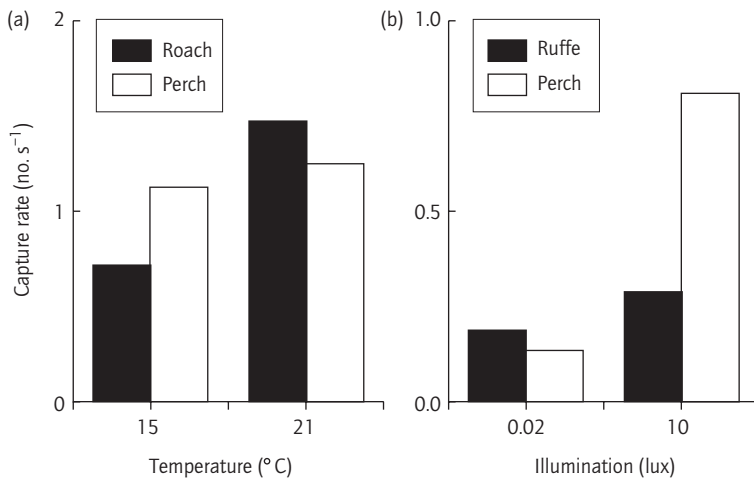
Fig. 15.2 (a) Maximum capture rates of roach and perch feeding on *Chaoborus* larvae at 15 and 21 °C. (Source: data from Persson 1986.) (b) Maximum capture rates of ruffe and perch feeding on *Chaoborus* larvae at 0.02 and 10 lx. (Source: data from Bergman 1988.)

development are reviewed by Jobling in Chapter 5, this volume, and effects on metabolism by Brix in Chapter 4, this volume.) Experimental studies have shown differences between species in temperature-dependent consumption and growth performance. Among salmonid fishes, brown trout *Salmo trutta* have their maximum consumption rate and growth rate at higher temperatures than do Arctic char *Salvelinus alpinus* (Elliott 1975; Jobling 1983). Temperature also influences the large-scale distributions of species. For example, Power (1990) found that temperature was important in explaining the geographical distribution of salmonid species. Within systems, Baltz et al. (1982) showed that temperature was a major determinant of species abundance in streams. A major route by which temperature affects the ecological performance of fish species is through its effect on foraging rate. Hammar (1998) suggested that differences in feeding performance of brown trout and Arctic char at different temperatures, particularly the fact that Arctic char may feed in winter under the ice, were important in explaining the distribution of these two species within and among lakes. Experimental studies have also demonstrated differences in functional responses of species as a function of temperature (for details of different functional responses see Juanes et al., Chapter 12, this volume). Persson (1986) showed

that the maximum consumption rate of Eurasian perch was higher than that of roach (*Rutilus rutilus*) at temperatures below 18 °C, whereas the opposite was the case at temperatures above 18 °C (Fig. 15.2a). This difference in temperature-dependent foraging ability relates in turn to the fact that perch are distributed further north in Scandinavian lakes and also penetrate deeper in stratified lakes. The impact of temperature on the ecological performance of fish led Magnuson et al. (1979) to advance temperature as a dimension along which fish species with different temperature optima could separate their niches.

Species differences have also been shown in response to light conditions (Schultz and Northcote 1972; Bergman 1988). Schultz and Northcote (1972) described Dolly Varden char (*Salvelinus malma*) as a more efficient forager in dim light conditions compared with cutthroat trout (*Oncorhynchus clarki*). Additionally, differences in foraging abilities have been suggested to be important for the ecological interactions between Arctic char and brown trout, with trout feeding on more visible surface prey and chironomidae pupae at night while Arctic char mainly feed on zooplankton during the same time period (Hammar 1998). Experimentally, Bergman (1988) showed that ruffe (*Gymnocephalus cernua*) had a higher foraging rate than perch under poor light conditions,

whereas the reverse was the case under good light conditions (Fig. 15.2b). This difference in light-dependent foraging ability can, in turn, be related to the ecological performance of ruffe and perch in lakes that differ in light conditions because of different productivities (Bergman 1988).

The ecological performance of different species as a function of abiotic conditions such as temperature and light is essentially a description of the fundamental niche of the species. In interactions with other species, or size cohorts within the same species, the realized niche of a species or size cohort will generally shrink to the part of the fundamental niche where individuals have the highest fitness. Operationally this can, for example, be measured by the attack rate of a particular species or size cohort on different prey types. The next section covers the implications of ecological interactions with a focus on the size-dependency of these interactions.

15.3 COMPETITION AND PREDATION AS STRUCTURING FORCES

15.3.1 Impact of competitive interactions

Comparative studies on fish communities were one of the first to document the impact of competition on species distributions within and among systems (Svärdson 1949; Nilsson 1963, 1978). In studies of Arctic char and brown trout, Nilsson demonstrated that the habitat and food use of the two species differed depending on whether they were sympatric or allopatric. In lakes where the two species lived in allopatry, both of them utilized the whole water volume. In contrast, in lakes where they lived in sympatry, Arctic char restricted their habitat use to the pelagic zone, whereas trout used the littoral shore habitat. The plasticity observed in habitat use of the two species was a result of interactive segregation, in contrast to selective segregation where the habitat uses of competing species have become genetically fixed (Nilsson 1978). In a review of species interactions in Scandinavian lakes, Svärdson (1976) advanced the hypothesis that it is the more planktivorous species, the Arctic char in the brown trout–Arctic char interaction, that will numerically dominate the system. This pioneering work by Swedish fish ecologists was relatively unnoticed by non-fish ecologists and remained so until the early 1980s (Schoener 1982). Similar studies on interactive segregation were also carried out on salmonids in North America (Schultz and Northcote 1972).

The presence of interactive segregation was substantiated by studies of changes in resource use. In temperate systems these changes were related to seasonal variation in resource levels or temperature (Nilssson 1960; Persson 1987a). In tropical systems, interactive segregation has been shown by comparing the degree of resource partitioning in dry versus wet seasons (Zaret and Rand 1971). Interestingly, data suggest that piscivorous and non-piscivorous species may show different responses to the wet season. Non-piscivorous species generally show an increase in food overlap in wet seasons, interpreted as a response to increased food supply that decreased competition (i.e. Zaret and Rand 1971). In contrast, Winemiller and Ponwith (1998) found that the diet similarity between piscivorous fish species decreased during the wet season when prey dispersed at lower per-unit-area densities.

The early studies on ecological interactions in fish communities were mainly based on comparative studies and the patterns observed were thus open to alternative explanations. The pioneering experimental work by Werner and Hall (1977, 1979) on sunfishes (*Lepomis*) was a qualitative step forward in that the presence of competition could be unambiguously demonstrated and also that a more predictive approach was developed. In a series of elegant experiments, Werner and Hall showed that the bluegill sunfish (*L. macrochirus*) was a superior forager to green sunfish (*L. cyanellus*) and pumpkinseed sunfish (*L. gibbosus*) in the open-water habitat. They also showed that the green sunfish was the superior forager in vegetation. In a pond experiment where resources in the vegetation were depleted over time, Werner and Hall (1979) predicted that the bluegill sunfish

should be the first to shift to the pelagic habitat and the green sunfish the last, a prediction corroborated by results (Werner and Hall 1979). The studies of the Centrarchidae subsequently evolved towards a more quantitative approach by utilizing optimal foraging theory to predict net energy intake from different habitats and thereby the optimal habitat to be in (Mittelbach, Chapter 11, this volume). In a pond experiment lacking predators, predictions of optimal habitat use were largely supported by empirical data (Werner et al. 1983a). In lakes with predators, predictions from foraging theory were upheld for size classes of bluegills that were not susceptible to predators (Mittelbach 1981). However, small bluegills that were susceptible to predation from predators like largemouth bass stayed longer in the vegetation than had been predicted, also pointing to predation risk as a possible cause of the habitat distribution of fish (see Chapters 11–13, this volume).

15.3.2 Size-dependent competitive interactions

The study of Mittelbach (1981) clearly pointed out the importance of size for ecological interactions in fish communities. Considering competitive interactions first, the classical study of Alm (1946) on Eurasian perch had already showed that interactions between size cohorts could lead to severe resource limitation resulting in stunted growth in this species. Persson (1983) showed that stunting in perch was not restricted to the low-productivity forest systems studied by Alm but also occurred in highly productive systems. It was suggested that low habitat heterogeneity of the system promoted slow-growing individuals, leading to stunted populations. In an enclosure experiment, Persson (1987b) also showed that smaller perch were superior to larger perch in competition for pelagic food resources due to the former's lower metabolic demands. Recent studies on very small stages of fish including larvae have underlined the influence of size-dependent foraging rates and metabolic demands on the outcome of competitive interactions (Byström and Garcià-Berthóu 1999). Although it has been shown that roach in general is a superior

competitor to perch (Persson 1988), young-of-the-year (YOY) perch were less affected by competition than 1-year-old roach due to the former's lower metabolic demands (Byström and Garcià-Berthóu 1999). This dependency of the outcome of competition between different-sized individuals on both size-dependent foraging (which affects attack rate and handling) and metabolic rates illustrates how size-structured interactions also lead to asymmetric competitive interactions between different-sized individuals (Werner 1986; Persson et al. 1998).

The intensity of resource limitation among size cohorts of fish may vary with size, causing a certain stage or size class to form a bottleneck for recruitment whereas other stages/sizes may not be resource limited (Werner 1986; Persson et al. 1999). For example, in bluegill populations, predation risk from largemouth bass forces small bluegill sunfish to stay in the vegetated littoral zone, where they experience reduced encounter rates with their preferred prey and, consequently, reduced individual growth rates (Mittelbach and Chesson 1987; Werner et al. 1983b; Mittelbach, Chapter 11, this volume). Food and habitat niche overlap between small and large bluegill is therefore very low but, despite this, small and large bluegill sunfish will affect each other through their coupled life cycle (Mittelbach and Chesson 1987). Because bluegills in the presence of piscivores use two different habitats during ontogeny and thereby have the potential to reduce resource levels in both habitats (Mittelbach 1988), negative indirect interactions between the resources of bluegill in these habitats are also present. For example, an increase in the food resources of juveniles translates into increased numbers of adults and increased consumption rates on the adult's food resources through higher juvenile growth rates and survival. This leads ultimately to a decline in the adult's resources. Conversely, an increase in food resources for adults increases juvenile abundance through increased adult fecundity, so leading to a decrease in abundance of juvenile food resources (Mittelbach and Chesson 1987; Mittelbach and Osenberg 1993). The crucial point here is that a life-history stage not limited by the

resources it needs but by recruitment from other life stages will not be able to take full advantage of an increase in its own resource. The abundances and growth rates of juvenile and adult fish in a population are ultimately determined by the productivities of resources available to them and, as a consequence, by the relative sizes of the littoral and pelagic habitats. Littoral macroinvertebrates are most often the resource that limits bluegill populations as a whole, resulting in negatively density-dependent growth rates in juveniles but positively density-dependent growth rates in adults (Mittelbach and Osenberg 1993). This topic also has a bearing on the evolution of life histories as discussed by Hutchings in Chapter 7, this volume.

In many lakes bluegill sunfish coexist with pumpkinseed sunfish, which leads to further stage-dependent interactions. Adult pumpkinseed use littoral snails, which are not used by adult bluegills, but juvenile pumpkinseeds share the macrophyte habitat with juvenile bluegill. An increase in the productivity of pelagic zooplankton will lead to an increase in the fecundity of adult bluegill, which leads to an increase in juvenile bluegill density. This then translates into decreased growth rate and survival of juvenile pumpkinseed. As a result, adult pumpkinseed abundance will decrease and snail abundance increase (Mittelbach and Chesson 1987; Mittelbach and Osenberg 1993).

15.3.3 Size-dependent mixed interactions

Stage- or size-structured dynamics prevalent in fish populations also mean that the nature of the interactions will change over ontogeny (Werner and Gilliam 1984; Werner 1986; Persson 1988; Mittelbach and Osenberg 1993; Olson et al. 1995). Changes in habitat and food resources used over ontogeny cause top predators to be exposed to both competitive and predatory interactions over their life (Persson 1988; Mittelbach and Osenberg 1993; Olson et al. 1995; Mittelbach, Chapter 11, this volume). Some species can be both predator and prey. The community consequences of these mixed in-

teractions were illustrated by the invasion of the redside shiner (*Richardsonius balteatus*) into Paul Lake (British Columbia). Up to 1950, this lake was inhabited only by rainbow trout (*Salmo gairdneri*) (Johannes and Larkin 1961), where all life stages fed on a mixture of plankton, benthos and terrestrial insects. After the invasion, adult trout started to feed on the redside shiner and dropped plankton from their diet. As a result, their growth rates increased. However, competition from redside shiners decreased the growth rate of juvenile trout, which negatively affected the recruitment of small trout to piscivorous size classes (Johannes and Larkin 1961). The different stages of trout were thus affected by the redside shiner in opposite ways, with a reduction in the trout population as an overall effect. The lake trout–redside shiner example also illustrates that the extent to which growing fish reach predatory stages is heavily influenced by different kinds of density-dependent interactions during different parts of their ontogeny (see also Mittelbach and Chesson 1987; Persson 1988; Persson and Greenberg 1990; Persson et al. 1999).

15.3.4 Ontogenetic constraints and trade-offs

In fish, as in many other taxa, changes in body size often necessitate a series of ontogenetic niche shifts toward larger prey sizes and shifts in habitat to allow for an optimal or even positive net energy intake (Werner and Gilliam 1984; Persson and Greenberg 1990). The presence of such size-dependent ontogenetic niche shifts imposes a series of constraints on the organism. This is because traits are expressed over several ontogenetic stages of an individual and are often highly intercorrelated because of pleiotropic mutations (ontogenetic covariance) (Werner 1988). As natural selection operates on morphological and behavioural traits over the whole life cycle, traits that are optimal in one ontogenetic niche may be suboptimal in others (Werner and Hall 1979; Werner 1986, 1988; Persson 1988). In such cases, genetic covariances will set profound constraints on how efficient an individual can be at each of these ontogenetic stages, which

typically results in ontogenetic trade-offs (Persson 1988; Werner 1988). A typical example of such a situation is piscivorous fish that can undergo two to three ontogenetic niche shifts over their life cycle. The body designs that are optimal for planktivory, benthivory and piscivory can be quite different. For the planktivorous stage, typical morphological traits are compressed body and a small gape size, which allows the fish to capture relatively small and non-evasive prey items efficiently at high swimming speed (Werner 1977). Benthivorous feeding, especially in vegetated habitats, requires a relatively low cruising speed, a relatively deep body, laterally inserted pectoral fins and enlarged dorsal fins (Eklöv and Persson 1995). Piscivorous feeding involves large evasive prey, which requires traits such as high attack speed, large gape size and an attacking foraging mode (Juanes et al., Chapter 12, this volume). Existing data suggest that different piscivorous species have solved the problem of ontogenetic trade-offs in different ways and that the different solutions have had feedback effects on the impact of different species on overall trophic dynamics (Mittelbach and Persson 1998).

Based on the constraints imposed by ontogenetic covariance, a general hypothesis has been advanced. This states that a species undergoing substantial niche shifts during its lifespan will have a lower maximum efficiency in any of the ontogenetic niches it utilizes than another species undergoing less substantial ontogenetic niche shifts (Werner and Hall 1979; Werner 1986; Persson 1988). For example, a juvenile of a species that is piscivorous as an adult will be an inferior planktivore feeder compared with a species specializing as a planktivore. Experimental support for this hypothesis has been provided for at least two species constellations: the perch–roach interaction and the largemouth bass–bluegill interaction (Werner 1977; Persson 1988).

As a consequence of ontogenetic trade-offs in piscivores, Persson (1988) suggested that the interactions between piscivores and planktivores are characterized by a high degree of asymmetry. By definition, piscivores have a predatory advantage but this is counteracted by the juveniles of plankti-

vores being better competitors than the juvenile stage of the piscivore. This is a result of ontogenetic trade-off costs in the piscivore when in their planktivore phase. Increased abundance of the competitively superior, smaller species will have a negative effect on the growth and survival of the juvenile size classes of the potentially larger species (competitive asymmetry). In contrast, there will be a positive effect on the growth and fecundity of the piscivorous adult size classes and a negative effect of the piscivores on the smaller species (predatory asymmetry) (Persson 1988). The outcome of such complex interactions will be determined by the relative strengths of predation and competition. Several cases have been described where the competitive asymmetry among juveniles is intense, leading to competitive juvenile bottlenecks in the recruitment to piscivorous size classes (Johannes and Larkin 1961; Persson 1988). This type of asymmetric interaction, particularly changes in the relative strengths of the predatory versus competitive advantage, may have major consequences for overall community and ecosystem dynamics as will be considered in the following. The topic of predatory and competitive interactions that change with ontogeny is also covered by Mittelbach (Chapter 11, this volume) but from a viewpoint determined by a theoretical perspective.

15.4 FISH COMMUNITY STRUCTURE, PRODUCTIVITY AND HABITAT STRUCTURE

15.4.1 *Size-structured community patterns and productivity*

Productivity is a major factor affecting trophic dynamics in ecological systems. Studies of fish communities in temperate lakes of different productivities have shown that substantial changes to the fish fauna take place along the productivity gradient (Leach et al. 1977; Persson et al. 1991). This shift involves a change from a numerical dominance of Salmoniformes in temperate systems of low productivity to a dominance of percids

in lakes of medium productivity. In highly productive lakes, the fish community is dominated by cyprinids. Studies on the relationship between productivity and fish community structure have mainly focused on European systems. Even so, studies of North American systems suggest a similar shift in fish community structure with the exception that centrarchids, not present in Eurasian systems, increase steadily in abundance with productivity as do cyprinids (Colby et al. 1972; Leach et al. 1977; Oglesby et al. 1987).

While shifts in fish communities along the productivity gradient have been recognized for a long time, the recognition of the implications of size-structured processes for these shifts and the trophic dynamical consequences is more recent (Persson 1988; Persson et al. 1991, 1992). The implications of the shifts in fish communities along the productivity gradient for the dynamics of trophic relations are a result of the high proportion of piscivores in the biomass of fish in systems dominated by percids. The proportion of piscivores is much lower in systems dominated by Salmoniformes or cyprinids (Persson et al. 1991, 1992; Persson 1994). In percid-dominated communities, the proportion of piscivores, mainly made up of piscivorous perch, forms up to 80% of total fish biomass (Fig. 15.3). In contrast, the proportion of the total fish biomass formed by piscivores in highly productive systems is low (≤20%) (Persson et al. 1991, 1992). Qualitatively, benthic and pelagic habitats show the same pattern of change in the importance of piscivores (Fig. 15.3). However, differences are present in that while piscivores are present in low numbers in the benthic habitat of very low productivity lakes, piscivores may be totally absent in the pelagic habitat of these lakes (Persson et al. 1992).

The change in fish community structure can be set in the general conceptual framework of ontogenetic trade-offs and asymmetric interactions discussed in the previous section. The shift in a numerical dominance from percids to cyprinids with increasing productivity has been related to the ability of roach to outcompete the adult piscivorous perch at the juvenile stage when they are feeding on zooplankton (Persson 1988; Persson and
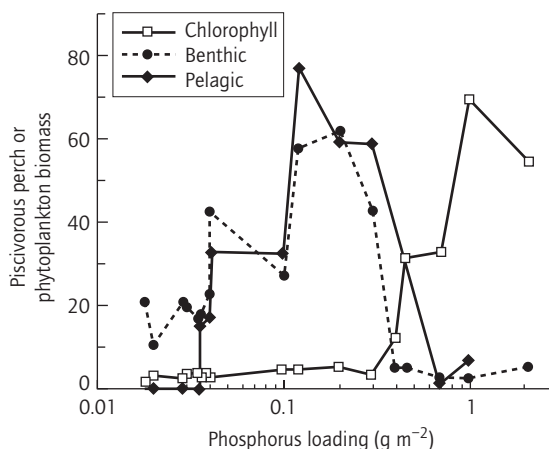
Fig. 15.3 Changes in the percentages of pelagic and benthic piscivorous perch biomasses of total pelagic fish biomass and phytoplankton biomass (chlorophyll *a*, µg l⁻¹) along a phosphorus loading gradient in Swedish lakes. (Source: data from Persson et al. 1991, 1992; Persson 1994.)

