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Introduction: Aquaculture and Behaviour

Felicity Huntingford, Sunil Kadri and Malcolm Jobling

Abstract: This chapter starts by providing a review of what aquaculture is, which finfish are farmed, for what purposes and in what kinds of culture systems. It then considers what behaviour is, why biologists are interested in behaviour and how they study and explain it. The question of the complexity of fish behaviour is addressed, leading into a discussion of fish welfare and how it can be defined, identified and measured. The issues of domestication, selective breeding and the extent to which fish are domesticated animals are then covered, as are the effects of captive rearing; in both cases, effects on behaviour are given special consideration. The criteria for effective, sustainable fish culture are then spelled out; these include efficient production, environmental protection (with respect to land, water and feed resources and to impacts on wild fish populations) and fish welfare. Possible strategies for improving the welfare of farmed fish are discussed and consideration given to what is required of the behaviour of fish cultured for food, for science and the ornamental trade and for release. Finally, an outline is given of the structure and content of the remaining 10 chapters of this book.

Keywords: behavioural biology; **c**aptive rearing; consciousness; conservation; culture systems; domestication; **e**nvironmental protection; fish in research; food fish; ornamental fish; production; selective breeding; supplementation; sustainability; welfare.

1.1 WHY BEHAVIOUR AND AQUACULTURE?

There are many problems to be overcome in the culture of fish, in terms of producing sufficient numbers of larvae and juveniles, in rearing these to the desired age and size and in ensuring that the fish have the characteristics appropriate to the purpose for which they were farmed. For long-established aquaculture species, the most immediate problems of cultivation have been solved; farmers can obtain a sufficient supply of fish and know about the environmental and food requirements for survival and growth. Even so new problems can arise, such as emerging diseases and concern about the environmental impact of farming operations. For both established and new species, scientists representing many disciplines have contributed to finding solutions to the problems encountered in culturing fish; engineering, veterinary science, nutrition, genetics, animal breeding and reproductive biology represent a few of these.

This book has been written in the belief that the biological discipline of animal behaviour can also make important contributions to promoting aquaculture. Many of the problems encountered in fish culture might stem from the

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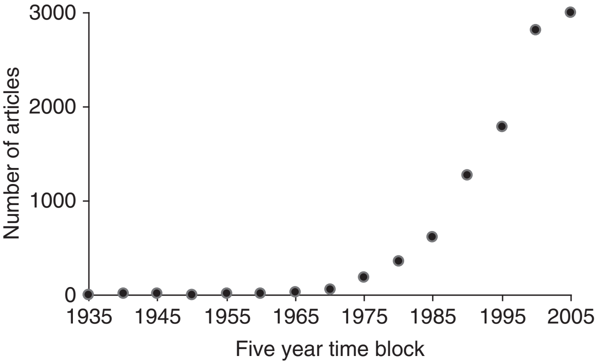

Figure 1.1. The number of papers on behaviour and aquaculture published in each 5 year period since 1935. Based on a Web of Science search using the key words behaviour (British and American spelling) and aquaculture.

natural behaviour of the fish concerned and solutions to these could emerge from an understanding of why animals behave as they do. Consequently, there is a growing interest in the application of behavioural concepts to aquaculture. This is reflected in the increasing number of published scientific articles on this topic (Figure 1.1). The overall aim of this book is to cover different aspects of behaviour that are relevant to fish culture, summarizing and illustrating the relevant fundamental behavioural biology and exploring its implications for aquaculture. The purpose of this introductory chapter is to provide the background information needed put this into context, starting with an overview of which finfish are cultured, for what reasons and how this is done. This includes an introduction to a group of species of fish cultured for various purposes that are used as 'spotlight species' to illustrate specific points throughout the book. There follows a brief review about what behaviour is and how biologists study and explain it, as well as a commentary on the degree to which fish are capable of the complex behaviour shown by other vertebrate groups that are farmed. This leads on to the tricky issue of the extent to which fish welfare is a meaningful concept about which it is legitimate to be concerned. The question of the effects of domestication and captive rearing on fish is addressed, both in general terms and in the context of potential effects on fish behaviour. Finally, criteria for effective and sustainable fish culture are considered, spelling out what it is that fish farmers aim to achieve; these include welfare-friendly, cost-effective production that is sustainable in terms of impact on the environment.

1.2 ABOUT AQUACULTURE

1.2.1 What aquaculture is

Aquaculture is the farming of aquatic organisms. In addition to finfish, which are the topic of this book, these include plants (both small phytoplankton and large macrophytes, such as seaweeds), molluscs (mussels, clams, scallops, marine gastropods, squid and octopus), crustaceans (freshwater and marine shrimps and prawns, crayfish and crawfish, lobsters and crabs), amphibians (frogs) and reptiles (sea turtles, freshwater turtles and terrapins, crocodiles and alligators). The fact that aquaculture is a form of farming implies that the organisms being cultivated are owned by farmers and that there is human intervention during the rearing process. The level of human intervention varies widely depending upon the species being cultured and the type of farming practice employed. For example, in the extensive cultivation of seaweeds and bivalve molluscs such as clams and mussels, there may be only a minimal degree of human intervention. This could involve no more than seed collection, selection of on-growing sites, occasional thinning of the stock and harvesting. On the other hand, the intensive farming of finfish and crustaceans may involve multiple interventions throughout the rearing cycle, from broodstock management, gamete collection and egg incubation to larval rearing and on-growing of the stock to market size. The interventions will often include regular feeding and observation of fish, management of water quality, treatment to combat diseases and infestation with parasites and protection from predators. The degree to which farmers intervene during the culture cycle will clearly have an impact on many aspects of the biology of their stock, including their behaviour.

1.2.2 Why finfish are cultured

Although understanding behaviour is important for culture of many kinds of animals, this book concentrates on behaviour and finfish aquaculture, since this in itself is a huge topic. When one considers finfish aquaculture, the first reaction is usually to think of the production of fish as a source of food for human consumption. The farming of fish for food undoubtedly accounts for the greatest proportion of finfish aquaculture, but it is by no means the only reason for which fish are farmed. Some are farmed for the ornamental fish trade, for use in domestic and display aquaria, whereas others are reared in large numbers for release into the wild to supplement wild populations used in recreational and commercial fisheries. A few species are raised in captivity for biomedical research or for environmental impact studies, while others have been taken into captivity in an attempt to conserve and save threatened natural populations. Finally, some fish species are farmed for use as pest control agents; for example, mosquitofish (*Gambusia affinis*) and guppies (*Poecilia reticulata*) are used to control the malarial mosquito and the grass carp (*Ctenopharyngodon idella*) is used to control aquatic vegetation that threatens to clog ponds, lakes, shipping canals and other waterways (Lever 1996; Shelton & Rothbard 2006).

1.2.3 Which finfish are cultured

The farming of finfish is recorded in antiquity, but a great expansion has occurred since the 1960s. The expansion has involved marked increases in production volumes and increases in the number of farmed species worldwide (http://www.fao.org/), driven by a combination of diminishing natural fisheries and an increased consumer demand for fish products (Shelton & Rothbard 2006; Le Francois *et al.* 2010). There are about 28 500 living species of finfish, inhabiting ponds, lakes, streams, rivers, estuaries and oceans throughout the world. About 40% of these species live in fresh water, particularly in tropical and subtropical regions, with freshwater species being most numerous in the river drainages of South-east Asia and South America. Just under 60% of the total number of species inhabit marine environments, the vast majority being found in shallow tropical and subtropical coastal waters. However, the coastal and shelf waters of temperate and polar regions also provide habitats for about 2000 species. Over 100 fish species are diadromous, migrating between marine and freshwater habitats for the purposes of feeding and breeding. Amongst these, most are anadromous, spawning in fresh water but having feeding grounds in the sea; however, a few are catadromous, spawning in the oceans but spending much of their life in fresh water. A major taxonomic division among finfish is between cartilaginous fish, such as sharks and rays, and bony fish, which include the lobe-finned fishes, such as the lungfishes, and the ray-finned fishes, which comprise the largest group of finfish.