Greenberg 1990). Correspondingly, it has been shown that roach are superior zooplankton feeders to perch (Persson 1988). This concerns both the capacity to depress zooplankton densities and the capacity to feed on smaller zooplankton forms, which are a result of intense predation pressure (Persson 1994). For example, the attack rates of roach when feeding on *Daphnia* and cyclopoid copepods are substantially higher than those of perch (Persson 1988). It has also been experimentally shown in both pond and whole-lake experiments that roach, by depressing resource levels of pelagic zooplankton, force juvenile perch to shift their feeding to benthic macroinvertebrates. This leads to a competitive juvenile bottleneck in the recruitment of perch to piscivorous stages (Persson and Greenberg 1990; Persson et al. 1999).

In highly productive systems, this competitive juvenile bottleneck leads to perch populations being dominated by small non-piscivorous size classes (Persson 1988; Persson and Greenberg 1990). In contrast, perch populations in moderately productive systems are generally characterized by having a greater proportion of large-sized

individuals. This change in the size structure of perch populations from highly productive lakes to moderately productive lakes has been related to at least two factors: (i) a decrease in the abundance of blue-green algae eaten by roach but not by perch with decreasing productivity; and (ii) a relative increase in the littoral zone and an increase in structurally complex habitats such as submerged vegetation, which favours perch (Persson 1988, 1993). Both of these factors provide possible mechanisms by which the competitive advantage of cyprinids may decrease, allowing a larger fraction of perch to reach larger size classes. An increased number of perch recruiting to larger size classes leads to the possibility that perch predation may affect the density of roach and other cyprinids (Persson 1988). The presence of a predatory impact by perch on roach is supported by the fact that the median size of roach populations is higher in lakes where the component of total fish biomass consisting of piscivorous perch is higher (Persson et al. 1991). The complex size-dependent interactions between roach and perch resulting from both predation and competition should be kept in mind when reading the chapters by Shepherd and Pope (Chapters 7 and 8, Volume 2), Schnute and Richards (Chapter 6, Volume 2) and Pauly and Christensen (Chapter 10, Volume 2).

15.4.2 Impact of piscivore life history

Depending on productivity, the abundance relationship between perch and its prey and competitors may be either positive or negative (Fig. 15.3). Similar studies on the Centrarchidae system have shown that the bluegill sunfish makes up the majority of total fish biomass in many lakes in central North America (Mittelbach and Osenberg 1993). Juvenile bluegill may have a negative effect on the growth of its competitors, including the juveniles of the major piscivorous predator, largemouth bass (Mittelbach 1988; Olson et al. 1995), via the same mechanism as outlined above for European perch and roach. Correspondingly, it has been experimentally demonstrated that the per-capita effect

of juvenile bluegill on YOY bass is larger than the reverse (Olson et al. 1995).

In contrast to the perch–roach system, the abundance relationship between bluegill and largemouth bass is always positive. This difference in density relationship between perch–roach and bass–bluegill can be related to differences in the life histories of the two piscivores (Olson et al. 1995). Bass become piscivorous in their first year, whereas it may take several years for perch to reach piscivorous stages. The potential for competing prey to affect perch recruitment to piscivorous stages is thus higher. A functional basis for the differences in life histories has been demonstrated by showing that largemouth bass have a larger gape width for a specific body length than do Eurasian perch (Mittelbach and Persson 1998). Furthermore, gape width is negatively related to size at switch to piscivory and positively related to size at age 1, suggesting a coupling between morphology and ecological performance. Finally, largemouth bass have shorter prey manipulation times on fish prey than perch (Mittelbach and Persson 1988). In conclusion, the studies on the perch–roach and the Centrarchidae systems suggest that size-structured interactions are of overwhelming importance in structuring fish communities and that the relationship between top predators and their competing prey may take different forms depending on piscivore life histories.

15.4.3 Habitat structure

Habitat structure, often in the form of submerged vegetation, affects both competitive and predatory interactions (Winfield 1986; Savino and Stein 1989; Persson 1993; Persson and Crowder 1998). Besides an overall reduction in predation efficiency of piscivores, complex habitats like vegetation may affect the relationship between body size and predation mortality of prey fish (Savino and Stein 1989; Persson and Eklöv 1995; Persson and Crowder 1998). The mechanisms behind the decreased predation efficiency in complex habitats can be both decreased encounter rate between predator and prey and decreased capture success of the predator

once the prey has been encountered (Savino and Stein 1989; Juanes et al., Chapter 12, this volume). Habitat structure in the form of vegetation may also reverse the outcome of competitive interactions among refuging prey fish. For example, the competitive advantage of juvenile roach over juvenile perch in open water was reversed in refuges in vegetation because of the effects of structure *per se* on roach foraging performance and because vegetation structure harbours prey that juvenile perch are better at foraging than are juvenile roach (Winfield 1986; Persson 1991, 1993).

Because habitat structure affects both predator–prey and competitive relationships, habitat structure is also expected to affect community patterns (see Mittelbach and Osenberg 1993 and bluegill example above). Although the major change in fish communities of European systems are associated with changes in productivity, it has been hypothesized that this change is more causally linked to changes in habitat structure than to productivity itself (Persson et al. 1992; Persson 1994). This hypothesis relates to the observation that the importance of submerged vegetation is generally at a maximum in moderately productive lakes (Wetzel 1979) where piscivore biomass is also at a maximum. Juvenile perch and roach prefer to forage in the vegetation if the risk of predation is high in the open water, and a high abundance of pelagic piscivores in lakes of intermediate productivity may thereby reverse the outcome of competitive interactions between juveniles in favour of perch (Winfield 1986; Persson 1993; Persson and Eklöv 1995).

15.5 EFFECTS OF FISH ON LOWER TROPHIC COMPONENTS

15.5.1 Fish predation and trophic dynamics

The classic paper by Brooks and Dodson (1965) showed that predation from planktivorous fish decreased both the abundance and mean size of zooplankton. Subsequently, a large number of papers have demonstrated the size-selective effects of planktivory on zooplankton communities. Moreover, studies by Hrbàcek et al. (1961), Henrikson et al. (1980) and other European researchers showed that the effect of fish predation was not restricted to an effect on zooplankton but also transformed into effects on phytoplankton. Studies by researchers including Shapiro and Wright (1984), Carpenter et al. (1987) and Carpenter and Kitchell (1993) subsequently demonstrated similar strong top-down effects of piscivorous and planktivorous fish on phytoplankton communities and nutrient dynamics in North American systems. More long-term studies carried out by Mittelbach et al. (1995) showed strong effects over several trophic linkages, covering piscivores to phytoplankton, following a winter-kill affecting largemouth bass. A most dramatic example of the impact of a piscivorous top predator is also provided by the introduction of the Nile perch in Lake Victoria (Kaufman 1992; Pitcher and Hart 1995; Kitchell et al. 1997). In this lake, the biomass of the native fish fauna, particularly *Haplochromis* species, have decreased to very low levels and many species have eventually gone extinct (Fig. 15.4). The effects of
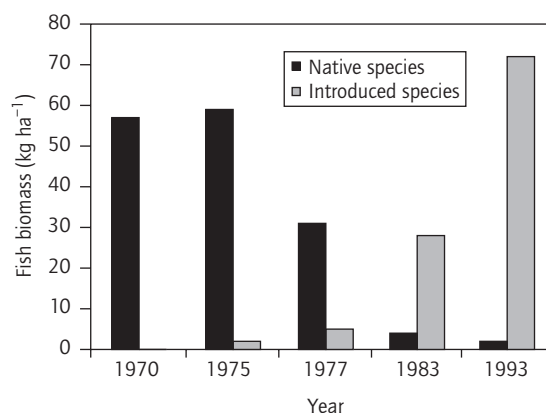
Fig. 15.4 Changes in standing stocks of native versus introduced fishes in Lake Victoria between 1970 and 1993. (Source: data from Kaufman 1992.)

these dramatic changes in fish fauna on lower trophic components are difficult to discern as the lake has undergone substantial eutrophication over the same time period. Comparative studies on lakes have provided evidence for the effects of top predators on lower trophic components. The changes in the importance of piscivores along the productivity gradient of Swedish lakes also involved feedback effects on other trophic levels such as zooplankton and phytoplankton (Fig. 15.3) (Persson et al. 1992; Persson 1994). For example, a ten-fold increase in phosphorus loading from 0.03 to $0.3\,\mathrm{g\,m^{-2}\,year^{-1}}$ only led to a minor increase in phytoplankton biomass, suggesting that an increased piscivore biomass may prevent an increased phosphorus loading leading to an increase in phytoplankton biomass within this range of phosphorus loadings. In contrast, phytoplankton biomass increased steadily with phosphorus loading in highly productive systems with a low proportion of piscivores (Fig. 15.3).

Many of the manipulations of fish populations have thus resulted in effects on planktivores and zooplankton to phytoplankton. Traditionally, these have been interpreted as direct effects of predator consumption. However, behavioural studies of predator–prey interactions have also emphasized non-lethal indirect effects of predators on community dynamics, such as effects on prey fish activity and habitat use (Power 1987; Turner and Mittelbach 1990). Power (1987) showed striking differences in the standing stock of algae between shallow margins and deeper central areas within pools of a Panama stream related to the distribution of the armoured catfish (Loricariidae). Data suggested that although large catfish were severely resource limited in the deeper parts of pools, they avoided shallow areas because of the greater risk of predation from birds (Power 1987). In contrast, small catfish were much more abundant in shallow water in order to avoid predatory fishes occupying deeper waters, but did not deplete algal resources there (Power 1987). Altogether, the evidence suggested that risk-sensitive foraging by large catfish resulted in a behaviourally induced indirect interaction between avian predators and benthic algae. Another example of a behaviourally

induced indirect effect has been demonstrated by piscivorous largemouth bass in pond experiments. Piscivore-mediated habitat choice in small bluegills caused an increase in zooplankton abundance in the open water compared with controls lacking largemouth bass (Turner and Mittelbach 1990).

15.5.2 Effects of fish on nutrient cycling

In addition to direct mortality and behavioural shifts in prey caused by fish predators, fish also affect trophic dynamics through their effects on nutrient cycling. In many systems, biota including fish represent major storage pools of nutrients that limit productivity, and consumer–resource interactions greatly affect nutrient cycling in different components of the food web. For example, Kaiser and Jennings (Chapter 16, Volume 2) review the importance of Pacific salmon (*Oncorhynchus* spp.) for movements of nutrients between marine and freshwater habitats. It may be important to consider nutrient recycling explicitly when the ratio of different essential resources, such as carbon, phosphorus and nitrogen, is different in ingested food compared with egested food (Sterner 1990). For example, when predation pressure from planktivorous fish on zooplankton is low, *Daphnia* dominate and they have a lower N : P ratio than do copepods, which often dominate when predation pressure from planktivorous fish on zooplankton is high (Sterner and Hessen 1994). Such differences in nutrient signatures can be used to trace links between members of a trophic web (Polunin and Pinnegar, Chapter 14, this volume). Nutrient recycling and transformation by zooplankton is widely recognized as an important source of nutrients for phytoplankton production (Vanni 1996). Experimental studies have also documented that direct nutrient recycling by fish will affect phytoplankton community structure. Vanni et al. (1997) showed that in lakes dominated by planktivores, fish effects on algal community composition can exceed the effects of nutrient recycling by zooplankton. As fish are rarely limited by phosphorus availability but are by energy, the N : P ratio ex-

creted from fish is generally low, which stimulates phytoplankton growth (Schindler and Eby 1997). The effects of size structure on nutrient recycling by fish will also be present because the ratio of phosphorus-rich bone mass to total body mass varies with fish size (Vanni 1996). However, the effect of fish body size on nutrient recycling is complex as a result of the interaction between physiological and ecological processes (Schindler and Eby 1997). The latter results from ontogenetic niche shifts, where larger fish generally eat larger prey with high phosphorus concentrations while smaller fish eat small prey with a generally lower phosphorus concentration.

If the effects of nutrient translocation between habitats due to benthivory are also considered, the impact of fish will become even larger (Schindler et al. 1996). It has for a long time been recognized that littoral habitats are linked biogeochemically to the open waters of lakes (Wetzel 1979). Because invertebrates in littoral zones generally have a higher biomass, production and diversity than those in open water, littoral zones form a potential resource base for pelagic production. Fish have a substantial impact on lake nutrient cycling because they function as vectors for transport of nutrients from littoral and benthic habitats through their feeding on littoral benthic prey (Schindler et al. 1996). Fish that migrate onshore–offshore may thus increase nutrient translocation above that accounted for by biogeochemical processes alone (Schindler et al. 1996). Under some circumstances, this nutrient translocation caused by fish may exceed the external loading of nutrients (Brabrand et al. 1990). The translocation of nutrients may also involve nutrient release from sediments (Brabrand et al. 1990; Vanni 1996). Finally, translocation of nutrients may occur over large distances, exemplified by anadromous sockeye salmon (*Oncorhynchus nerka*) (Kaiser and Jennings, Chapter 16, Volume 2). The salmon were a major vector for the transport of nutrients from marine systems to nutrient-poor freshwater systems, and human-caused inhibition of their upwards migration into fresh waters resulted in major decreases in the productivity of these systems (Stockner and MacIsaac 1996).

In correspondence with the observation that fish may translocate nutrients from the littoral/benthic habitats to pelagic habitats, recent biogeochemical analyses of phosphorus cycles in the pelagic zones of lakes suggest that observed levels of primary productivity are too high to be supported by pelagic recycling alone. For example, one-third of the pelagic primary production of Mirror Lake (New Hampshire, USA) has been estimated to be supported by phosphorus coming from elsewhere (Caraco et al. 1992). Correspondingly, both Vanni (1996) and Schindler et al. (1996) argue strongly in recent reviews that pelagic nutrient budgets can only be balanced by considering biologically driven phosphorus from the littoral. The current knowledge therefore suggests that the littoral zone is a source of nutrients for pelagic food webs and that the pelagic habitat consequently is a sink for littoral productivity in most lakes.

15.5.3 Alternative states in highly productive systems

The interaction between vegetation structure and trophic structure and the different pathways through which fish may affect nutrient recycling has led to the proposal that there exists a potential for alternative stable states in highly productive systems (Scheffer 1990, 1998; Blindow et al. 1993). One state is characterized by high phytoplankton biomass, low biomass of zooplankton and high biomasss of planktivore/benthivore fish; the other state is characterized by high biomass of macrophytes, low biomass of phytoplankton, high biomass of zooplankton and a high biomass of piscivores. Theoretical studies have suggested that the existence of the two alternative states should be restricted to shallow highly productive lakes, whereas in deep highly productive lakes only the state with high biomass of phytoplankton should be present (Scheffer 1990, 1998). Correspondingly, field evidence that highly productive lakes may be dominated by macrophyte production is restricted to shallow lakes (Blindow et al. 1993; Scheffer 1998). Nevertheless, the evidence for the presence of alternative stable states in shallow highly productive lakes provides a nice

illustration of the impact of fish on lake ecosystem dynamics.

15.6 FROM INDIVIDUAL-LEVEL PROCESSES TO POPULATION DYNAMICS

So far individual-level capacities, like the abilities to forage and avoid predators, have been connected to community patterns, such as how trade-offs between maximizing energy gains and minimizing predation risk may affect the size distribution of size cohorts and species (Mittelbach 1981; Werner 1986; Osenberg et al. 1988; Persson 1988). Essentially, community patterns have thus been predicted from individual, size-dependent, capacities. Although this approach has been relatively successful in increasing our understanding of community patterns, a major impediment has been that the population dynamics between interacting species has been neglected. Stage-based population models based on just two life stages, juveniles and adults, have been shown to successfully predict the abundance patterns of different stages and species in some cases (Mittelbach and Chesson 1987; Mittelbach and Osenberg 1993). At the same time, the fact that fish grow during most of their lives and that individual growth is strongly limited by food availability (Jobling, Chapter 5, this volume) calls for an approach that explicitly handles these features.

Physiologically structured models represent an approach that explicitly links the dynamics that takes place at the level of population to the behaviour of individual organisms (De Roos 1997). These models are based on a state concept at each of two levels of organization: an *i*-state, which represents the state of the individual in terms of a collection of characteristic physiological traits such as size, age, sex and energy reserves, and a *p*-state, which is the frequency distribution over the space of possible *i*-states (De Roos 1997). The core of physiologically structured models is the description of the individual state. The population state becomes a matter of book-keeping of the individuals in different *i*-states. Although representing a recently

developed theoretical framework, physiologically structured models have been successfully applied to the study of cohort interactions and cannibalism in fish (Persson et al. 1998; Claessen et al. 2000). A different perspective on individual-based models that predict population processes is given by Huse et al. (Chapter 11, Volume 2).

Considering intercohort competition first, the foraging rate as a function of body weight is commonly described by a power function (Werner 1988). For a given prey size, the attack rate $a(w)$ as a function of weight (w) has been found to be a hump-shaped function of predator size (Byström and Garcìa-Berthóu 1999). The initial increase in the foraging capacity with consumer size is due to an increase in visual acuity and locomotor ability, both of which will affect the encounter with prey (Persson et al. 1998). The decreasing part of the function is due to a decrease in retinal rod density and hence the capacity to discern small prey (Breck and Gitter 1983). Furthermore, attack efficiency may also decrease above a given body size due to decreased ability to make fine-tuned manoeuvres (Persson 1987b). A function that encapsulates these aspects is the following formula:

$$a(w) = A\left[\frac{w}{w_o}\exp\left(1 - \frac{w}{w_o}\right)\right]^{\alpha} \qquad (15.1)$$

where A is the maximum attack rate, w_o is the body size at which the maximum rate is achieved and α is a size scaling exponent (Fig. 15.5) (Persson et al. 1998). Empirical support for the form of this function is found in Byström and Gàrcia-Berthóu (1999). Using the same principle, the function for handling time as a function of body size can be derived (Persson et al. 1998; Claessen et al. 2000).

The metabolic rate of fish also increases with body size and for many fish species a size scaling exponent (α) around 0.75 has been found (Persson et al. 1998; Claessen et al. 2000). Taking both foraging gains, expressed as the attack rate times energy content per prey and assimilation efficiency, and metabolic costs associated with gaining this energy into consideration allow us to derive the minimum level of the resource that will allow the fish to maintain itself. For planktivorous prey,
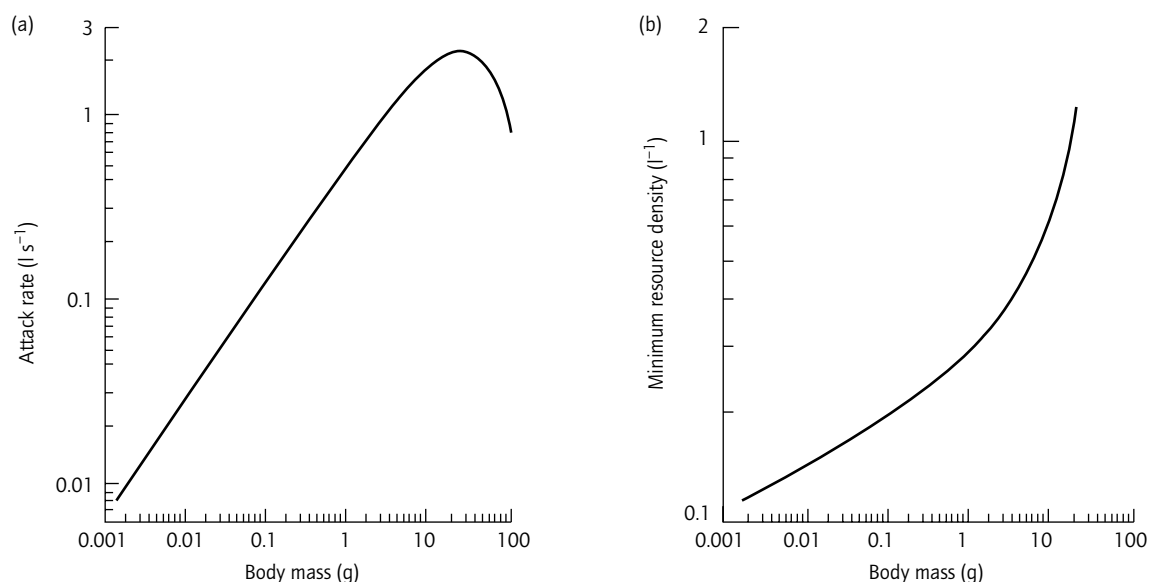
Fig. 15.5 (a) Attack rate and (b) minimum resource requirements of a planktivorous fish as a function of fish size. Parameter values: $A = 2.31\,s^{-1}$, $w_o = 17.4\,g$, $\alpha = 0.5$ and zooplankton size $= 0.6\,mm$. (Source: see Persson et al. 1998 for derivation.)

where the weight exponent in equation 15.1 has been shown to vary between 0.59 and 0.67 (Mittelbach 1981; Byström and Garcìa-Berthóu 1999), the minimum resource level is a monotonically increasing function of body size (Fig. 15.5). The interpretation of this is that smaller-sized individuals will have the lowest minimum resource demand level and hence be competitively superior to larger individuals with respect to exploitative competition.

A general result derived from this model is that consumer–resource interactions, for example the interaction between planktivorous fish and zooplankton, are likely to result in population oscillations. These oscillations are driven by recruiting fish individuals that by their pulsed appearance will heavily depress the zooplankton resource and thereby reduce fecundity and increase starvation risk in larger mature fish. There are a number of examples of planktivorous fish that support this modelling result. A classic example is population oscillations in zooplanktivorous cisco (vendace) (*Coregonus albula*) (Aass 1972; Hamrin and Persson 1986; Auvinen 1994). The cycle length in these populations varies between 2 and 5 years (Aass 1972; Hamrin and Persson 1986) (Fig. 15.6) and is probably driven by variation in recruitment caused by the adults suffering severe mortality due to starvation. Roach populations have been shown to demonstrate similar oscillations (Townsend et al. 1990).

So far, I have only considered a size-structured population and a non-structured population of zooplankton. In fish populations, both predator and prey are generally size-structured, which particularly concerns the interaction between piscivorous predators and their fish prey (Hambright 1994; Christensen 1996). The vulnerability of larval fish to raptorial predators has been found to increase to a maximum and thereafter decrease as prey fish size increases. An important consequence of such a form of the attack rate is that newborn prey fish, depending on the size distribution of potential predators, may subject these predators to competition for a shared resource such as zooplankton before the prey fish are effi-

ciently captured by their predators. With a further increase in size, prey fish vulnerability will increase with size to a peak and thereafter decrease. As it is often the case that both piscivores and prey fish increase in size over time, the time span over which a prey fish cohort is susceptible to predation will depend on the growth rates of both predator and prey.

Investigations of a physiologically structured model including both cannibalism and com-

Fig. 15.6 Abundances of young-of-the-year cisco (*Coregonus albula*) (catch per unit effort, $g \times 10^{-2}$) and cladoceran zooplankton (no. per litre) in Lake Bolmen in the years 1970–77. (Source: data from Hamrin and Persson 1986.)

petition for a basic resource suggested that the dynamics can be characterized by a mixture of high-amplitude recruiter-driven dynamics interspersed with periods of cannibal-driven dynamics (Claessen et al. 2000; Juanes et al., Chapter 12, this volume). The amplitude of cannibal-driven dynamics varies from high-amplitude dynamics to stable equilibrium (Claessen et al. in press). Interestingly, cannibalistic individuals with accelerating growth rates (Fig. 15.7) may appear under several conditions given that the cannibals feed on relatively large victims. An empirical study of the population dynamics of an allopatric cannibalistic perch population showed that the dynamics of the perch population could be separated into two phases (Persson et al. 2000). In one phase, adult perch dominated and recruitment of YOY perch to 1-year-old perch was low due to high cannibalism on young and small stages of YOY perch. In these years, adult perch had an asymptotic length of around 180 mm. This phase was interrupted by a phase when the number of adult perch decreased possibly due to starvation, leading to a period of strong recruitment of 1-year-old perch. The growth of the few surviving adult perch accelerated as a result of the energy that older and thus larger YOY perch represented, leading to a 'double asymptotic' growth curve (Fig. 15.7). Interestingly, the growth patterns of perch in the two different phases were the same as the growth patterns predicted by the model (Fig. 15.7) (Claessen et al. 2000).

Fig. 15.7 Growth rates of cannibalistic perch in years when young-of-the-year (YOY) perch were cannibalized (a) early and (b) in years when YOY perch survived for a longer period in Lake Abborrtjärn 3 (squares, solid lines) and as predicted by the model (circles, dotted lines). In (b), YOY perch surviving for a longer period were present from the time when cannibalistic perch were 4 years old. (Source: data from Claessen et al. 2000; Persson et al. 2000.)
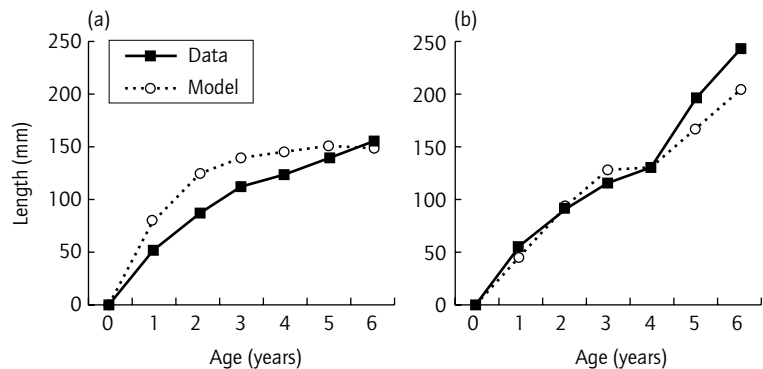
15.7 CONCLUSIONS

The analyses of the dynamics of fish populations using physiologically structured population models are so far restricted to intercohort competition and cannibalism. The results of these analyses are encouraging and suggest that physiologically structured models are a useful tool for increasing our understanding of the dynamics of fish populations. The analyses of intercohort competition and cannibalism also suggest that there is potential to reach a substantial degree of generality in results. Is it possible to go further to more complicated scenarios, involving, say, two size-structured fish populations of which one is a predator on the other species, and continue to have a substantial degree of generality in model predictions? Examples might be perch–roach and largemouth bass–bluegill interactions. If this is the case, physiologically structured population models may turn out to be a valuable approach for the analysis of fish community dynamics, including the impact of fish on their resources as discussed in this chapter. Ongoing research suggests that this may be possible. The dynamics of more complex configurations appear to be largely driven by combinations of the mechanisms analysed in the simpler configurations, such as recruit-driven and cannibal-driven cycles. These analyses and the analysis of Claessen et al. (2000) also suggest that important elements of the dynamics observed in both the models and empirical systems are not accessible to analysis outside the domain of physiologically structured population models. Thus, to substantially increase our theoretical understanding of the implications of size-structured interactions for fish community dynamics, physiologically structured population models may be indispensable.

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16 Comparative Ecology of Marine Fish Communities

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16.1 INTRODUCTION

Fish of a particular species do not occur in isolation from others but as members of ecological communities. They interact with fish of other species, with invertebrate prey, with bird and mammal predators, and with the plants and sessile animals that provide much of the physical structure of their environments. It has been traditional to refer to fish communities, meaning all fish species in a location, and we follow this tradition while noting that many of the important biotic interactions are with non-fish organisms (cf. Pauly and Christensen, Chapter 10, Volume 2 for definition of an ecosystem). Our goal is to describe marine fish communities, particularly to contrast communities of fishes in temperate and tropical demersal locations and in the pelagic realm. Are structure and dynamics of fish communities in these different types of location similar or not and why might differences exist? In contrast to Polunin and Pinnegar (Chapter 14, this volume) we focus on the disparate perspectives of tropical and temperate communities given by different sampling methods and on the role larval ecology plays in determining community structure. Polunin and Pinnegar are more concerned with how to establish trophic links and in understanding how ecosystem structure determines stability.

Our knowledge of the ecology of marine fishes has derived from three rather different approaches driven by different questions, and from different ancestries that have yielded different perspectives.

First, fisheries management has required ecological information on the populations being fished and, to a considerable degree, has obtained that information by sampling the catch of the fishery being managed (Evans and Grainger, Chapter 5, Volume 2; Sparre and Hart, Chapter 13, Volume 2). Second, study of the ecology of many fishes that are of recreational or only marginal fishery interest has necessarily used fishery-independent sampling methods, but has still relied largely on samples of fish removed from their environment as the source of ecological data. Third, in certain environments where the approach is feasible, the ecology of fishes has been explored by putting the scientist into the water. Methods similar to those used in terrestrial ecology are used to observe the fish in its habitat or to perform field experiments. Each of these three approaches has its own biases as well as its own methods. Each focuses on its own set of questions and tells its own version of reality (see Hart and Reynolds, Chapter 1, this volume).

Because these general methods are differentially used among different environments, our pictures of fish communities are incomplete in different ways in different places. Fisheries science began with the need to manage commercial fisheries (Smith, Chapter 4, Volume 2). Its early development was largely a north-temperate marine endeavour, perhaps even a North Atlantic activity. The study in temperate regions of the ecology of freshwater species and coastal marine species of limited commercial value primarily used methods

that kept scientists more or less dry and ensured fish were more or less dead before they were examined. The use of techniques that put the scientist into the water has been most extensive in the tropics and the warm temperate zone. Our thesis will be that the differences in community structure and dynamics reported among temperate, tropical and pelagic fish communities may be as much due to the different approaches used as to real differences in ecology. This chapter examines patterns in biodiversity, habitat associations and production and recruitment dynamics, all in the context of community structure and dynamics, and attempts to identify real differences among these different environments.

16.2   BIODIVERSITY

16.2.1   *Biogeographic divisions of the world's oceans*

The world's oceans are expansive and continuous bodies of water, but compartmentalization into somewhat distinct regions occurs on many spatial scales. On a large spatial scale, significant boundaries occur primarily due to physical oceanographic factors, such as currents, fronts and other boundaries between water masses, the positions of the continents and suboceanic topography (Briggs 1974; Longhurst 1981; Sharp 1987; Helfman et al. 1997; Polunin and Pinnegar, Chapter 14, this volume). Briggs (1974), the classic reference to marine biogeography, recognizes cold temperate, warm temperate and tropical groupings of littoral–continental shelf species, as well as epipelagic, deep pelagic and deep demersal or abyssal fish species. Temperate biogeographic regions are restricted to single ocean basins or even to single shorelines. Four tropical biogeographic regions are recognized for littoral fishes: Indo-West Pacific, East Pacific, Western Atlantic–Caribbean and Eastern Atlantic–Mediterranean (see Gill and Mooi, Chapter 2, this volume, who give a much broader categorization of biogeographic regions).

The world contains in excess of 25 000 described species of fish (Eschmeyer et al. 1998), and about 60% of the world's fishes are marine (Nelson

1984; Helfman et al. 1997; Holmlund and Hammer 1999). The bulk of this marine diversity (78%) is found in coastal waters; 89% of these littoral–continental shelf species occur in tropical waters (Moyle and Cech 1996; Helfman et al. 1997). Epipelagic fishes occupy the open ocean from the surface down to 200 m and constitute just 2.2% of the total number of marine species, although they are the major component of the world's marine fish landings. Coastal pelagics, particularly clupeoids, make up one-third of the total 80–90 million tonnes landed per year (Cushing 1995; Holmlund and Hammer 1999; Pauly et al. 2000), and offshore pelagics such as tunas and billfishes make up an additional 15% (Blaxter and Hunter 1982; Groombridge 1992). Deep pelagic fishes are those that live in the water column below 200 m and constitute 8.6% of species. Deep demersal species live on the bottom below 200 m and comprise 11% of total species. The number of species in these little explored regions is increasing with time (Mooi and Gill, Chapter 3, this volume).

Because the focus of this chapter is to compare temperate and tropical fish communities, it is inappropriate to attempt a survey of all biogeographic regions. Instead, we focus on (i) tropical demersal, chiefly coral-reef, communities of littoral fishes in the Caribbean and the vast Indo-West Pacific, (ii) temperate demersal communities of littoral species of the north temperate, and (iii) epipelagic communities of temperate and subtropical seas.

16.2.2   *Levels of biodiversity in different systems*

Trend of diversity with latitude

Within large geographic regions, several patterns of faunal diversity have been reported in the literature, with various explanations to account for these patterns (Paine 1966; Pianka 1966; Briggs 1974; Stevens 1989; Thresher 1991; Krebs 1994; Rosenzweig 1995). The most widely known and accepted pattern of global faunal diversity lies in the trend of decreasing species diversity with in-
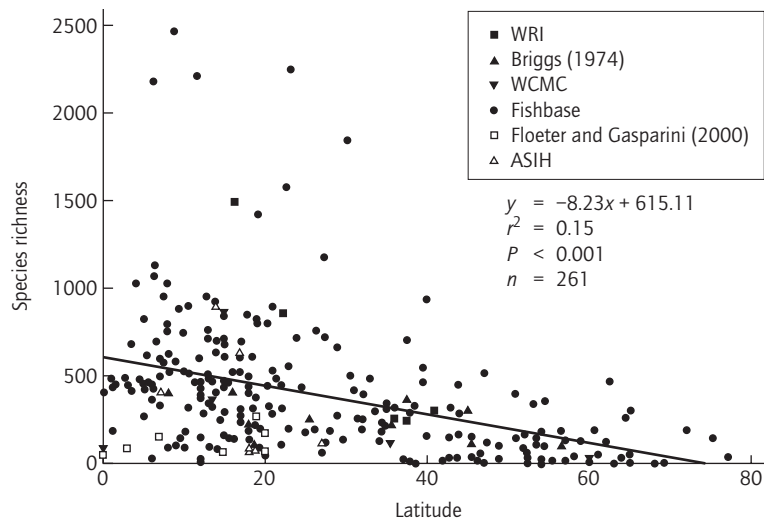
Fig. 16.1 Plot of species richness against latitude for shore fish assemblages. Although the regression of declining richness with distance from the equator is significant, it accounts for only 15% of variance in the data. Data were compiled from various sources as shown: Briggs (1974); Floeter and Gasparini (2000); FISHBASE, ICLARM's Fishbase website (http://www.cgiar.org/iclarm/fishbase/); WCMC, World Conservation Monitoring Centre website (http://www.wcmc.org.uk/marine/data/statistics/); WRI, World Resource Institute website (http://www.wri.org/wri/biodiv/marihome.html); ASIH, personal communications from colleagues at American Society of Icthyologists and Herpetologists conference, La Paz, Mexico, 2000, details available on request.

creasing latitude (Fischer 1960; Briggs 1974; Craig 1984; Crossland 1988; Stevens 1989). This is not such a simple case in the marine environment. For example, marine mammals reach their maximal diversity in polar regions, seaweeds reach their maximal diversity in temperate regions and corals reach their maximal diversity in the tropics (Gee and Warwick 1996). For most groups of marine organisms, the latitudinal pattern is unknown, partly because the comparative data are lacking (Gee and Warwick 1996). Several comparative studies (Horn and Allen 1978; Stevens 1989; Floeter and Gasparini 2000) have found evidence of the expected pattern of decreasing fish diversity with increasing latitude, excluding fishes that have extensive migrations. However, this conformity with the general trend is due almost entirely to the much greater richness of fish communities in some tropical coastal, especially coral-reef, locations. Indeed, when species lists from a broad geographic range of locations are plotted against latitude, the trend in richness with latitude is seen to be quite weak (Fig. 16.1). More comparative studies on fishes are needed but, at present, it appears unlikely that a simple pattern with respect to latitude will emerge.

Global clines, biodiversity hotspots

Other aspects of global faunal diversity, including centres of distribution ('hotspots'), patterns of endemism and geographic patterns of composition of taxa, have attracted the attention of researchers interested in the diversity of marine fishes (Ekman 1953; Briggs 1970, 1974; Gilbert 1972; Springer 1982; Thresher 1991). Here we review patterns in littoral fish faunas.

Tropical littoral Because of the presence of coral reefs, tropical littoral regions include locations possessing the highest faunal diversity, greatest gross photosynthesis and highest standing stock

biomass of all marine ecosystems (Crossland et al. 1991; Birkeland 1997). Yet coral reefs are uncommon, covering anywhere from $255\,000\,km^2$ (Spalding and Grenfell 1997) to $617\,000\,km^2$ (Smith 1978) depending on how narrowly they are defined. This represents just 0.1–0.2% of ocean area scattered through suitable coastal locales throughout the tropics. The four littoral biogeographic regions in the tropics all contain coral reefs, and are separated chiefly by faunal characteristics of reef-associated fauna. Reef development is far more extensive in the Indo-West Pacific than elsewhere and very sparse in the Eastern Atlantic. Of the four, the Indo-West Pacific and the Caribbean–Western Atlantic regions contain the greatest biodiversity (Briggs 1974; Springer 1982; Thresher 1991; Floeter and Gasparini 2000), although recent work is adding to the richness of the East Pacific region – the coastal waters of Mexico and Central America and the few island groups east of the 'East Pacific Barrier' of deep oceanic waters (Allen and Robertson 1994; Robertson and Allen 1996).

Total fish species richness reaches in excess of 600 species in Caribbean locations and can exceed 2000 species in central Indo-West Pacific locations. In the latter, one can often see in excess of 100 species in a single dive. As one travels away from the centre of either region, in any direction, species richness on coral reefs declines until it is comparable to species richness on warm temperate rocky shores, around 200 species or fewer (Gilbert 1972; Sale 1980; Thresher 1991). This pattern of decline with distance from the centre of the region is both more pronounced and far better documented in the Indo-West Pacific, perhaps simply because it is a much larger region than the Caribbean–Western Atlantic.

There is a high degree of taxonomic similarity among the four regions at the level of family and even of genus; however they are well differentiated at the species level. This taxonomic similarity reflects the circumtropical oceanic system due to the existence of the shallow Tethyan Seaway during the time the tropical fish fauna was evolving (Bellwood 1996, 1997). The differences among regions, particularly between the Caribbean–Western Atlantic and the Indo-West Pacific, re-flect the considerable interregional barriers that have existed since the late Eocene. The relative numbers of species in each of the families varies substantially among regions so that some families are of quite different importance in terms of species richness even if represented in different regions (Thresher 1991); there are also measurable differences of this type in taxonomic composition among locations within the Indo-West Pacific (Springer 1982; Thresher 1991). There are also high levels of endemism, and only a handful of circumglobal coral-reef fishes (Briggs 1974; Thresher 1991; Allen and Robertson 1994; Robertson and Allen 1996). Recently, Jones et al. (2002) have shown that endemism is well distributed throughout the Indo-West Pacific and the Caribbean, though with a tendency for it to be more pronounced in the more isolated island groups within the Pacific.

Temperate littoral   In the north temperate region, boundaries are hard to fix because the change in fauna from one location to the next is gradual and the ranges of many fishes fluctuate throughout the year in response to seasonal climatic changes. Despite this, marine biogeographers have recognized four main north temperate regions: Mediterranean–Atlantic, North American Atlantic, North American Pacific and Asian Pacific (Briggs 1974). The southern portions of these regions possess representatives of tropical faunas, such as Labridae, Serranidae, Haemulidae and Lutjanidae; as one travels northward, fish more typical of cold water are found, such as Pleuronectidae, Gadidae and Cottidae. Species richness is notably lower than in tropical littoral regions and declines towards the north. In the North American Atlantic region, for example, there are about 350 littoral species south of Cape Hatteras, 200–250 south of Cape Cod, about 225 in the Gulf of Maine, 100 in the Gulf of St Lawrence, 61 on the Labrador coast and 34 in Greenland (Briggs 1974). Similar clines are evident in each of the other temperate biogeographic regions. Briggs (1974) suggests that the North Pacific has been the primary centre of species evolution for north temperate regions and has largely determined the faunal composition of

the less rich northern Atlantic. The Antarctic region has played a similar role in the south.

Different faunas, different fisheries, different questions and approaches

Littoral fish faunas are far richer in the tropics than in the temperate zone. As a consequence, tropical coastal fisheries involve localized multispecies harvests of the same suite of many species over broad areas (Munro 1996; Arreguin-Sanchez and Manickchand-Heileman 1998; Pauly et al. 2000), while temperate fisheries are usually more closely targeted to single species. In general, fisheries research, which developed with commercial fisheries in the temperate zone (Smith, Chapter 4, Volume 2), has focused on the interactions of a target species stock and the fishery, with limited regard to other aspects of the environment or the ecosystem of which the fished species is a part. Yet the fundamental difference in the nature of temperate and tropical coastal fisheries has not led to different management approaches nor to different types of fisheries research, and tropical coastal fisheries are poorly managed as a consequence. The story is complicated further by the fact that the far more limited financial, human and information resources available in developing countries diminish the capacity to do fisheries research and management in the tropics (Sale 2002).