Thus, living finfish represent a very large and diverse group in terms of both their taxonomy and their ecology. Only a small proportion of finfish is suitable for culture; for example, of the 300 species that are farmed for human consumption, less than half are produced in large quantities and farmed fish production is dominated by species from a few families (Shelton & Rothbard 2006; Le Francois *et al.* 2010; http://www.fao.org/figis). The majority of farmed species belong to the teleosts, which is the largest and most advanced division of the ray-finned bony fishes, containing almost 27 000 extant species. Some representatives of other groups of ray-finned fish, perhaps most notably the sturgeons, are also farmed. All the 25 species of sturgeons (family Acipenseridae) occur in the northern hemisphere and all spawn in fresh water, although some species are diadromous, moving seasonally between fresh water and the sea. The life history characteristics of the sturgeons make them susceptible to overexploitation by humans; they are long-lived, late-maturing species and mature females may not spawn each year. All sturgeon species are endangered as a result of overfishing, damming and regulation of waterways and industrial pollution of their habitats. Several species are being raised in captivity as a conservation measure. Sturgeons are also highly prized as food fish, both for their meat (which may be smoked) and for their roe (caviar), which is one of the most valuable fish products in the world. Sturgeon farming is carried out in some Middle Eastern countries, in parts of Europe and the former Soviet Union and in North America (Le Francois *et al.* 2010).

Among the teleosts, the ostariophysans dominate the fresh waters of the world in terms of both numbers of species (about 7500) and individuals, accounting for about two-thirds of all freshwater fish species; they include the minnows, carps, loaches, piranhas, tetras, freshwater catfishes and electric eels. Culture of carps and freshwater catfishes dominates fish farming in fresh waters, and fish culture production as a whole. Although generally considered freshwater fish, about 120 ostariophysan species are marine; for example, the milkfish (*Chanos chanos*) is an important food fish in the Indo-Pacific region where it is farmed in brackish-water ponds and lagoons. The family comprising the carps and carp-like fishes (Cyprinidae) is the largest family of freshwater fishes, with about 2200 species and with its greatest diversity in Eurasia, followed by Africa and North America. Several species are popular as aquarium fishes, including the goldfish (*Carassius auratus*), koi carp (a variety of *Cyprinus carpio*), zebrafish (*Danio rerio*) and other rasboras. The zebrafish is now widely cultivated for use in laboratory-based research on subjects including developmental biology and genetics, toxicology and biomedicine. Box 1.1 gives more details of the species in this large group of teleost fish that are cultured and for which purposes.

The cichlids (Cichlidae) make up another family with many freshwater species (about 1400 species). There are almost 400 species in the Americas, but the great majority of cichlids occur in Africa and a few species are found in the Middle east and on the Indian subcontinent. Several cichlids are popular aquarium fishes; South American species include the freshwater angelfishes (*Pterophyllum* spp.), discus (*Symphysodon* spp.), oscars (*Astronotus* spp.) and convict cichlids (*Archocentrus* spp.), whereas amongst

Box 1.1 Further details of some cultured groups of Ostariophysi

See Tucker & Hargreaves 2004, 2008; Shelton & Rothbard 2006 and http://www.fao.org/figis for details

***Cyprinids*:** Several species of carp are farmed in South-east Asia, on the Indian subcontinent, and in Europe, but there is little interest in carp culture in North America. World-wide, the annual production of cyprinids is about 15–20 million tonnes. The common carp (*Cyprinus carpio*) is farmed in many countries and dominates cyprinid culture in Europe, making up about 64% of the approximately 225 000 tonnes of farmed cyprinids produced in that continent. A variety of cyprinid species, often referred to as Chinese carps, are farmed in large quantities in South-east Asia. These include grass carp (*Ctenopharyngodon idella*), mud carp (*Cirrhina molitorella*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Aristichthyes nobilis*) and *Carassius* spp. (crucian carp and gibel carp). *Carassius* spp. are produced in several Asian countries and in Eastern Europe, but production is low outside China. Similarly, grass carp and bighead carp are farmed in over 20 countries, mostly in South-east Asia, but also in Europe and on the American continent, though fewer than 10 countries report production figures over 1000 tonnes. On the Indian subcontinent, Indian major carps, catla (*Catla catla*), mrigal (*Cirrhina mrigala*), rohu (*Labeo rohita*) and calbasu (*Labeo calbasu*) are farmed, along with some production of Chinese carps. The majority of carp farming takes place in ponds by extensive or semi-intensive methods, and pond-based, semi-intensive polyculture of cyprinids is the norm in many south-east Asian countries.