Scientists interested in fish communities rather than single fished species or fishery management have tended to study those communities most amenable to direct observation and experimentation (but see Pauly and Christensen, Chapter 10, Volume 2). These are rarely the relatively depauperate groundfish communities of the North Atlantic continental shelves where fisheries research developed. Instead, studies of marine fish communities have predominantly examined the diverse communities of shallow tropical and subtropical shores, and for some quite simple reasons (Roberts 1996; Sale 1996). Use of SCUBA is effectively limited to depths less than 25 m for meaningful ecological research, although use of Nitrox gas mixtures can extend that limit slightly. Other in-water techniques, such as underwater habitats or submersibles, are very much more expensive. In-water methods also require good visibility, moderate current regimes and tolerable temperatures. While approaches that put scientists into the water are used in cold temperate regions like Greenland and the Gulf of Maine (Green 1975; Green et al. 1984; Levin 1993), the physical conditions are not conducive to this activity the way they are further south, and many parts of the continental shelf are outside the depth range for conventional SCUBA. It is hardly surprising that the bulk of ecological research on fish in north temperate waters has used various types of gear to catch fish for subsequent analysis and that this research has focused on questions of population ecology. Catch your fish, measure it, take scales, gut and gonad samples – this could very well be the mantra driving ecological research on temperate fish species.

By contrast, in the tropics it is unpleasant to be out on the water and not in it, and the highly diverse fish communities are predominantly in shallow clear waters, usually with moderate current regimes. The high diversity of fish on coral reefs as well as the ecological background of many primary researchers led initially to an interest in the structure and dynamics of these assemblages rather than to a study of the ecology of single species (Sale 1988). Of course, in the same shallow tropical seas there are the turbid waters of mangroves and other estuaries in which direct observation is far more difficult. Methods conventionally used in temperate waters are employed there, often to answer the same size, age, gut and gonad questions of population ecology. Yet we have yet to meet an ecologist who works on tropical coastal fishes and prefers working in mangroves and seagrass beds rather than coral reefs.

The community-level questions that dominated early coral-reef studies were derived from terrestrial ecology rather than from study on fishes in other systems (Sale 1980). Even now, 50 years after serious coral-reef research on fishes began and 90 years since the first attempts by diving scientists to make in-water observations of reef fishes, there is remarkably little cross-referencing of tropical and temperate ecological research on fishes.

16.2.3   Why and how are the tropics more diverse?

Much of the earliest ecological research on coral-reef fishes was directed to the question of biodiversity. Why were these systems so rich in species? What ecological processes permitted the continued coexistence of such large numbers of species relative to temperate systems? Despite much effort (Sale 1980, 1991a), definitive answers to these seductive questions do not yet exist.

There is substantial evidence that reef fishes can be highly specialized with respect to microhabitat (Sale 1980; Tolimieri 1995, 1998; Caselle and Warner 1996). That so many of them are quite sedentary once their pelagic larval phase has been completed makes such specialization possible, and the topographically and biotically rich structure of their environment enhances possibilities for microhabitat differentiation. A coral reef is structurally far more complex than any rocky reef, and both make the structural complexity of a soft sediment plain something to be pitied!

However, the early expectation that such microhabitat specialization would permit effective habitat partitioning and stable coexistence of otherwise very similar species has not been borne out (Sale 1991b). Indeed, there is growing evidence that coral-reef environments are subject to frequent disturbances and are otherwise unpredictable habitats (Connell 1978; Wellington and Victor 1985; Williams 1986). There is also evidence that in many instances reef fishes are not limited by the availability of habitat or other reef-based resources (Doherty 1983; Doherty and Fowler 1994a,b; Caley et al. 1996; Hixon 1998).

At present, if there is a consensus view, it is that reef fish exist as metapopulations composed of numerous local open populations interconnected by their larval stage. Reef fish larvae are nearly uniformly pelagic for periods ranging from 1 week to several months but averaging 4 weeks, and are highly specialized for pelagic existence during this time. They also appear to be substantially more capable pelagic organisms than the larvae of the temperate species that have been examined, prob-

ably because they are taxonomically predominantly advanced perciforms (Leis 1991; Leis and Carson-Ewart 1997, 1998, 1999; Stobutzki 1998; Stobutzki and Bellwood 1998). Reef fish communities, then, are metassemblages of species, each protected from permanent local extinction by its metapopulation properties (Sale 1991b, 1996; see also Polunin and Pinnegar, Chapter 14, this volume; Polunin, Chapter 14, Volume 2). This consensus does not answer why these tropical faunas are so diverse but it diverts the question from the ecological to the evolutionary realm, leaving it as a problem for somebody else. Indeed, the question may even be backwards. Should we not ask why it is that temperate fish communities are so depauperate?

16.3   HABITAT ASSOCIATIONS

16.3.1   Demersal species

In demersal systems, our understanding of habitat is dominated by coral-reef investigations, although there are some parallel investigations in temperate systems (e.g. Holbrook et al. 1990; Tupper and Boutilier 1997). Demersal fishes select habitats for various reasons, including food resources (Love and Ebeling 1978; Choat 1982; Jones 1986; McCormick 1995), spawning and nesting sites (Fricke 1975; Walsh 1987; Danilowicz 1995; Warner 1995), sleeping sites and protection from predation (Shulman 1985; Jones 1988; Holbrook et al. 1990; Anderson 1994) and protection from stressful environmental conditions. Some of the patterns of fish–habitat associations may be conserved in more depauperate systems, whereas others involving the effect of species interactions on these associations may not.

Coral reefs

Relative to temperate demersal species, coral-reef species exist in a relatively stable environment with respect to temperature, salinity and oxygen

conditions. Common disturbances they face are severe yet episodic, including hurricanes, point source siltation from localized erosion, or destructive fishing methods (Bohnsack 1996). When comparing one reef locale to another within a region such as the Western Atlantic, for example, features that are relatively similar across reef habitats include temperature, salinity, characteristically limiting nutrient levels, high water clarity and gross productivity, which is typically high. In contrast, features that may show marked differences are physiographic features such as live coral cover, reef profile, extent of lagoon or shallow areas around the reef where mangroves and sea-grass beds are found, and tidal range (Marshall 1985; Sharp 1987).

Reef fish are strongly segregated by these physiographic features at spatial scales of 10–100 m (Sale 1991b), resulting in patterns of zonation where the species found in zones such as forereef, reef flat and backreef are usually predictable and conserved, although actual numbers within each species may fluctuate (Sale 1980). Another common pattern observed for coral-reef species is the increase in the number of large individuals with increasing depth. Fishing pressure usually attenuates with depth and may amplify this pattern, but it is likely pre-existing since many unfished coral-reef species show the same trend.

A weak positive relationship often exists between numbers of species present and habitat structure or structural complexity (Roberts 1996; Adjeroud et al. 1998; reviewed in Jones and Syms 1998). However, this is not a universal pattern even within coral-reef systems. Studies in different tropical regions or with different assemblages of species have demonstrated strong positive and negative effects of habitat structure as well as weak or no relationships (Sale 1991a; Jones and Syms 1998).

At spatial scales of metres, microhabitat segregation only occurs among certain particularly specialized species. Other processes, especially spatiotemporal variation in patterns of recruitment, may have a much greater effect on the fish species we see at particular locations (Doherty and

Fowler 1994a,b; Caley et al. 1996; Sale 1996). Habitat selection at the time of settlement can be precise, and is facilitated in some cases by olfactory cues deriving from adult fishes or coral species (Sweatman 1988; Sweatman and St John 1990; Roberts 1996). However, two factors act to prevent consistent microhabitat segregation by species: (i) coral-reef habitats have high heterogeneity with complex spatial arrangements of corals and resident fishes, thus providing multiple cues as attractants to various potential recruits; and (ii) recruits are patchy in space and time and may therefore not be available to respond to the cues provided (Caley et al. 1996).

Presently and historically, coral-reef managers have felt that limits of available habitat restrict abundances of adult fish populations. This is likely incorrect much of the time. The recent paradigm shift in marine ecology that emphasizes the role of recruitment in setting local species abundances (Doherty and Fowler 1994a,b; Bohnsack and Ault 1996; Caley et al. 1996; Sale 1996) may be beginning to filter into management of coral-reef fishes (Roberts 1996; Murray et al. 1999). Managers must recognize the fact that presence of a pelagic larval phase, and very high mortality during the pelagic existence, ensure a large degree of serendipity with respect to the species and numbers of recruits that colonize adult habitats.

Other tropical demersal environments

Other tropical demersal environments such as mangrove, estuarine, sea-grass and 'hardbottom' habitats have received more attention in recent years (Thayer et al. 1987; Bell and Pollard 1989; Ley et al. 1999; Lindeman and Snyder 1999). Observations of diverse fish assemblages in high densities in these environments, coupled with threats of anthropogenic stresses, have heightened concern and awareness of these highly productive habitats. Furthermore, there has been increasing evidence to suggest that mangrove, sea-grass and estuarine habitats serve as nursery grounds for important sport and commercial fishery species (Livingston 1982; Heck and Thoman 1984; Sogard et al. 1989;

Cabral and Costa 1999). Environmental factors that influence fish distributional patterns in mangroves and estuaries include gradients in salinity, water clarity, depth, abundance of prey and temperature (Ley et al. 1999).

Temperate demersal environments

Most temperate studies of habitat associations have focused on the effect on species distribution of a primary environmental factor, such as depth, structural relief or substratum type. Recent findings are revealing many relationships between temperate fishes and their environment, and continental shelves are no longer thought of as simple homogeneous environments with uniform assemblages of fishes (Craig 1984; Grimes et al. 1986; Hobson 1986; Pihl and Ulmestrand 1993; Gregory and Anderson 1997; Rhodes 1998; Swain et al. 1998). For example, beam trawl surveys in the northeast Atlantic by Rogers et al. (1999) found that more heterogeneous, rocky substrata supported a more diverse fauna of smaller-sized fish, such as gurnards (*Trigla* spp.), sole (*Solea solea*) and elasmobranchs, than more homogeneous, muddy bottoms. These results were similar to those of Platell and Potter (1999), who found partial segregation of Triglidae and Pempheridae in temperate muddy and rocky bottoms. Tupper and Boutilier (1997) have demonstrated the importance of habitat on various aspects of temperate reef fish ecology, including settlement, growth, predation risk and survival. Ebeling and Hixon (1991) argued convincingly for the general similarity of patterns in temperate rocky reef fish assemblages and those on coral reefs.

Identifying detailed patterns of association of fishes with habitat structure is difficult when techniques like trawling are used to determine distribution of fish (Larkin 1996; Walters et al. 1997; Pennington and Strømme 1998; Millar and Fryer 1999). Trawl efficiency varies with habitat and with overall abundance of fish (Godø et al. 1999), and discrepancies between path of vessel and paths of towed instruments introduce significant additional errors (Engås et al. 2000). Patchy distributions of fish within habitats cause further

problems in data interpretation (Pennington and Strømme 1998; Parrish 1999; Engås et al. 2000; Sparre and Hart, Chapter 13, Volume 2). Overall, despite the difficulty, direct observations by SCUBA or submersible are invaluable if a detailed picture of habitat responses is to be gained.

In contrast to coral-reef systems, temperate demersal environments show marked spatial differences in temperature, oxygen, salinity and primary production (Coutant 1990; Sharp 1987). In fact, one of the steepest latitudinal temperature gradients in the world, at 1 °C for every 1° latitude, occurs along the east coast of North America, combining in some parts with an annual range in sea surface temperature of up to 20 °C (Conover 1992). Such pronounced latitudinal and seasonal changes have led to numerous studies on the relationship of temperature to commercially important species, for example for groundfish (Swain et al. 1998) Atlantic cod, *Gadus morhua*, (Pihl and Umestrand 1993) and Alaskan coastal fishes (Craig 1984). These studies have frequently identified broad-scale spatial structure in fish populations. Yet in addition to temperature or other physicochemical factors, there is often significant habitat structure created by the sponges and other sessile invertebrates that grow even where the substratum is uniformly sand or clay. Indeed, awareness that temperate continental shelves frequently contain significant structure of importance to fishes appears to have coincided with the realization that commercial trawling in many regions is now so intense that most patches of substratum are trawled annually, with resulting serious degradation to structure (Dayton et al. 1995; Watling and Norse 1998; Turner et al. 1999; Kaiser and Jennings, Chapter 16, Volume 2).

For example, directed movements of Atlantic cod related to temperature have been associated with aggregations for feeding, overwintering and spawning among inshore and offshore habitats (Templeman 1966; Garrod 1988; Serchuk and Wigley 1992). While the earlier perspective was one of broadly uniform distribution over entire offshore banks and embayments, more recent studies have identified meso- and small-scale genetic heterogeneity that is being attributed to known

oceanic features besides cod biology and ecology, and implies far greater association of individuals with specific places than previously suspected. By using microelemental analysis of otoliths, individual spawning aggregations have been shown to be associated with unique elemental fingerprints; these infer population structure on a scale as small as inshore and offshore zones of individual bays and within specific locations on Georges Bank, the Grand Banks and the Labrador Shelf (Ruzzante et al. 1999, 2000; Campana et al. 2000). Stock-specific spawning occurs in the presence of topographically induced eddies and gyre-like circulation that result in the consistent deposition and retention of eggs and larvae in a particular habitat.

Habitats thought to be contiguous are now being described as patchy due to the presence of submarine channels, saddles and trenches that isolate populations. Such physical features can also promote coordinated movements of large numbers of fish among habitats. These are termed 'migration highways'. Habitat structure can also focus spawning aggregations, termed 'spawning columns', at specific sites (Rose 1993). Described in these contexts, Atlantic cod appear to resemble the larger snappers and groupers of coral reefs that live closely associated with a topographically rich substratum but undertake substantial annual migrations to traditional spawning locations tens of kilometres distant in characteristic outer reef slope locations (Colin 1992; Sadovy et al. 1994; Domeier and Colin 1997; Zeller 1997, 1998). Such work suggests that the well-recognized similarities between fish communities on coral reefs and rocky reefs (Ebeling and Hixon 1991) are likely extendable to many other temperate demersal communities.

Home ranges and territories

Overall, we suggest there is a general trend for long-term site attachment in demersal species in all environments. Long-term site attachment refers to the occupation of an area by an individual for its entire adult life. In most this will take the form of a long-term home range, while in a minor-

ity of species this range, or a portion of it, may be defended as a territory. Many fish may undergo periodic foraging and spawning migrations away from their home range, and in some species these movements may cover tens of kilometres. On coral reefs, home ranges are dependent on fish size and species and the typical relationship is for larger species to move over larger home ranges (Sale 1978). Familiarity with an area that comes with the establishment of home ranges offers many advantages, such as accurate knowledge of feeding, mating and shelter sites (Braithwaite 1998; Kramer and Chapman 1999). These advantages would not be expected to differ substantially between tropical and temperate systems (Barrett 1995), although the tendency for year-round residency may decrease with increasing latitude because some temperate regions experience large seasonal variation in water temperature, forcing reef residents into deeper waters to avoid environmental extremes (Barrett 1995). The findings for cod presented earlier provide support for this hypothesis. Home ranges may be very restricted, exemplified by gobies (Gobiidae) and damselfish (Pomacentridae) that commonly reside within $1–2\,m^2$ around a coral head, and by pricklebacks (Stichaeidae) and sculpins (Cottidae) that occupy small temperate tidepools (Barrett 1995; Helfman et al. 1997; Kramer and Chapman 1999). Intermediate ranges of a few hundred square metres characterize many kelp-bed and reef species (see Kramer and Chapman 1999 for examples).

16.3.2 Habitats for pelagic species: Water masses, fronts and eddies

When managers and scientists discuss habitat with reference to pelagic fisheries, they generally refer to physical oceanography such as frontal zones, oxygen, nutrient, salinity and temperature gradients (Sharp 1987; Cushing 1995). Pelagic regions are characterized by large volumes of water that lack obvious physical structure, have high solar insolation and have variable production that can be very high in regions of upwelling or convergence of major currents (Walsh 1981; Mann 1993;

Cushing 1995; Verity and Smetacek 1996). Fronts or upwelling areas represent concentrated productivity in temperate marine waters and can be seen from aircraft or satellites via infrared radiometry, provided there are temperature differences (Cushing 1995). These frontal zones represent boundaries between water masses that differ in temperature, salinity or both, and possess an accumulation of material including planktonic organisms and fishes that feed on the plankton (Walsh 1981; Sherman 1994). Although frontal zones change rapidly (Grioche and Koubbi 1997), they are predictable through the use of oceanographic modelling (Sharp 1987; Cushing 1995). There is abundant evidence that epipelagic fishes aggregate at these discontinuities and that targeting such zones is an effective fishery practice (Kirby et al. 2000). Fronts also may occur between masses of water differing in salinity but not temperature. In these cases the water masses may be indistinguishable from satellite radiometry data, yet they may differ significantly in fauna (Walsh 1981; Sharp 1987; Castillo et al. 1996).

16.4   DIFFERENCES IN TROPICAL AND TEMPERATE PRODUCTION CYCLES

Production cycles and trophic relationships are covered by Pauly and Christensen (Chapter 10, Volume 2) and Polunin and Pinnegar (Chapter 14, this volume) respectively, so we limit comment to geographic trends in fish production. Fish community structure and population dynamics are linked to physical oceanography by primary production cycles (Woods 1988; Cushing 1995; Mann and Lazier 1996). The primary production within each system shapes the characteristic annual production efficiency and quantity of fishery stocks and the communities they comprise (Woods 1988; Daly and Smith 1993; Mann 1993; Cushing 1995; Mann and Lazier 1996). The primary source of energy is incoming solar radiation and carbon fixation is performed by phytoplankton, macroalgae

and vascular plants. The role of detritivores that remobilize carbon into food webs is important but also easily forgotten (Wood 1967; DeAngelis et al. 1989; Daly and Smith 1993). Marine fish communities are supported by three different production cycles that are differentially important in different regions.

The water column supports two alternative phytoplankton production cycles. Both are exploited by zooplankton and fishes (Daly and Smith 1993; Cushing 1995; Mann and Lazier 1996). First, in regions where upwelling returns nutrients to surface waters, bursts of primary production of phytoplankton, mainly diatoms, are promoted. Upwelling can be the product of wind stress from above or tidal currents impinging on the bottom from below and may depend on submarine topography. Such zones occur in association with the continental shelves, estuaries, tides and current boundaries. The phytoplankton are kept in an environment rich in essential nutrients and light. Maximal rates of primary production result. Phytoplankton production can be used as a source of food directly by vertebrate grazers, such as herbivorous fishes, or indirectly by zooplankton that are then available for consumption by planktivorous fishes. Many fishes have evolved specialized gill arches or jaws that allow for efficient and maximal consumption of available phytoplankton or zooplankton resources. Any production not consumed by fish is recycled back into the food web by the microbial loop or settles to the bottom and is consumed by the benthic invertebrate community (Daly and Smith 1993; Cushing 1995; Mann and Lazier 1996). The majority of offshore fisheries in temperate and tropical systems are sustained by this production cycle.

The second production cycle is associated with zones that experience well-stratified conditions through extended periods, such as tropical oceanic waters year-round and most temperate waters during the summer months. In these zones, lack of upwelling allows the euphotic zone to become depleted of nutrients. Primary production is at relatively low rates and dominated by bacteria and small flagellates. These producers are predomi-

nantly taxa that are small in size. They tend to support several trophic levels of zooplankton and are relatively quickly recycled by the microbial loop. They are considered to be a poor source of energy for the production of fishes. For weakly stratified water, production of phytoplankton, again dominated by diatoms, will be favoured over production of bacteria and flagellates when conditions promote a low ratio of respiration to photosynthesis (Daly and Smith 1993; Cushing 1995; Mann and Lazier 1996).

In addition to these two water-column production cycles, demersal fishes in shallow waters, typically <30 m, have access to benthic primary production in the form of algae and sea-grasses. Demersal primary production can operate at the highest known rates in very shallow systems with efficient nutrient recycling mechanisms, and is of major importance as a food source for herbivores in coral-reef communities (Hatcher 1990). Herbivorous fishes that feed on demersal algae and sea-grasses typically comprise 25–40% of coral-reef fish biomass (Polunin 1996). This is in marked contrast to their near absence on cold temperate reefs, where demersal production enters the fish community principally by way of invertebrate intermediates. The cold temperate, Southern Hemisphere Odacidae are particularly capable digesters of algal material and an exception to the rule that algal herbivory by fish is a tropical lifestyle (Choat and Clements 1998). As a consequence, tropical demersal habitats support fish communities that depend on benthic as well as pelagic production to a degree not seen in the temperate zone. The high rates of production of fish on coral reefs and other tropical shore waters would not be possible without this direct use of demersal primary production.

16.5 VARIATION IN RECRUITMENT DYNAMICS

We include brief discussion of recruitment dynamics in this chapter because there is a real possibility, at least in tropical demersal systems,

that variation in the recruitment of new juvenile fishes plays a significant role in determining the structure of fish communities. Myers (Chapter 6, this volume) provides a comprehensive review of recruitment and density-dependence in fish populations. We use the term 'recruitment' not in the fisheries but in the ecological sense of 'addition of a new cohort to a population' (Caley et al. 1996). It is an important process in communities such as those on coral reefs, which are made up of species with pelagic larval stages and at least a modest degree of mixing of larvae from adjacent breeding populations. In such systems, the process of 'settlement' from the pelagic stage, and the usually synchronous metamorphosis from a larval to a juvenile phenotype, are dramatic moments in life history when one lifestyle is exchanged for another radically different one (Leis 1991). The great majority of other marine fishes also have dispersive larval stages that differ dramatically from the adults, so these species may also experience pronounced variations in recruitment to the juvenile stage.

16.5.1 Spatiotemporal variation in recruitment to reef habitats

A number of studies in various coral reef regions have now demonstrated a conspicuous spatiotemporal variation in recruitment of fish to the juvenile stage (Williams and Sale 1981; Doherty and Fowler 1994a,b; Caselle and Warner 1996; Tolimieri et al. 1998; reviewed in Doherty and Williams 1988; Caley et al. 1996). The variation can frequently be orders of magnitude in extent, both in space and time. Little of the variation among years and locations is accounted for by variation in habitat quality or resident population size. Doherty and Fowler (1994a,b) showed for one long-lived pomacentrid fish, *Pomacentrus moluccensis*, that differing patterns of recruitment success over a decade left measurable and different 'recruitment signatures' in the age structure of populations at each of seven nearby coral reefs. With the exception of one reef, which received particularly strong rates of recruitment and on which the population

'might' have demonstrated some compensatory density-dependent mortality, the data strongly supported an absence of any compensatory mortality to adjust the varying input of new fishes. These populations were 'recruitment limited' (Doherty 1983; Victor 1983, 1986) in the sense that their abundances and age compositions were set by the varying input of new settlers.

It follows, from this and other studies of recruitment variation, that community structure may be continuously modified by the varying recruitment of many of the component species. This is clearly the case for the small but isolated communities of fish that occur in habitat composed of small patch reefs (Sale 1991b; Sale et al. 1994). However, it is very likely also the case for the larger communities of fish on more contiguous reef habitat. The difficulty of accurately censusing communities over large areas of contiguous reef and the likelihood that spatial averaging will reduce the extent of variability seen in large study sites make this difficult to test in the way it has been tested on small patch reefs (but see Ault and Johnson 1998).

Accepting the notion that community composition is continuously modified by recruitment variation requires acceptance of the idea that reef fish populations are normally not at limits set by the resources available in reef habitat, although those limits are undoubtedly reached for some species at some times and places. Indeed, reef fish ecologists are currently strongly divided over the whole question of population regulation, and some are not convinced that density-dependence is a particularly important regulatory phenomenon in such systems (Sale 1991b; Hixon and Carr 1997; Chesson 1998; Hixon 1998; Sale and Tolimieri 2000).

16.5.2   *Temporal variation in recruitment to temperate populations*

The substantial variation in recruitment has been the bane of fisheries management from the outset (Hjort 1914; Myers, Chapter 6, this volume). Here, recruitment is used in the fisheries sense, as 'entrance of new individuals into the fishable population', and occurs substantially later in life than the

recruitment of reef fishes to the demersal population. Nevertheless, given that fishery recruitment is so frequently highly variable in space and time, it is reasonable to assume that entrance into earlier life stages of fishery species will also be highly variable, as on coral reefs, and there is some direct evidence that this supposition is correct.

While the lower diversity and stronger dominance of most temperate communities will ameliorate the community-level effect, it follows that at local scales the communities of fishes that occupy demersal habitat on temperate shores may also be expected to have their composition constantly modified, in relative abundances if not in species composition, due to the varying pattern of delivery of new cohorts of their component species. The extent of this variation is not well known, partly because it has seldom been looked for. Its potential importance lies in the impact on such aspects of community dynamics as the trophic web that transfers nutrients and energy through the community. We suggest that it is time to recognize that such ecosystem properties as patterns of transfer of energy and nutrients must be seen as flexible and constantly changing. Predator–prey dynamics may also change as particular prey or predator species change in abundance relative to those they interact with.

16.6   CONCLUSIONS

In this chapter we have used the richer body of in-water direct data from tropical demersal systems to infer patterns and processes likely to be present in temperate demersal and pelagic fish communities. We have used direct data from these other systems to confirm or modify these inferences. Our sense is that there are substantial similarities among demersal fish communities and that a greater cross-referencing of work on demersal systems should take place than has been the case in the past. We suspect that the pelagic habitat makes for somewhat different community organization.

Biotic diversity of fishes does not follow any simple latitudinal cline, despite the existence of a

significant negative trend with latitude in most sets of data on demersal shorefish. Variation in diversity of shorefishes along the equator is just as great, and some isolated islands close to the equator have fish faunas no richer than north temperate coasts. The order of magnitude variation in species richness among shorefish faunas is likely to be a result of history rather than a direct response to environmental conditions.

Pelagic environments are structured by temperature, salinity and currents, at both small and large scales, although the structures are transient. Individual fishes, their populations and communities respond to this structure and restrict their activities appropriately. We are beginning to understand the complexity of these responses. However, while knowledge of the details of these responses may enable a more effective targeting of fishery species, it is unlikely that management can be implemented at other than broader scales as done at present.

There is good evidence that demersal fish respond predictably to structural habitat features and reside within appropriate habitats. We know far more about this phenomenon in tropical coral-reef environments than in temperate or pelagic systems. The microhabitat structure created by sponges and other sessile invertebrates on otherwise featureless sandy or silty plains is only now becoming recognized as important for temperate demersal fish. In pelagic systems, fish respond to the large- and smaller-scale structure of the water mass due to physical oceanography. Our knowledge of these patterns has grown with our ability to define the physical structures using synoptic sampling of fish and physical structure and via remote sensing. We suggest that the interactions of demersal marine fishes and their habitats are defined by spatial homogeneity of habitats, seasonality of conditions and the spatial scales at which fish live their lives.

The highly variable pattern of recruitment from larval to juvenile stages is apparent across marine fish species. Its consequences for community structure will depend on the interaction with habitat complexity. Productivity of fish is notably different among tropical demersal faunas with their herbivorous taxa and the temperate demersal and pelagic faunas that depend on intermediary invertebrate herbivores.

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17 **Interactions Between Fish, Parasites and Disease**

I. BARBER AND R. POULIN

17.1 INTRODUCTION

Water provides the ideal medium for the survival, dispersal and proliferation of disease-causing organisms. Fish are particularly important hosts of parasites in aquatic ecosystems, harbouring a wide variety of adult and immature forms and acting either as the sole host in a parasite's life cycle or as one in a series of hosts. Some parasites may be responsible for acute, economically important outbreaks of disease in exploited fish populations or reduce productivity through nutritional effects; others may be responsible for chronic long-term changes in population structure. Infection-associated changes to host phenotype may influence the outcome of intraspecific or interspecific interactions and have important consequences for individual performance, whether measured by an ecologist in terms of evolutionary fitness or by a fisheries manager as reductions in stock biomass. Finally, since some fish parasites are transmittable to humans, and others reduce the market value of fish products by either spoiling host tissues or reducing the demand for fish as food, infections may have socioeconomic or human health importance. There is indeed some aspect of fish parasitology that is relevant to every modern fish biologist.

17.1.1 Aims and scope of this chapter

Given the remarkable breadth of fish parasitology research hinted at above, we are clearly unable to review all aspects of the subject. Our approach has been to concentrate on what we regard as currently dynamic research fields, highlighting those that examine the evolutionary and ecological consequences of parasite infections. We have attempted to present our review in a manner that is of interest and use to both theoretical and empirical scientists and those involved in fisheries management and, where possible, we have illustrated our text with examples drawn from studies of ecological, fisheries or aquaculture relevance. However, many of the studies that have given greatest insight have utilized a small number of model systems and our review inevitably reflects this literature bias. Our approach means we have omitted various topics perhaps expected in a more traditional review of fish parasitology. Readers seeking insight into the pathology and treatment of economically important fish diseases are referred to Roberts (1989) and Bruno and Poppe (1996). Similarly, for specific aspects of the biology of the various parasite groups themselves, we refer the reader to the modern and classic texts documented in Table 17.1. We have attempted to draw the reader's attention to other specialist texts in other areas where we feel our coverage has been necessarily compromised.

We begin by introducing the taxonomic diversity of organisms parasitic in and on fish, their equally varied life cycles and the effect of different environmental parameters on the richness and types of fish parasite communities. We continue by discussing host–parasite coevolution and other

evolutionary aspects of host–parasite relationships, particularly examining how the effects that parasites have on host phenotype may influence the ecology and 'fitness' of infected fish. We then develop this individual-based approach to an examination of the types of population-level effects parasite infections may have in natural habitats, and ask what may happen when such systems are upset by anthropogenic change. Turning our attention to the socioeconomic and human health implications of fish parasites, we examine how the real and perceived threat of fish-borne human infection may impact on fisheries and aquaculture, and then look at how parasite infections may be controlled in natural and artificial populations. We conclude our chapter by highlighting two recently developed applications of fish parasitology; using infections as ecological markers and as pollution monitoring systems.

17.2   FISH PARASITE DIVERSITY

17.2.1   *Important groups of fish parasites*

In this review we consider as fish parasites all organisms that have a requirement to live on or in fish hosts for at least part of their lives and which, during that time, have some negative influence on their fish hosts. We therefore include some vertebrates (lampreys) but not egg predators or the 'sneaky' conspecific males of some fish species that are often described as 'parasitizing' the mate resources of other fish (Forsgren et al., Chapter 10, this volume). Parasite taxa may be conveniently, though arbitrarily, separated into two major groups, based primarily on their size and mode of multiplication. The microparasites of fish, which are generally capable of asexual multiplication within or on a single fish host, comprise the viruses, bacteria and fungi, as well as the flagellated and ciliated protozoa; these are frequently important pathogens of fish in culture (Sommerville 1998). The metazoan macroparasites of fishes include the monogenean, digenean and cestode platyhelminth worms, nematodes, acanthocepha-

lans, leeches, certain copepod, branchiuran and isopod crustaceans, the glochidia larvae of certain molluscs and lampreys. References to classic and modern texts dealing with the major groups of fish parasites are provided in Table 17.1.

17.2.2   *Parasite life-cycle variation*

Parasites show tremendous variation in the types of life cycles they exhibit. A useful distinction can be made between those parasites with direct life cycles, which involve individuals of a single host species but sometimes interspersed with a free-living stage, and those with indirect life cycles that utilize a series of different host species. Such a functional distinction is not related perfectly to parasite taxonomy, since closely related members of a particular parasite group may exhibit either type of life cycle. However, it is useful because it identifies the mode of transmission, an important determinant of the importance of specific pathogens under particular situations. Knowledge of the life cycle and the mode of transmission of any parasite is the key to effective control; however life-cycle details are not known for many parasites. For example, *Kudoa* spp. are myxosporean parasites of marine fish that produce proteolytic enzymes to break down muscle filaments, providing nutrients for the parasite and causing the characteristic 'black tail' condition. Because the parasite does not have direct access to the external environment, spores are only released following the disintegration of muscle tissue. How the parasites get into a new fish host is not known (Moser and Kent 1994); the life cycle could either be direct or involve an intermediate host, as do other myxosporean life cycles (Kent et al. 2001).

In this section we highlight life cycles from several important parasite groups, drawing on specific examples from species of ecological, economic or evolutionary importance for which conclusive life-cycle details have been determined.

Directly transmitted parasites

Parasites with direct life cycles reproduce either by sporulation, fission, budding, egg production or in

Table 17.1 Taxonomy and key references to the major groups of organisms parasitic on or in fishes.

Parasite group	Representative taxa	Reference
Microparasites		Woo and Bruno (1999)
Viruses	Infectious pancreatic necrosis (IPN), viral hemorrhagic septicaemia (VHS), infectious haematopoietic necrosis (IHN), channel catfish virus (CCV)	Wolf (1988)
Bacteria	*Aeromonas, Pseudomonas, Yersinia, Flexibacter, Renibacterium*	Austin and Austin (1993)
Fungi	*Ichthyophonus, Saprolegnia*	
Macroparasites		Woo (1995)
Protista		Lom and Dyková (1992)
Apicomplexa	*Cryptosporidium*	
Microspora	*Glugea*	
Myxozoa	*Kudoa, Myxobolus* (*Myxosoma*)	Kent et al. (2001)
Ciliophora	*Ichthyophthirius, Trichodina*	
Platyhelminthes		Williams and Jones (1994)
Monogenea	*Gyrodactylus, Dactylogyrus*	Dawes (1947)
Cestoidea	*Diphyllobothrium, Bothriocephalus, Ligula, Eubothrium, Schistocephalus*	Khalil et al. (1994)
Trematoda	*Diplostomum, Allocreadium, Cryptocotyle*	Dawes (1947)
Nematoda	*Anisakis, Pseudoterranova, Contracaecum*	Moravec (1994)
Acanthocephala	*Corynosoma, Neoechinorhynchus, Acanthocephalus, Pomphorhynchus*	Crompton and Nickol (1985)
Mollusca		
Unionidae	Glochidia larvae	
Annelida		
Hirudinea	*Piscicola, Hellobdella, Hemibdella*	Sawyer (1986)
Arthropoda		
Copepoda	*Caligus, Lernaeocerca, Salmonicola, Thersitina*	Kabata (1979)
Isopoda	*Lironeca*	
Branchiura	*Argulus*	
Metazoa		
Agnatha	*Petromyzon*	Hardisty and Potter (1971)

some cases viviparity (Sommerville 1998). Parasite groups with members that exhibit direct life cycles include the viruses, bacteria, fungi, protozoans, microsporeans and ectoparasitic monogeneans, crustaceans and leeches. Even though such parasites only rarely cause problems in natural populations, when outbreaks do occur they may have catastrophic effects on fish stocks (e.g. Rahimian and Thulin 1996). Such parasites are particularly important pathogens in aquaculture as a consequence of the high stocking densities, reduced water quality and general stress levels of fish, which provide ideal opportunities for their transmission and proliferation (Sommerville 1998). Here we present two illustrative examples of direct life cycles.

Ichthyophthirius multifiliis ('white spot' disease; Ciliophora: Ichthyophthiriidae*)* *Ichthyophthirius multifiliis*, the causative agent of 'white spot', a common and pathogenic disease of fish in temperate and tropical aquaculture, is a directly transmitted ciliate. The endoparasitic trophont stages, located within the epidermis of infected fish, grow and divide for a period of about 1 week before actively leaving the host and encysting as a tomont stage in the aquatic environment. Each tomont undergoes binary fission for a period of up to 24 h to

produce up to 10^4 tomites, which differentiate into motile, positively phototactic theront stages that are infective to fish. Once a host is located, penetration of the epidermis is swift and is followed by growth to the mature trophont stage within 7 days (Matthews 1994).

Caligus spp. (Crustacea: Copepoda: Siphonostomatoida)   These important parasites of marine fishes begin life as non-parasitic, planktonic naupliar stages that moult to form the first copepodid stage. The copepodid is parasitic and must locate a fish host, to which it clings using prehensile antennae before moulting into a specialized chalimus stage. This stage is followed by three more instar phases, which are all attached to the host by an invasive frontal filament. Two preadult stages follow, which detach from the frontal filament and become capable of movement over the fish's body surface and of transfer between hosts, feeding on epidermal tissue using specialized mouthparts (Schmidt and Roberts 1989).

Indirectly transmitted parasites

Indirect life cycles are particularly common in some myxosporeans, most digenean trematodes, cestodes, acanthocephalans and nematodes, where transmission to the fish host is generally via predation events or skin penetration by free-living motile stages. Fish may be used as intermediate hosts by larval stages or as definitive hosts by adult parasites capable of sexual reproduction. Here we outline basic life cycles of representative species of these groups.

Myxobolus cerebralis (Myxozoa: Myxosporea)   Spores released into the aquatic environment when infected fish die and decompose, or are consumed by predators or scavengers, are ingested by tubificid oligochaete worms. After 3–4 months in the worm's gut epithelium, these spores develop into the infective 'actinosporean' phase. These are released into the water and enter susceptible fish, mainly salmonids, through the epithelial cells of the skin, fins, the base of the gills in the buccal cavity and elsewhere in the mouth, upper oesophagus and lining of the digestive tract. Transformation into *M. cerebralis* spores within the fish takes 2–3 months (El-Matbouli and Hoffmann 1989).

Diplostomum spathaceum (Trematoda: Digenea)   *Diplostomum spathaceum* is a trematode that infects a wide range of freshwater fish when free-swimming cercariae, released from parasitized lymnaeid snails, penetrate the fish's skin. The parasites migrate to the eye of the fish host, where they occupy the lens, causing exophthalmia (Chappell et al. 1994) and impairing vision to the extent that host foraging success is reduced (Crowden and Broom 1980). The definitive hosts of the parasites are piscivorous birds, particularly gulls (Laridae), which acquire the parasite after feeding on infected fish. High levels of infestation may cause losses in aquaculture and lead to a reduced catch rate by anglers in salmonid sport fisheries (Moody and Gaten 1982).

Schistocephalus solidus (Cestoda: Pseudophyllidea)   This common parasite of lacustrine populations of three-spined stickleback (*Gasterosteus aculeatus*) utilizes the fish as its second intermediate host (Fig. 17.1). Fish acquire the infection after ingesting procercoid parasites, harboured by cyclopoid copepods, which penetrate the fish's intestine and grow to a large size in the body cavity, significantly distending the abdomen of the host as they do so (Fig. 17.2). The increased nutritional demand of the parasite and its combined effects on host appetite, locomotion and competitive ability have severe consequences for the behaviour of infected sticklebacks, changes that have been intensively studied (reviewed by Milinski 1990; Barber and Huntingford 1995). Many behaviour changes are likely to facilitate transmission to bird and mammal definitive hosts, which become infected after feeding on infected fish. This life-cycle pattern is repeated for many other cestode parasites of economic or zoonotic importance, including *Ligula intestinalis* (Fig. 17.3) and *Diphyllobothrium* spp.