***Characiforms*:** The majority (about 1300) of characids are South American; some occur in Central America and the southern states of the USA and about 200 species occur in Africa. The order contains many popular aquarium fishes, including the tetras and silver dollars and some of the larger species are important as food fishes in certain South American countries; a few of these, such as *Colossoma* and *Brycon* spp., are farmed for human consumption.

***Siluriformes*:** There are almost 3000 species of catfishes, which mostly inhabit freshwater and as a group have a worldwide distribution, predominantly in South America, south-east Asia and Africa. Freshwater fish farming in the USA is dominated by catfish culture (family Ictaluridae) in the southern states bordering the Gulf of Mexico, with several species and their hybrids being cultured. Catfish farming in the USA is dominated by semi-intensive and intensive pond culture of the channel catfish (*Ictalurus punctatus*). Catfish culture is widespread globally, being practised in several Asian, African and European countries. In these regions, farming tends to be based upon the rearing of native catfish species (families Siluridae, Pangasiidae, Clariidae). In South-east Asia, pangasius (*Pangasianodon hypophthalmus*) farming has undergone explosive growth, driven by a rapid expansion in Vietnam and other countries of the Mekong River basin (Thailand, Cambodia and Laos), but also in Indonesia, Malaysia, Bangladesh, Myanmar (Burma) and China. The development of pangasius farming has played an important role in the socioeconomics of rural communities in these countries, with most of the farmed pangasius being processed for export to markets in Europe, the Americas and countries of the former Soviet Union. Pond culture is the norm for the farming of catfishes, but there is some intensive cultivation of catfish in Europe, carried out in land-based, water re-use tank and raceway systems.

the African cichlids several species within the genus *Haplochromis* have attained popularity with aquarists. In parts of the world, some cichlids, commonly known as the tilapias, are important as food fishes. Tilapia farming has a long history, but has experienced a recent rapid expansion; within the space of two to three decades tilapias changed from being fish that were reared by poor farmers in developing countries for local consumption to being an important export commodity that is traded in global markets. Annual production of farmed tilapia is over 2 million tonnes and rivals or exceeds that of farmed salmonids, so tilapia is now familiar in international fish markets.

All salmonid species, about 70 in total, occur naturally in the northern hemisphere, but several species have been introduced to the southern hemisphere, where they are farmed or form the basis of recreational fisheries. There are both freshwater and anadromous species of salmonids, but some of the anadromous species also have populations that are confined to fresh waters. The farming of salmonids expanded rapidly in the late 20th century, with production reaching 1.5 million tonnes by the turn of the century and expanding further during the early years of the present century. Just over half of the production is Atlantic salmon (*Salmo salar*). Much of the remainder is rainbow trout (*Oncorhynchus mykiss*), global annual production of farmed rainbow trout being about 500 000 tonnes (http://www.fao.org/figis). Traditionally, the farming of salmon and trout has been carried out in Europe and North America, although Chile and Australia have become significant producers in recent years (http://www.fao.org/figis; Shelton & Rothbard 2006; Solar 2009; Le Francois *et al*. 2010). Atlantic salmon and rainbow trout are farmed primarily as food fish, but both species are sometimes used for supplementation to support recreational fisheries. The brown trout (*Salmo trutta*) is reared in several European countries for both food and supplementation. Several species of Pacific salmon, some charrs and whitefish are also reared, either directly for human consumption or for supplementing natural populations.

Representatives from several marine finfish families are also farmed, including sea breams and porgies (family Sparidae), drums and croakers (family Scianidae), sea basses (family Serranidae), the temperate basses (family Moronidae), Atlantic cod and sablefish (Gadidae) and marine flatfishes (families Scophthalmidae, Paralichthydae, Pleuronectidae and Soleidae; Stickney 2000; Tucker & Hargreaves 2008; Le Francois *et al*. 2010; http://www.fao.org/figis). Production of farmed marine species is generally moderate in comparison with the quantities of the major freshwater (cyprinids, freshwater catfishes and tilapias) and anadromous (salmon and trout) species that are produced by farming.