Anisakis simplex (Nematoda: Anisakidae)   This and other members of the genus *Anisakis* are
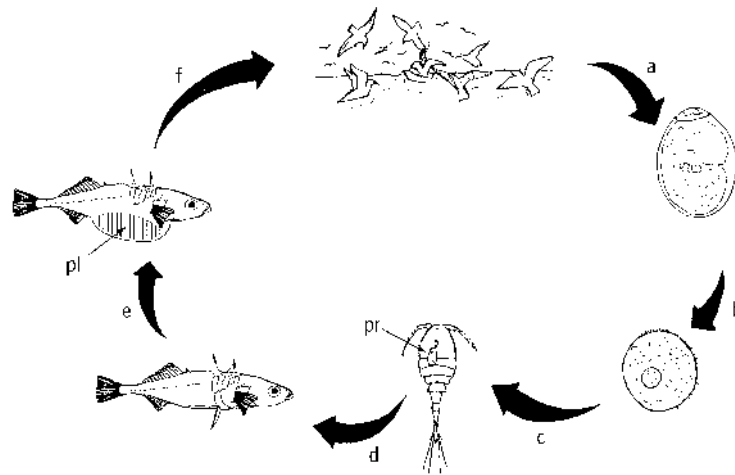
Fig. 17.1   Birds harbouring the adult cestode in their intestine transmit the parasite eggs into the aquatic environment with their faeces (a) where they hatch, releasing free-swimming coracidia (b). If these coracidia are ingested by copepods (c) then they pass into the body cavity and develop to form the procercoid stage (pr). If infected copepods are ingested by a three-spined stickleback (d) then the parasites move to the body cavity of the fish, where they undergo rapid growth (e), developing into plerocercoids (pl). The life cycle is completed when fish-eating birds ingest sticklebacks harbouring plerocercoids (f), allowing development to the egg-producing adult form in the avian intestine.

parasites that utilize marine fish as intermediate hosts. Fish acquire the parasite following the ingestion of infected crustaceans, whereupon the worm penetrates and invades the flesh of the fish where it remains until eaten by the definitive host, a marine mammal. It is likely that definitive hosts may also become infected following the consumption of infected crustaceans, meaning that the fish is a non-essential, or 'paratenic', host in the life cycle. The life cycle is completed when parasite eggs pass out with the faeces of the definitive host and are ingested by susceptible crustaceans.

17.2.3   *Environmental parameters affecting parasite communities*

It is rare for individual fish to be infected with just one single parasite species in nature; it is far more common to find fish harbouring a suite of infections. The factors governing the development of such parasite 'communities' within fish hosts are complex but largely depend on the geographic range, diet, local habitat use and size of the host fish. As such, the examination of parasite communities may also be used as indicators, or markers, to give an insight into the biology and habits of the host species, and this theme is taken up again in later sections of this chapter. Here we consider the major factors affecting the abundance and complexity of parasite communities in host fish.

Parasite communities of tropical vs. temperate fishes

Like those of free-living species, fish parasite communities in tropical aquatic habitats are typically more diverse and rich than their temperate counterparts. Latitudinal variation in parasite community structure has been demonstrated in congeneric freshwater eels from the UK and the Australian tropics, where the tropical hosts harboured a far greater parasite species richness than their temperate counterparts (Kennedy 1995). Two main hypotheses have traditionally been proposed to explain the increased diversity of communities

(a)

(b)

(c)
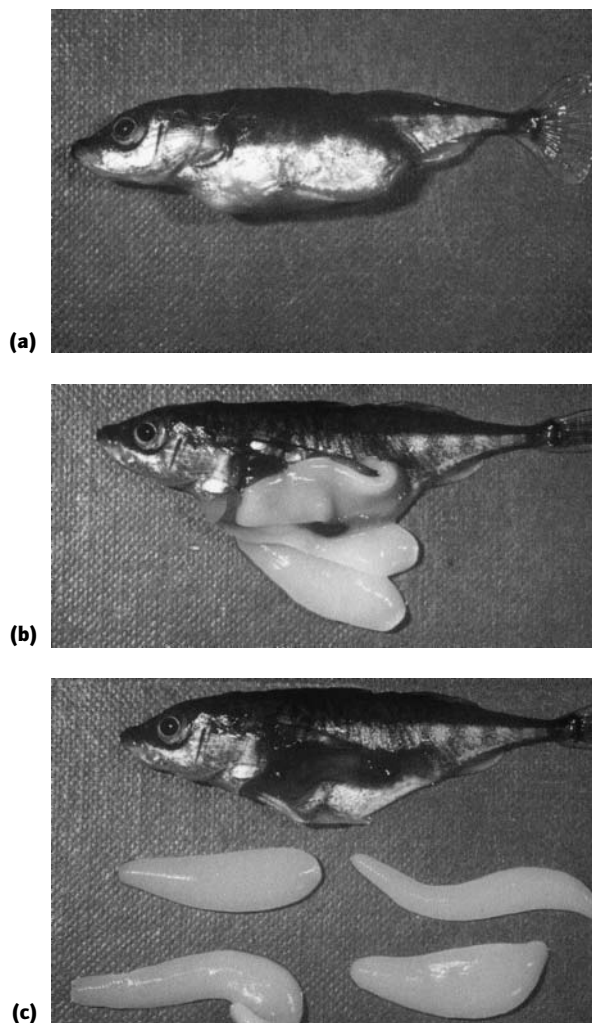
Fig 17.2 Three-spined stickleback naturally infected with four *Schistocephalus solidus* plerocercoids (a) before, (b) during and (c) after dissection.

Fig. 17.3 Two plerocercoids of the pseudophyllidean tapeworm *Ligula intestinalis* removed from the body cavity of a naturally infected European minnow.

of both parasitic and free-living animals in tropical habitats: the evolutionary time hypothesis and the evolutionary rate hypothesis, which relates to temperature (Rohde 1993). Increased parasite diversity in tropical fish may be explained by either. Elevated non-seasonal temperatures lead to increased growth and reproduction rates of hosts and parasites, increasing the opportunity for mutation and subsequent speciation events, whereas the tropics also hold ancient species with equally ancient host–parasite associations. Poulin and Rohde (1997) attempted to separate these two factors by comparing the species richness of ectoparasitic metazoans on the heads of 111 marine fish species selected to span both temperate and tropical regions. After controlling for phylogeny, to ensure results are a real effect and not just phylogenetic artefacts, they found that tropical species exhibited higher species richness and that richness was better explained by water temperature than latitude alone, supporting the evolutionary rate explanation.

Parasite communities of marine vs. freshwater fishes

Similar variation in parasite community structure is typically found when comparing marine and freshwater fish species. Holmes (1990) compared the findings of a study examining the parasite community structure of marine rockfishes with a study on freshwater fish and found parasite communities of the marine species to be more 'complex', defined as having more species for a given

number of individual parasites. Holmes attributed the difference in parasite community complexity to the greater mobility of, and habitat diversity encountered by, marine fish hosts and the broader host specificity of marine gastrointestinal helminths. However, we are aware of no studies that have examined the parasite fauna of groups with both marine and freshwater congeners, such as the sticklebacks or gobies, or of different populations of single species found in the different habitats. Both types of study would give useful comparative data.

Other factors affecting parasite communities

Within a particular geographic range, other factors are likely to determine both the number and species composition of parasite infections harboured by individual species. Habitat diversity and species richness both increase the likelihood that the correct hosts and habitat requirements for parasites with indirect life cycles or those with free-living stages will be met. The body size of a particular fish host species may be important, since it affects host diet and determines both the size of the space available for colonization and the size of the 'target' the host presents to parasites that infect via mobile free-living stages. Poulin and Rohde (1997) found that host body size correlated closely with the number of individual ectoparasites but not the species diversity harboured by marine fish. For parasites transmitted via the food chain, diet may also be an important determinant of the types of parasites that infect fish hosts. A study into the parasite fauna of two trophic morphs of Arctic charr *Salvelinus alpinus* in Loch Rannoch, Scotland, illustrates this. Parasite communities of the pelagic morph, which feeds on planktonic prey, were dominated by copepod-transmitted cestodes whereas those of the benthic morph were dominated by acanthocephalans, transmitted via bottom-dwelling fauna, and diplostomatid trematodes, the cercaria of which are released from benthic snails (Dorucu et al. 1995).

17.3 EVOLUTION OF HOST–PARASITE RELATIONSHIPS

17.3.1 Host–parasite coevolution

Cospeciation of fish and parasites?

From a historical perspective, the main question regarding fish–parasite relationships has to do with their evolutionary origins. Is a parasite present on a fish because of an association with the ancestors of the host that has been passed down through the host's lineage or because of a relatively recent colonization event, that is, a switch from another host lineage? The first scenario implies that associated fish and parasite lineages cospeciate over evolutionary time such that their phylogenies should be significantly congruent; host switching events, on the other hand, would disrupt this congruence. Monogenean and copepod ectoparasites of fish are often assumed to have cospeciated with their hosts because of their high host specificity (Poulin 1992). The few phylogenetic analyses available tend to support this view (Guégan and Agnèse 1991; Paterson and Poulin 1999). Coevolutionary patterns between fish and endohelminths have not yet been examined but host switching may have played an important role, as it has in the coevolution of endohelminths and other marine vertebrates (Hoberg 1995).

Recent coevolutionary studies have shown that parasite speciation and diversification can take place on shorter time-scales. Molecular analyses have revealed that what were previously considered single species of fish parasites actually consisted of several distinct species or genetic entities (Renaud and Gabrion 1988; De Meeüs et al. 1992). Sympatric congeneric species, though highly similar and easily confused for one another, are often produced rapidly through reproductive isolation following host switches. No doubt the use of molecular approaches will reveal other complexes of cryptic species within 'single' parasite species known to occur in several fish species.

Parasites as agents of natural and sexual selection in fish

Three requirements are necessary for parasites to act as selective agents: (i) their numbers must vary among individual hosts in a population; (ii) variation in parasite numbers among hosts must be associated with variation in host fitness and (iii) the trait under selection must either directly influence the number of parasites in an individual host or the host's ability to tolerate parasites, or the expression of the trait must depend on the number of parasites per host. Parasites in general meet these conditions and can thus be direct agents of selection (Goater and Holmes 1997). However, examples of parasite-mediated evolution in fish are few. The striped bass (*Morone saxatilis*), introduced a century ago from the east coast of North America to the west coast, at first suffered severe pathology and mortality from infection by a west-coast fish tapeworm. Today, bass from the west coast are more tolerant of the parasite than fish of east-coast populations from which they derived (Sakanari and Moser 1990), suggesting that they evolved to cope with infections and illustrating how rapidly parasite-mediated natural selection can act in fish populations. Similarly, European minnows (*Phoxinus phoxinus*) infected experimentally with *Diplostomum phoxini* are less likely to die from the infection when challenged with sympatric parasites than if the parasites are cultured from separate, genetically isolated host populations (Ballabeni and Ward 1993).

Much work has focused on the role of parasites as agents of sexual selection (Forsgren et al., Chapter 10, this volume). Hamilton and Zuk (1982) hypothesized that male secondary sexual characteristics serve as costly indicators of resistance to parasites and that females should prefer males with the most elaborate sexual characteristics. Several studies have confirmed that parasite load and the expression of sexual traits in male fish are often negatively correlated and that females prefer the showiest males (reviewed by Kodric-Brown 1990); in sex-role-reversed pipefish, males avoid mating with heavily parasitized females (Rosenqvist and Johansson 1995). The avoidance and rejection of

heavily infected mates may have direct benefits, such as the avoidance of potentially harmful directly transmitted contagious parasites or a reduced chance of passing microparasites to fry through vertical transmission. Alternatively, in species where male fish provide some degree of parental care, females may avoid selecting mates that are poor carers for eggs or young. In contrast Stott and Poulin (1996) found that parasitized males may invest heavily in nest defence. Evidence for indirect benefits in fish, where choosy individuals are proposed to benefit from mate choice by selecting 'good genes' for their offspring, are scarce. However, recent studies do suggest that the offspring of bright male sticklebacks may have higher resistance to *S. solidus* infections, attained at the expense of slower growth (Barber et al. 2001; Hutchings, Chapter 7, this volume).

Parasites could ultimately be the reason why male fish have evolved complex courtship displays, bright coloration or other forms of sexual ornamentation. At the same time, the proximate debilitating effects of parasites can affect the sensory acuity of females or reduce the effort that they invest in mate selection, making them less likely to discriminate among males differing in quality (Poulin 1994; López 1999). Thus the evidence available to date suggests that parasites can mediate sexual selection either by driving it or slowing it down.

Across species, Hamilton and Zuk (1982) proposed that host species exposed to strong selection pressure from parasites should evolve sexual characteristics that are more elaborate or pronounced than those of species incurring little pressures from parasites. A comparative analysis of British freshwater fish revealed a positive correlation between sexual dichromatism and the number of parasite genera per fish species (Ward 1988). However, a separate analysis of North American freshwater fish showed that the relationship between fish coloration and the number of parasite taxa exploiting a fish species is an artefact of sampling effort (Chandler and Cabana 1991). There is therefore no solid evidence at present that parasites have played a role in sexual selection at the macroevolutionary level.

17.3.2 Evolution of host modification: why does it occur?

Parasites often induce various physiological and behavioural changes in their hosts. These changes have three possible causes (Poulin 1995). First, they may simply be non-adaptive coincidental side-effects of infection. This is the most parsimonious explanation for simple changes in behaviour or performance, such as a reduction in swimming speed in parasitized fish (Sprengel and Lüchtenberg 1991). Second, alterations in host behaviour following infection may be the expression of parasite genes modifying the phenotype of the host. In other words, changes in hosts may be adaptive manipulations by the parasite that should facilitate the completion of its life cycle. The complex phenotypic alterations in sticklebacks induced by the cestode *S. solidus* appear to fall into this category; most observed changes seem likely to increase predation on infected sticklebacks by the predatory birds that serve as definitive hosts for the parasite (LoBue and Bell 1993; Tierney et al. 1993). Third, changes in infected hosts may represent host responses to infection, aimed at eliminating the parasites or compensating for their effects. The greater risks taken by sticklebacks harbouring *S. solidus* whilst foraging can be interpreted as a fish strategy aimed at compensating for the energy lost to the parasite (Milinski 1985; Godin and Sproul 1988). The stickleback–cestode example illustrates that the above three explanations are not always mutually exclusive and that they are difficult to disentangle from one another.

A single parasite larva may often be enough to induce a measurable phenotypic modification in an invertebrate host. In fish, however, as in other vertebrates, the influence of parasites on host phenotype is usually proportional to the numbers or biomass of parasites harboured by a fish. This is true whether the phenotypic changes are reductions in swimming speed (Sprengel and Lüchtenberg 1991), visual acuity (Crowden and Broom 1980) or antipredator behaviours (Poulin 1993; Lafferty and Morris 1996). This means that the consequences of parasite-induced changes in host phenotype are probably limited to the most heavily infected individuals in a fish population. We discuss these consequences after reviewing the mechanisms responsible for these alterations and the specific types of parasite-induced phenotypic alterations observed in fish.

17.3.3 Infection-associated behaviour change

Behaviour changes are frequently the most visible manifestations of physiological or pathological effects of parasite infections and, in an ecological and evolutionary context, may be the most important sublethal effects. Fish naturally perform a wide variety of behaviours: on a daily basis they need to locate and compete for food and avoid predators (Juanes et al., Chapter 12, this volume; Krause et al., Chapter 13, this volume), whereas over longer time periods they need to find mates and spawn successfully. The fulfilment of these requirements may involve long-distance migrations (Mctcalfe et al., Chapter 8, this volume) or competition over a territory or limited resources. If infections interfere with host nutrition, physiology or motor–sensory function, then changes to such behaviours may be expected.

There has been considerable recent interest in host behavioural change in fishes associated with parasite infections (see review by Barber et al. 2000), and we provide an overview of major studies that have revealed changes to specific behaviours associated with parasite infections in Table 17.2. A common problem in many studies has been that of distinguishing between cause and effect (Poulin 1998). Deviation from 'normal' behaviour patterns in naturally infected fish is insufficient to identify parasitism as the causal mechanism, since an individual already behaving differently as a result of some other factor could be more susceptible to infection. Yet despite providing the strongest design for detecting infection-mediated behaviour change, studies in which infection status is conferred on a random sample of an experimental population are scarce, and in the majority of cases causality is yet to be ascertained.

Mechanisms of behaviour change

Even in cases where behavioural change in fish hosts has been convincingly attributed to infecting parasites, the mechanisms of behavioural modification have rarely been identified. Yet the elucidation of the mechanistic basis of behaviour change can provide important clues to the evolutionary background and likely ecological consequences of behaviour change. Here we outline the major types of mechanism that have been identified.

Parasites that live in the intestine, grow in the body cavity or absorb nutrients from an invasive connection from the outside – as well as those that increase the metabolic cost of locomotion, stimulate large immune responses or increase activity levels – may cause a significant drain on the energy reserves of host fish. Many behavioural changes undoubtedly arise from these energetic effects of infection, including altered foraging behaviour and appetite (Milinski 1990). Concurrent increases in respiratory demand, which may also result from parasite-inflicted damage to gill surfaces, may lead fish to have a higher requirement for oxygen, leading to changes in the habitat preferences in order to exploit higher oxygen tensions.

Certain infections have significant local pathological effects and for parasites that occupy sense organs, muscles or neural tissue, local effects may be sufficient to bring about changes to host behaviour. Metacercariae of the trematode *Diplostomum phoxini* (Fig. 17.4) occupy specific brain lobes of European minnows (Barber and Crompton 1997) and infection is associated with erratic surface swimming of host fish (Rees 1955). Myxosporeans that destroy the cartilage of the inner ear have similar effects on the swimming behaviour of salmonid hosts, causing 'whirling disease' (Markiw 1992), and reduced swimming performance is also found in sheepshead minnows infected with digeneans that encyst in the bulbus arteriosus and obstruct blood flow (Coleman 1993). Parasites that grow to a large size and distend the abdomens of host fish, such as cestode plerocercoids, increase host cross-sectional area and frictional drag (Rodewald and Foster 1998), as well as causing atrophy of body musculature (Sweeting
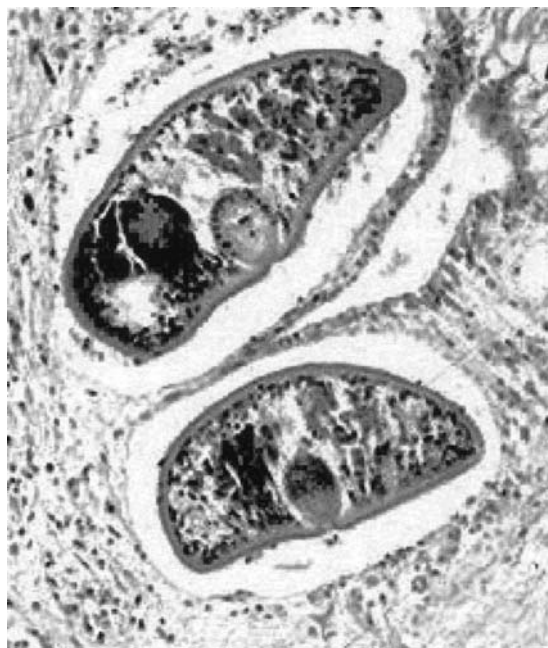
Fig. 17.4   Histological section showing two *Diplostomum phoxini* metacercariae in the brain tissue of a naturally infected European minnow. Metacercaris measure ~300μm × 100μm.

1977). These changes typically reduce body flexibility, locomotory speed and efficiency (Videler 1993).

Parasites may also alter host behaviour through more direct mechanisms, for example by producing host-modifying secretions. Alcohol and ketone waste products from encysted nematodes anaesthetize host musculature and reduce swimming performance (Ackman and Gjelstad 1975). The production of host hormone analogues is considered one of the strongest types of circumstantial evidence that behaviour change is an adaptive strategy by the parasite (Poulin 1998). Although hormonal modification of host behaviour has been demonstrated in invertebrate host–parasite systems, it has been difficult to detect in fish. *Ligula intestinalis* plerocercoids apparently castrate their hosts through interactions with the pituitary–gonadal axis of infected cyprinid fishes (Arme 1968), although the precise mechanism by which

this is achieved is yet to be discovered, despite extensive research effort (Williams et al. 1998).

Types of behaviour change

Table 17.2 outlines the major studies that have examined infection-associated changes in the behaviour of fish hosts, including changes in host foraging, swimming, antipredator, habitat selection and reproductive behaviour. Here we summarize the major effects on each of these behaviours.

Fish harbouring parasite infections are frequently reported to be poor competitive foragers as a result of impaired prey detection ability, poor prey handling ability or impaired swimming performance associated with infection. Such infections therefore present twin problems for host fish, since as well as increasing nutritional demand, they reduce the host's ability to compete for food, and infected fish need to overcome this problem (Milinski 1990). Demonstrated mechanisms by which hosts mediate these disabilities include modifying their time budget to increase the proportion of time spent foraging, switching prey-size choice to exploit prey of lower quality and for which there is less competition, and foraging in risky habitats avoided by non-parasitized fish.

Commonly reported effects of parasites on swimming behaviour take the form of either quantifiable reductions in swimming performance, measured as maximum sustainable velocity, burst speed or stamina, or changes in swimming form. The latter changes are rarely quantified, comprising mainly descriptive or anecdotal accounts of 'erratic' or otherwise conspicuous swimming movements. Both types of changes, which are unlikely to be mutually exclusive, may be important in determining predation pressure on hosts, either by increasing their visibility to predators or by impairing escape responses.

Since changes to antipredator behaviour potentially have immediate consequences for host survival and for positively or negative effects on parasite transmission, they have attracted a good deal of attention from evolutionary ecologists interested in adaptive host manipulation by parasites (see Lafferty 1999 for review). Although changes in antipredator behaviour of host fish associated with parasite infections have been demonstrated at every step of the predation cascade, from detection to identification, avoidance, susceptibility and capture, few studies have shown that these behaviours increase susceptibility to predators (see Section 17.3.4). Studies that demonstrate rapid changes in host antipredator behaviour around the period of parasite infectivity (Tierney et al. 1993) are particularly interesting, since they provide strong evidence for adaptive manipulation by the parasite. For many small fishes inhabiting open water, shoaling is the primary antipredator defence strategy (Krause et al., Chapter 13, this volume), and infections have been shown to influence both shoal membership and performance within polarized schools (see Barber et al. 2000). The extent to which antipredator behaviour is affected by infection may also depend on the host's particular life-history strategy. For longer-lived iteroparous species reduced antipredator performance should be more costly for young fish, which have high expected future reproductive success, than for older individuals. Young individuals should therefore invest more heavily in opposing the effects of infection. Poulin's (1993) results are consistent with this theory, as they show that the negative effects of trematodes on the antipredator responses of upland bullies (*Gobiomorphus breviceps*) are more pronounced in 2+ and 3+ age-group fish than in 1+ fish.

Common infection-associated changes in the spatiotemporal distribution, or habitat choice, of infected fish are the occupation of inshore (cf. offshore) waters, their position in the water column and preference for vegetation and cover (Mittelbach, Chapter 11, this volume discusses non-parasite reasons for habitat switching). Although such changes are often viewed as being host or parasite adaptations, care must be taken when interpreting the findings of field studies showing differences in the habitats occupied by infected and uninfected fish. This is because fish occupying certain habitats or regions of a water body may also be more or less likely to pick up certain parasites. For example, minnows in

Table 17.2 Selected studies documenting effects of parasites on host behaviour in teleost fishes.

Behaviour category	Specific behaviour	Host species	Parasite group	Parasite species	Site of infection	Marine (M)/ Fresh water (FW)	Laboratory (L)/Field (F)	Direction of change	Notes	Reference
Foraging	Time spent foraging	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Increase		Giles (1987)
	Reactive distance to prey	Dace, three-spined stickleback	Digenea	*Diplostomum spathaceum*	Lens	FW	L	Decrease		Crowden and Broom (1980), Owen et al. (1993)
	Attack success	Dace	Digenea	*Diplostomum spathaceum*	Lens	FW	L	Decrease		Crowden and Broom (1980)
	Competitive ability	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Decrease	Under certain conditions	Barber and Ruxton (1998)
	Handling time	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Increase		Cunningham et al. (1994)
	Prey choice	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Change	Preferred lower quality (smaller) items	Milinski (1984)
	Prey choice	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Change	Preferred higher quality (larger) items	Ranta (1995)
	Diet	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	F	Change	Switched from planktonic cladocerans to benthos	Jakobsen et al. (1988)
	Diet	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	F	Change	Less full stomachs during winter and summer	Tierney (1994)
Swimming	Ability to sustain maximum velocity	Sheepshead minnow	Digenea	*Ascocotyle pachycystis*	Heart	FW	L	Decrease		Coleman (1993)
	Swimming speed	Smelt, eels	Nematoda	*Pseudoterranova decipiens*		M	L	Decrease		Sprengel and Lüchtenberg (1991)
	Burst swimming speed	Coho, steelhead	Digenea	*Nanophyetus salmonicola*		FW	L	Decrease		Butler and Millemann (1971)

Behaviour		Host	Parasite group	Parasite species	Site	Habitat	L	Effect	Description	Reference
Activity levels		Guppy	Digenea	Diplostomum spathaceum		FW	L	Decrease		Brassard et al. (1982)
Swimming speed		Sockeye	Myxosporidea	Myxobolus arcticus		FW	L	Decrease		Moles and Heifetz (1998)
Fatigue distance		Sockeye	Cestoda	Eubothrium salvelini	Intestine	FW	L	Decrease		Smith and Margolis (1970)
Migration performance		Sockeye	Cestoda	Eubothrium salvelini	Intestine	FW	L	Change	Concentrated towards the end of the run	Smith (1973)
'Conspicuous locomotion'		European minnow	Digenea	Diplostomum phoxini	Brain	FW	L	Change	Infected fish exhibit 'intermittent swimming movements'	Rees (1955)
'Conspicuous locomotion'		Various salmonids	Myxosporidea	Myxosoma cerebralis	Cranium	FW	L	Change	Infected fish exhibit erratic circular swimming at water surface	Markiw (1992)
'Conspicuous locomotion'		Common shiner	Cestoda	Ligula intestinalis	Body cavity	FW	L	Change	Infected fish display 'jerky' or 'sluggish' swimming movements	Dence (1958)
'Conspicuous locomotion'		Pejerrey	Digenea	Diplostomum mordax	Brain	M	L	Change	Fish harbouring infective parasites impair movement	Szidat (1969)
Antipredator behaviour	Risk avoidance	Three-spined stickleback	Cestoda	Schistocephalus solidus	Body cavity	FW	L	Decrease	Infected fish fed closer to predatory fish	Milinski (1990)
		Three-spined stickleback	Cestoda	Schistocephalus solidus	Body cavity	FW	L	Decrease		Tierney et al. (1993)
		Upland bully	Trematoda	Telogaster opisthorchis	Body cavity	FW	L	Decrease	Reduction in antipredator behaviour increased with host age	Poulin (1993)

Table 17.2 *Continued*

Behaviour category	Specific behaviour	Host species	Parasite group	Parasite species	Site of infection	Marine (M)/Fresh water (FW)	Laboratory (L)/Field (F)	Direction of change	Notes	Reference
	Risk avoidance	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Decrease	Infected fish return quicker to food patch after being disturbed	Godin and Sproul (1988)
Social behaviour	Shoal membership	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Decrease	Infected fish left shoals quicker when food deprived	Barber et al. (1995)
	Schooling behaviour	European minnow	Cestoda	*Ligula intestinalis*	Body cavity	FW	L	Change	Increased nearest neighbour distance	Barber and Huntingford (1996)
	Schooling behaviour	Killifish	Trematoda	*Crassiphiala bulboglossa*	Skin	FW	L	Change	More often on periphery	Krause and Godin (1994)
Habitat selection	Inshore water occupancy	Pollack, whiting	Copepoda	*Lernaeacerca branchialis*	Gills	M	F	Change	Delayed seaward spring migration	Sproston and Hartley (1941)
	Inshore water occupancy	Menhaden	Copepoda Isopoda	*Lernaeenicus radiatus* *Olencira praegustator*	Skin, gills	M	F	Change	Infected adults remained with juvenile schools in estuaries	Guthrie and Kroger (1974)
	Position in the water column	Gudgeon, roach	Cestoda	*Ligula intestinalis*	Body cavity	FW	F	Change	Infected fish swam higher in the water column	Bean and Winfield (1992)

Behaviour	Fish species	Parasite group	Parasite species	Site	Habitat	L/F	Direction	Effect	Reference
Position in the water column	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	L	Change	Infected fish more buoyant and swam higher in water column	LoBue and Bell (1993)
Position in the water column	Fathead minnow	Digenea	*Ornithodiplostomum ptychocheilus*	Brain	FW	L	Change	Infected fish swam closer to water surface	Radabaugh (1980)
Position in the water column	Dace	Digenea	*Diplostomum spathaceum*	Lens	FW	L	Change	Infected fish swam closer to water surface	Crowden and Broom (1980)
Vegetation preference	Three-spined stickleback	Cestoda	*Schistocephalus solidus*	Body cavity	FW	F	Change	Infected fish found more distant from vegetation	Jakobsen et al. (1988)
Sexual behaviour — Attractiveness to opposite sex	Deep-snouted pipefish	Digenea	*Cryptocotyle lingua*	Skin	M	L	Decrease	Males avoid mating with infected females	Rosenqvist and Johansson (1995)
Display rate	Guppy	Monogenea Nematoda	*Gyrodactylus* sp. *Camallanus cottii*	Skin, gut	FW	L	Decrease	Infected males displayed less frequently and were chosen as mates less often	Kennedy et al. (1987)
Egg care	Upland bully	Trematoda	*Telogaster opisthorchis*	Body cavity	FW	L & F	Increase	Infected males fanned more than uninfected males	Stott and Poulin (1996)
Mate inspection	Upland bully	Trematoda	*Telogaster opisthorchis*	Skin	FW	L	Decrease	Females spent less time inspecting males	Poulin (1994)

isolated estuarine sloughs have high digenean loads because of their proximity to snail intermediate hosts (Coleman 1993) and the high frequency of eyeflukes in fish at specific sites in one lake has been explained by the local abundance of herons (Balling and Pfeiffer 1997). Unless it is possible to eliminate the effects of differential exposure to parasites caused by association with different habitats, then observational studies will generally be insufficient to demonstrate infection-mediated habitat shifts. In addition, since habitat type may determine the level of exposure to certain types of parasite, fish may use habitat selection as a primary strategy to avoid infection (see Section 17.6). In this way, parasites may interfere with the behaviour of (potential) hosts without actually infecting them.

Changes to sexual and reproductive behaviour of parasitized fish has been well documented (see Kodric-Brown 1990; Table 17.2; Forsgren et al., Chapter 10, this volume) and may stem from either reduced gonadal development (Pampoulie et al. 1999) or more subtle effects on sexual 'attractiveness', parental ability or the discriminatory ability of the choosing sex.

17.3.4 Ecological consequences of host manipulation

Whatever the phenotypic trait modified by parasites, and whether or not the modification is adaptive for host or parasite, the consequences for fish populations may be important. In the majority of cases, the potential population effects of even well-documented changes in fish phenotype caused by parasites remain unknown. What evidence there is, however, suggests that the influence of parasites can be substantial. Lafferty and Morris (1996) demonstrated in the field that fish parasitized by larval trematodes behave differently and are much more susceptible to bird predation than unparasitized conspecifics. Other studies have also found that parasitized fish are more vulnerable to predators than healthy ones (van Dobben 1952; Brassard et al. 1982). Combined with the results of studies that report decreased antipredator responses or greater conspicuousness

in parasitized fish (LoBue and Bell 1993; Poulin 1993; Krause and Godin 1994; Ness and Foster 1999), these findings suggest that phenotype-altering parasites can indirectly increase fish mortality by increasing their risk of predation.

The ecological and economic effects of phenotype modification are not limited to enhanced predation. As reviewed above, infected fish may, for a variety of reasons, have reduced reproductive output. Parasite infection may also influence migration success. Since its introduction to Europe from Asia in the early 1980s, the nematode parasite *Anguilicolla crassus* has been causing severe pathology and mortality in European eel populations (Moravec 1992). Sublethal nematode infections reduce haematocrit and stamina of eel hosts and cause important reductions in swimming ability (Sprengel and Lüchtenberg 1991), possibly making them less successful at completing their extensive migration. Considering that helminth infections can also impair orientation in migrating fish (Garnick and Margolis 1990), it is clear that parasite-induced changes in host behaviour or physiology can have profound impacts on fish populations.

17.4 EFFECTS OF PARASITES ON FISH POPULATION ECOLOGY

17.4.1 Patterns of parasite distribution amongst host populations

The level of parasite infection can be quantified in terms of the numbers of parasites of a particular species harboured by an individual ('intensity') or by the proportion of a host population that are infected ('prevalence'). To understand the potential influence of a particular parasite on host population ecology, it is important that the specific pattern of infection within the host population is recognized. In natural host populations, it is generally the case that parasites are not distributed equally amongst the population of hosts. Instead, macroparasites typically exhibit an aggregated dis-

tribution, with most host individuals harbouring low numbers of parasites and a small proportion of the host population harbouring a disproportionate load. The mechanisms leading to parasite overdispersion may involve individual-level variation in immunity or exposure to infective parasite stages, or may result from stochastic processes (Poulin 1998).

For longer-lived parasites, infection levels frequently covary with host age, since parasites are acquired over the lifespan of the fish. Body size, which may covary with age, may additionally be important if larger hosts provide a bigger 'target area' for infecting parasites. The combination of the two mechanisms may account for the frequent disproportionately high burdens harboured by large host individuals. In temperate regions, or where hosts undertake regular migrations between habitats differing in their intrinsic risk of parasite infection, there may additionally be a seasonal effect on parasite load.

17.4.2 Effects of parasites on host population structure

The medium and long-term consequences of parasite infections for fish populations are of great interest to fisheries managers and parasitologists alike. One of the most extensive long-term studies of host–parasite population change in a natural system has been that of the population consequences of *Ligula intestinalis* infection of the roach population in Slapton Ley, a freshwater lake in Devon, south west England (summarized in Kennedy et al. 1994). *Ligula intestinalis* was recorded for the first time in the roach population in 1973, its introduction coinciding with the arrival and successful breeding of great-crested grebes *Podiceps cristatus*, major definitive hosts of the parasite. The parasite spread rapidly through the roach population, reaching a prevalence of 28% 2 years later and causing a crash in the host population. *Ligula intestinalis* became gradually less prevalent and eventually disappeared from the population by 1985. The parasite was detected again at the site in 1990, and 12 months later the prevalence of the parasite had risen to 71%. This

second outbreak typifies the destructive and opportunistic nature of such parasites in small lowland lakes, where intense year-round avian predation on the host population ensures the parasite's rapid transmission following a chance introduction to the system. Interestingly, the patterns in Slapton Ley are very different to those in a lacustrine population of minnows infected with *Ligula* in the highlands of Scotland, where the parasite persisted at a low level for at least 10 years (I. Barber, unpublished data). The differences are probably attributable to the vastly differing predation regimes at the two sites: transmission of the parasite at the highland site by gulls, the only piscivorous birds of note at this site, is restricted to their presence during a short breeding period in early summer. Lake size may also be important in determining the stability of infections, and in larger lakes *L. intestinalis* may reach a state of equilibrium (Kennedy 1985).

However, such documented effects of parasites on natural fish populations are relatively few, and generally our best indications of population-level effects of parasites are various types of circumstantial evidence. For example, the small number of extremely heavily infected fish predicted from mathematical models of parasite distributions are often completely missing from host populations, suggesting that they have been removed by predators or have died naturally. This truncates the expected negative binomial distribution. Another clue is given by the absence of large heavily infected individuals from natural populations in field surveys; again, the implication is that these fish, which may carry the majority of the parasite population, are not present because they have been removed from the population by predators (Poulin 1998).

17.4.3 Parasites and conservation: what happens when natural systems are upset?

Natural and anthropogenic change may affect fish parasites, and hence diseases, in a number of ways. Firstly, parasites that have free-living stages will be susceptible to the same ecological parameters

that control the distribution and abundance of free-living animals. Secondly, their reliance on hosts means that they will be affected by changes to host populations. However, there is little direct evidence linking environmental changes to fish parasites, and most evidence is circumstantial.

Environmental impact on established parasites

The consequences of environmental change, either long term or acute, natural or anthropogenic, is an important area for research in parasitology (Hominick and Chappell 1993). Transmission between hosts is the most important rate-limiting step in all parasite life cycles, and both natural and anthropogenic environmental changes that affect the rate at which parasites are transmitted potentially have massive impact on fish populations. For example, many parasites in temperate ecosystems that have free-living stages in their life cycles have a lower temperature below which transmission does not occur (Chubb 1976). Where natural water temperatures are artificially raised as the result of thermal pollution resulting from the input of cooling water from power plants, such thermal limits may be constantly exceeded and infection possible year round, leading to increased parasite loads in host fish (Högland and Thulin 1990). The importance of long-term global climate change in this respect is particularly relevant. Other types of pollution, such as nutrient loading resulting from the input of sewage effluent, may alter communities of invertebrates, which often act as intermediate hosts, and of predators, which are often definitive hosts of fish parasites. Changes to such communities have the potential for knock-on effects on fish parasites (see Section 17.7.2).

Anthropogenic parasite introductions

Introduction of a novel parasite species into a naïve population may have especially serious consequences for the fish hosts. Kennedy (1994) discusses the biology of parasite introductions and identifies several characteristics of successful 'pioneering', or colonizing, parasites, including the existence of a life cycle that is direct or, if indirect, has wide host specificity for intermediate hosts. The economically important eel parasite *Anguillicola crassus* (see above) is ideally equipped for colonization (Kennedy 1994). Although it has an indirect life cycle, a wide range of copepod species are utilized as intermediate hosts and the parasite can also use a multitude of fish species as paratenic hosts. The parasite species need not always be completely novel to have such serious consequences; a novel strain of an existing parasite may also be highly pathogenic in the 'wrong' host population. Fish populations that have been separated for significant periods of time may support highly coevolved populations of the same parasite species that are significantly more pathogenic than local coevolved strains (Ballabeni and Ward 1993).

One of the most damaging outbreaks of a fish parasite in Europe in recent decades has resulted from the introduction of *Gyrodactylus salaris* into the salmonid-rich rivers of northern Norway. This monogenean parasite was first documented in 1973 and the subsequent decimation of salmonid stocks in these rivers over the following years led to the parasite being deemed a notifiable disease in 1983. Controversial treatment of infected rivers with rotenone in 1981 was successful in exterminating the parasite locally (Johnsen and Jensen 1991). The parasite is thought to have been introduced with stocked fish from infected hatcheries, possibly from eastern Scandinavia where local salmonid populations are resistant to the parasite (Bakke et al. 1990).

17.5 SOCIOECONOMIC AND HUMAN HEALTH IMPLICATIONS OF FISH PARASITES

17.5.1 *Economic importance of parasites in fisheries and aquaculture*

There are four main ways in which parasites may impact on economically important fisheries (Sinderman 1990). Firstly, direct mortality associated with highly pathogenic infections, or indirect mortality resulting from increased levels of preda-

tion on exploited stocks, may reduce the numbers of fish available in the harvestable stock. Parasitic fungi (*Ichthyophonus*) have been associated with recent mass mortalities of economically important species (Rahimian and Thulin 1996). Secondly, nutritionally demanding parasites or those that impair foraging behaviour may cause poor growth performance. Chronic low-level cestode infections of salmonids in aquaculture lead to economically significant reduced body weight at harvest (Bristow and Berland 1991), as do microsporidean infections (Hauck 1984) (but see Arnott et al. 2000 for a demonstration of parasite-induced gigantism in fishes). *Kudoa thyrsites* has an intensity-dependent effect on muscle texture in Atlantic salmon *Salmo salar*, with heavily infected fish exhibiting 'soft flesh' disease (St-Hilaire et al. 1997), which reduces market value and host survival. Thirdly, consumer aversion to visibly detectable infections can increase wastage and processing costs and may severely reduce a fishery's viability. Consumer rejection may be based on the presence of the parasites themselves, which in some cases may present a real human health risk (see Table 17.3); more frequently it is based on damage caused to host musculature, which reduces palatability, aesthetic quality and hence marketable value (for marketing issues see Young and Muir, Chapter 3, Volume 2). This is particularly problematic for aquaculture species, which are very often long-lived, high-value products. Finally, changes in the size or structure of an infected host population may have consequences for the performance of other species in the community (some of which may also have commercial value). These mechanisms are likely to be complex but may be positive, for example if they result in emancipation from predation or competition, or negative, for example if the parasite exhibits density-dependent host switching.

The microparasites are generally the most important parasites in aquaculture (Sommerville 1998), since high stocking densities mean that parasites with direct life cycles have a greater likelihood of finding a host. Inevitable reductions in water quality may also irritate sensitive external fish surfaces, and the subsequent oversecretion of mucus may serve as a substrate for ectoparasitic protozoans. Certain discrepancies in the importance of various groups between different types of systems are evident; for example, the microsporideans are more important pathogens in mariculture than in freshwater systems. However, indirectly transmitted parasites, such as digenean trematodes, may also become problematic in aquaculture because invertebrate populations, which are potential intermediate hosts, build up quickly in fish farms in response to nutrient availability. The availability of definitive hosts also provides ample possibility for such infections to become established (Kennedy 1994), and predators attracted to the farm potentially facilitate the completion of complex parasite life cycles. The clinostomatid and heterophyid trematodes in particular cause problems in warmwater aquaculture because of their large size and infectivity to humans respectively.

17.5.2 Human health implications of fish parasites

The risks of infection with fish-borne parasites present a potential or realized threat to the health of human consumers particularly in societies where the consumption of raw, undercooked or cold-smoked or lightly salted fish is traditional. In their review of human helminths, Coombs and Crompton (1991) describe 76 registered helminth pathogens of *Homo sapiens* that involve fish in their life cycles, the majority of which are acquired by humans following the consumption of infected fish (Table 17.3). Sinderman (1990) highlights three major groups of marine fish parasites with demonstrated public health significance: the anisakid nematodes, the diphyllobothriid cestodes and the heterophyid trematodes. These three groups of parasites give rise to major diseases. Over 1000 cases of anisakiasis, resulting from the invasion of the wall of the human digestive tract by *Anisakis* or *Pseudoterranova* sp. nematodes, were reported between 1969 and 1977 in Japan, whereas diphyllobothriasis, resulting from the ingestion of infective *Diphyllobothrium* sp. cestode plerocercoids, is an important disease in Asia.

Table 17.3 Parasites of humans that are acquired from fish or that otherwise involve fish in their life cycle (Source: data from Coombs and Crompton 1991).

Parasite taxon	Species	Definitive host	First intermediate host[a]	Second intermediate host[a]	Paratenic host[a]	Geographic distribution	Infection route
Trematoda							
Digenea							
Clinostomatidae	*Clinostomum complanatum*	Humans	Snail	Fish (FW species including *Cyprinus, Perca*)		Asia	Ingestion
Cathycotylidae	*Prohemistomum vivax*	Humans	Snail	Fish (FW and BW species including *Clarias, Mugil, Tilapia*)		Africa	Ingestion
Diplostomatidae	*Diplostomum spathaceum*	Piscivorous birds	Snail	Humans, Fish (FW species)		Europe	Skin penetration
Echinostomatidae	*Echinochasmus japonicus*	Humans	Snail	Fish (FW species including *Perca*)		Asia	Ingestion
	Echinochasmus perfoliatus	Humans	Snail	Fish (including *Acheilognathus, Mogarnda, Pelteobargus*)		Asia, Europe	Ingestion
	Echinostoma hortense	Humans	Snail	Fish (including *Misgumus*)		Asia	Ingestion
	Echinostoma malayanum	Humans	Snail	Fish (including *Barbus*)		Asia	Ingestion
Psilostomatidae	*Psilorchis hominis*	Humans	?	?Fish (FW species)		Asia	Ingestion
Nanophyetidae	*Nanophyetus salmonicola salmonicola*	Humans	Snail	Fish (Salmonidae)		N.America	Ingestion
	Nanophyetus salmonicola schikhobalowi	Humans	Snail	Fish (FW species)		Europe	Ingestion
Opisthorchidae	*Metorchis albidus*	Humans	?	Fish (Cyprinidae)		N. America, Europe	Ingestion
	Metorchis conjunctus	Humans	Snail	Fish (Cyprinidae)		N. America	Ingestion
	Opisthorchis felineus	Humans	Snail	Fish (Cyprinidae)		Europe	Ingestion
	Opisthorchis guayaquilensis	Humans	?Snail	?Fish		C. America	Ingestion
	Opisthorchis sinensis	Humans	Snail	Fish (Cyprinidae)		Asia	Ingestion
	Opisthorchis viverrini	Humans	Snail	Fish (FW species)		Asia	Ingestion
	Pseudoamphistomum truncatum	Humans	?	Fish (Cyprinidae)		Europe	Ingestion

Heterophyidae	*Apophallus donicus*	Humans	Snail	Fish (FW species)	N. America	Ingestion
	Centrocestus armatus	Humans	Snail	Fish (Cyprinidae)	Asia	Ingestion
	Centrocestus formosanus	Humans	Snail	Fish (FW and BW species)	Asia	Ingestion
	Cryptocotyle lingua	Humans	Snail	Fish (M and BW species)		Ingestion
	Haplorchis pumilio	Humans	Snail	Fish (including *Puntius*)	Africa, Asia	Ingestion
	Haplorchis taichui	Humans	Snail	Fish (including *Puntius*)	Africa, Asia	Ingestion
	Haplorchis vanissimus	Humans	?Snail	?Fish	Asia	?Ingestion
	Haplorchis yokogawai	Humans	Snail	Fish (including *Puntius*)	Africa, N. America, Asia	Ingestion
	Heterophyes dispar	Humans	Snail	Fish (including *Barbus, Mugil, Solea*)	Asia	Ingestion
	Heterophyes heterophyes	Humans	Snail	Fish (including *Mugil, Tilapia, Aphanius*)	Africa, Asia Europe	Ingestion
	Heterophyes nocens	Humans	?Snail	Fish (including *Acanthogobius, Lateolabrax, Mugil*)	Asia	Ingestion
	Heterophyopsis continua	Humans	Snail	Fish (including *Acanthogobius, Lateolabrax, Mugil*)	Asia	Ingestion
	Metagonimus minutis	Humans	Snail	Fish	Asia	Ingestion
	Metagonimus yokogawai	Humans	Snail	Fish (Cyprinidae)	Asia	Ingestion
	Procerovum calderoni	Humans	Snail	Fish (including *Butis, Chanos, Mugil*)	Asia	Ingestion
	Procerovum varium	Humans	Snail	Fish (including *Glossamia*)	Asia	Ingestion
	Pygidiopsis summa	Humans	Snail	Fish (including *Acanthogobius, Liza, Mugil*)	Asia	Ingestion
	Stellantchasmus falcatus	Humans	Snail	Fish (including *Acanthogobius, Liza, Mugil*)	N. America	Ingestion
	Stictodora fuscata	Humans	Snail	Fish (BW species)	Asia	Ingestion
Cestoidea						
Pseudophyllidea						
Diphyllobothriidae	*Diphyllobothrium cameroni*	Humans	?Copepod	?Fish (M species)	Asia	Ingestion
	Diphyllobothrium chordatum	Humans	?Copepod	?Fish (M species)		Ingestion
	Diphyllobothrium dalliae	Humans	?Copepod	Fish (FW species including *Dallia*)		Ingestion

Table 17.2 *Continued*

Parasite taxon	Species	Definitive host	First intermediate host*	Second intermediate host[a]	Paratenic host[a]	Geographic distribution	Infection route
	Diphyllobothrium dendriticum	Humans	Copepod	Fish (FW species)			Ingestion
	Diphyllobothrium elegans	Humans	?Copepod	?Fish (M species)		Asia	Ingestion
	Diphyllobothrium erinaceieuropaei	Humans	?Copepod	?Fish		Asia	Ingestion
	Diphyllobothrium giljacicum	Humans	?Copepod	?Fish			Ingestion
	Diphyllobothrium hians	Humans	?Copepod	?Fish (M species)			Ingestion
	Diphyllobothrium klebanorskii	Humans	?Copepod	Fish (Salmonidae, including *Onchrynchus*)			Ingestion
	Diphyllobothrium lancelatum	Humans	?Copepod	Fish (including *Coregonus*)			Ingestion
	Diphyllobothrium latum	Humans	Copepod	Fish (FW species)			Ingestion
	Diphyllobothrium mansoni	Carnivorous animals (including cat and dog)	Copepod	Humans; Fish (FW species)		Asia	Ingestion (of infected copepod)
	Diphyllobothrium minus	Humans	?Copepod	?Fish			Ingestion
	Diphyllobothrium nenzi	Humans	?Copepod	?Fish			Ingestion
	Diphyllobothrium nihonkaiense	Humans	?Copepod	Fish (Salmonidae)		Asia	Ingestion
	Diphyllobothrium pacificum	Humans	?Copepod	Fish (M species including *Sarda, Scomberomorus*)			Ingestion
	Diphyllobothrium scoticum	Humans	?Copepod	?Fish		Asia	Ingestion
	Diphyllobothrium skrjabeni	Humans	?Copepod	?Fish			Ingestion
	Diphyllobothrium tingussicum	Humans	?Copepod	?Fish			Ingestion
	Diphyllobothrium ursi	Humans	Copepod	Fish (Salmonidae, including *Oncohrynchus*)			Ingestion
	Diphyllobothrium yonagoensis	Humans	?Copepod	?Fish		Asia	Ingestion
	Diplogomoporus balaenopterae	Humans	?	Fish (M species including *Eugraulis, Sardinops*)		Asia	Ingestion
	Diplogomoporus branni	Humans	?	?Fish		Europe	
	Diplogomoporus fukuokaensis	Humans	?	?Fish		Asia	
	Ligula intestinalis	Humans	Copepod	?Fish		Asia	
	Pyramicocephalus anthocephalus	Humans	?	Fish (M species including *Elinginus, Megalocottus*)		N. America	
	Schistocephalus solidus	Humans	Copepod	Fish (FW species including *Gasterosteus*)		Europe	Ingestion

		Definitive host	Source	Fish host	Geography	Transmission
Nematoda						
Dioctophymatidae	*Dioctophyma renale*	Humans	Oligochaete	Fish (FW species including *Ameirus*)		Ingestion
	Eustrongyloides sp.	Humans	Oligochaete	Fish (FW species including *Fundulus*)	N. America	Ingestion
Trichinellidae	*Trichinella nativa*	Humans	Humans/fish?		N. America	Ingestion
Trichuridae	*Aonchotheca (Capillaria) philippinensis*	Humans	Fish (FW and BW species, including *Hypseleotris*)		N. America Africa, Asia	Ingestion
Anisakidae	*Anisakis simplex (marina)*	Humans	Euphausiid crustaceans	Fish (M species)	Asia, N. America, Europe	Ingestion
	Contracaecum osculatum	Humans	Euphausiid crustaceans	Fish (M species)	Europe	Ingestion
	Pseudoterranova decipiens	Humans	Marine crustaceans	Fish (M species)	N. America, Asia	Ingestion
Dracunculidae	*Philometra* sp.	Fish (Humans accidental)	Marine copepods		N. America	Via wound
Gnathostomatidae	*Gnathostoma doloresi*	Humans	FW copepod	Fish (Salmonidae)	Asia	?Ingestion
	Gnathostoma hispidum	Humans	FW copepod	Fish (FW species including *Misgurnus*)	Asia	?Ingestion
	Gnathostoma spinigerum	Humans	FW copepod	Fish (FW species)	N. America, C. America, Asia	Ingestion
Acanthocephala						
Echinorhynchidae	*Acanthocephalus rauschii*	Humans	Marine crustacea	?Fish (M species)	N. America	Ingestion
Polymorphidae	*Bolbosoma* sp.	Humans	?Marine crustacea	?Fish (M species)	Asia	?Ingestion
	Corynosoma strumosum	Humans	?Marine amphipods	Fish (BW and M species)	N. America	?Ingestion

a FW, freshwater; BW, brackish water; M, marine. *? denotes non-confirmed or unknown host.

17.6 CONTROLLING
PARASITE INFECTIONS

17.6.1 Natural parasite control mechanisms

Fish can adapt to tolerate infections. Tolerance is defined as minimizing the fitness effects of the parasite infection. However, two other strategies are available for limiting parasite load: avoiding parasites or eliminating them following infection. Several behavioural mechanisms can serve to decrease fish exposure to the infective stages of parasites. For instance, sticklebacks can avoid certain microhabitats or form large shoals to decrease their risk of being infected by ectoparasitic branchiuran crustaceans (Poulin and FitzGerald 1989a,b). Parasites, or more correctly the threat of infection they pose, also have the potential to alter prey selection if fish have evolved to avoid either prey items that contain infective parasite stages or whole prey taxa, if their consumption is potentially associated with subsequent infection. Few studies examining behavioural avoidance in fish have been undertaken, but the results of Wedekind and Milinski (1996) suggest that although they are identifiable through altered behaviour, copepods infected with *S. solidus* are not avoided by foraging sticklebacks.

Once infected, fish rely mainly on their immune system to combat pathogens and parasites. Although its intricacies are not as well known as those of the mammalian system, the fish immune system appears capable of controlling infections by both microorganisms and metazoan parasites (Iwama and Nakanishi 1996). Antibodies against endoparasitic worms have been found in diverse fish taxa (Harris 1972; Sharp et al. 1989), and both natural and acquired resistance against monogeneans has been demonstrated in guppies and salmonids (Madhavi and Anderson 1985; Bakke et al. 1990). Much of the regulation of parasite numbers in wild fish may be due to immune responses (Lysne et al. 1997).

Other modes of regulation can be used against ectoparasites. For example, fish are known to rub their body against hard substrates to rid themselves of sources of irritation such as skin parasites (Wyman and Walters-Wyman 1985). Cleaning symbioses represent a more sophisticated ectoparasite control method (see Losey 1987; Poulin and Grutter 1996; Côté 2000 for reviews). This interaction involves the removal of ectoparasites, mucus or diseased tissues from the surfaces of fish by a cleaning organism. Certain crustaceans and fish, especially the wrasse *Labroides* spp., are specialized cleaners of a wide range of fish species; cleaning is also sometimes observed between conspecific fish (Sikkel 1986). The benefits of cleaning for fish are not always clear. Despite the large numbers of ectoparasites ingested by cleaners, experiments in which cleaners were removed from reefs have revealed no changes in infection levels by ectoparasites or no sign of fish emigrating to other reef patches (see Poulin and Grutter 1996). The latest of these field experiments is the only one suggesting that the action of cleaners benefits fish: the action of cleaner wrasses led to a decrease in the numbers of ectoparasitic gnathiid isopods per caged fish relative to fish caged on reefs without cleaners (Grutter 1999).

17.6.2 Biological control of parasites in fish farms

Cleaner fish have recently been used as an alternative to chemicals in order to control ectoparasite infections on cultured fish. Specialized and/or potential cleaner fish can reduce the number of monogeneans or copepods per fish when introduced in tanks or sea cages containing cultured fish such as tilapia or Atlantic salmon (Cowell et al. 1993; Costello 1996). Temperate wrasses not known as specialized cleaners, but related to the tropical genus *Labroides*, show much potential for the biological control of sea lice (caligid copepods) on Atlantic salmon. A new inshore fishery has recently appeared to supply wrasses to salmon farms. However this has other potential environmental implications, and wrasses themselves are now being cultured to meet the demand (see Costello 1996). If these supply problems are solved, there is no doubt that the tendencies of certain fish to clean, and of most other fish to pose

for cleaners, can be further exploited for parasite control.

17.6.3   Chemical control, vaccine development and other approaches

Reactive treatment or prophylaxis of disease was the primary mechanism of dealing with parasite outbreaks, and the preventative use of chemical agents has been the typical approach taken to disease in aquaculture. The development of vaccines against fish parasitic diseases was not considered feasible until very recently, yet it is now an important industry. Vaccine development is a complex new field, the specific details of which lie beyond the scope of this chapter; we refer the interested reader to recent reviews by Evelyn (1997) and Vinitnantharat et al. (1999).

Low-tech solutions may also be effective in controlling outbreaks of indirectly transmitted parasites, principally by removing or controlling intermediate hosts. Field and Irwin (1994) describe how a management strategy of increased water flow and weed-bed, algae and snail removal at a fish farm in Northern Ireland reduced the prevalence of *Diplostomum spathaceum* in rainbow trout from 100% to 20%.

17.7   RECENT APPLICATIONS OF FISH PARASITOLOGY

17.7.1   Parasites as ecological markers

Parasites can serve as biological tags to obtain information on various aspects of fish biology (see Williams et al. 1992 for an extensive review). Many parasite taxa have all the characteristics of ideal biological markers, including infection levels that vary widely among the different parts of the study area but remain stable locally from year to year, a relatively long lifespan, and being easily detected and identified (Williams et al. 1992). Parasites often provide valuable information on their own, but they should ideally be seen as a complementary method for validating or supplement-

ing results obtained using genetic markers, meristic data or any other type of biological indicator.

In recent years the use of parasites as ecological markers has been particularly important for the stock separation of commercially important fish species and the elucidation of recruitment migrations of fish from nursery grounds to feeding and spawning grounds (Moser 1991; Williams et al. 1992; Metcalfe et al., Chapter 8, this volume). The spatial scale over which infection levels by one parasite species in a fish species show significant variation can be relatively small, and allows other uses for parasites as ecological markers. For instance, on coral reefs, fish from the reef flat can have significantly different ectoparasite and endoparasite loads compared with conspecifics from the reef slope just a few hundred metres away (Rigby et al. 1997). Parasites can therefore shed light on the limited movements of fish and on their local population structure. However, the fact that some parasites have the potential to alter host behaviour, including swimming performance and migratory patterns (see Table 17.2), should be taken into account when identifying ideal indicator parasites.

Other uses of parasites as biological tags include the determination of fish diets and spatiotemporal feeding patterns, as well as the reconstruction of food webs (Williams et al. 1992; Marcogliese and Cone 1997; Polunin and Pinnegar, Chapter 14, this volume describe other methods). Such studies focus on parasites transmitted via the food chain that show some degree of specificity for their intermediate hosts, thus providing clues about what fish are eating. Finally, parasites can be used as specific characters in phylogenetic reconstructions of fish lineages (see Williams et al. 1992) or in studies of the recent origins of congeneric fish species (Marcogliese and Cone 1993). Their potential as biological markers is thus vast and mostly untapped.

17.7.2   Parasites as early warning systems for pollution detection

Aquatic pollution can influence, directly or indirectly, the infection levels and pathogenicity of

fish parasites (see Khan and Thulin 1991 for review). On the one hand, pollutants can suppress the immune responses of fish and lead to greater acquisition of parasites. On the other, pollutants can either harm the free-living stages of fish parasites or reduce the populations of their invertebrate intermediate hosts and thus cause reductions in infection levels in fish. The interaction between toxic pollution and parasitism can therefore have important ecological implications for fish populations. Beyond that, fish parasites can also be used as indicators in environmental impact studies and in pollution monitoring. Because different types of parasites respond differently to different pollutants, a detailed knowledge of the expected effect of pollution on a parasite species is needed if this species is to serve as an indicator. For instance, a review of published studies suggests that ciliate and nematode parasites may be reliable indicators of eutrophication and thermal pollution, whereas acanthocephalans and cestodes should make good indicators of heavy metal pollution (Lafferty 1997). In fact, acanthocephalans and cestodes of fish accumulate heavy metals at concentrations that are orders of magnitude higher than those in fish tissues or the external environment (Sures et al. 1999). As always, a combination of indicators is better than a single one when assessing water or environmental quality. The great sensitivity of parasites to many types of pollution should make them indicators of choice.

17.8   CONCLUSIONS

Fish harbour a wide range of adult and immature forms of taxonomically diverse parasites, many of which have significant sublethal effects that have important consequences for the ecology, evolution and management of host fish. Parasite infections impact on almost every aspect of fish biology, from individual behaviour to population-level processes, but there remain many gaps in our knowledge of the mechanisms by which parasites influence host individuals and populations. We are only beginning to understand the ecological and fitness consequences of parasites that infect fish,

yet many of these are likely to be of considerable importance for the way in which we design strategies for the conservation, exploitation and management of populations. The adoption of a multidisciplinary approach to fish parasitology, in which controlled experimental infections are used to examine changes in the biology of parasitized fish in conjunction with carefully designed studies of host and parasite in more natural environments, should go some way to filling these gaps.

In this necessarily brief review, we have tried to highlight recent research, examining a range of topics of current interest, including the role of parasites as agents of natural and sexual selection in their fish hosts, the consequences of infection-associated behaviour change for parasite transmission, and the effects of parasites on host population biology. Since many parasites have the potential to cause direct and indirect losses in commercial and subsistence fisheries and in aquaculture, and because others may be transmissible to humans and cause disease or death in extreme cases, we have discussed the often considerable socioeconomic importance of infections. We also briefly introduce the use of parasites as indicators of pollution and as biological tags and the potential of parasites to influence fish conservation programmes.

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