1.2.4 Kinds of culture systems

Extensive and intensive fish culture

Culture systems for finfish aquaculture can be classified on a continuum with extensive systems such as natural ponds that require little management at one extreme and intensive, closed, recirculating systems requiring continuous monitoring at the other (Figure 1.2; Tucker & Hargreaves 2008; Le Francois *et al*. 2010). As increasing control over the rearing environment is exerted by the farmer, culture intensity is said to increase, as does the production capacity of the system. The sophistication of the technology required to develop and operate a culture system is usually higher as intensification increases, though there can be variation even within a given type of culture system. As culture intensity increases, both initial and operating costs, as well as the chances of system failure, tend to rise. When fish are held at high stocking densities, there is greater dependence upon complex equipment and power supplies and a failure in the water supply will rapidly lead to deterioration in water quality, with the risk of death of the fish. Rearing conditions within closed, recirculating systems may be independent of the local climate and there may be strict control over water quality and other rearing conditions, but the risk of failure is increased and the margin of error reduced compared to low-technology systems.

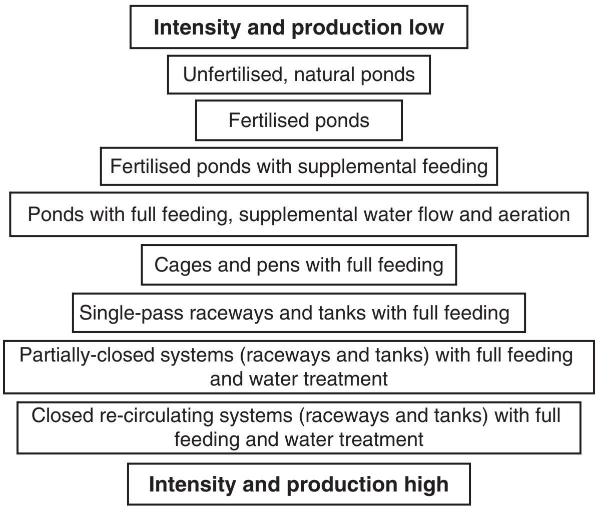

Figure 1.2. Schematic depiction of culture systems used for producing fish, classified in terms of intensity. Reproduced with permission from Le Francois *et al*. 2010.

Although culture systems vary in design and degree of intensification, all fish production systems have the common feature that they require abundant water of correct quality and temperature. Variation in water quality beyond acceptable ranges leads to reduced rates of growth of the fish, distress, increased incidence of disease outbreaks and in extreme cases mortality of the stock. Water characteristics are influenced by factors such as the type of production system, stocking density of the fish and the types and amounts of feed introduced into the system. Ponds, flow-through tanks and raceways rely on different amounts of water exchange and aeration to maintain water quality. When cages (or net-pens) are placed in the sea or lakes, water quality is maintained by the water exchange that results from water currents or tides. In water re-use and re-circulating systems, temperature and water quality parameters such as oxygen, carbon dioxide and ammonia concentrations, and pH are controlled mechanically or biologically (Tucker & Hargreaves 2008; Le Francois *et al*. 2010).

Pond culture

Natural earthen ponds, typical extensive production systems, are dynamic ecosystems under the influence of factors such as weather that are uncontrollable and

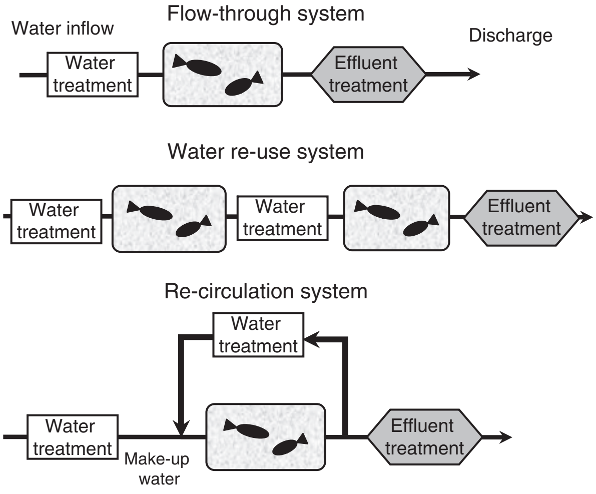

Figure 1.3. Schematic depiction of three water management systems used for producing fish. Reproduced with permission from Le Francois *et al.* 2010.

unpredictable and so are difficult to manage. Although earthen ponds are usually associated with extensive production, intensity of pond production varies depending upon external inputs and the effort expended in pond management. Intensification of pond culture increases from the unfertilized natural pond, through fertilized ponds and ponds with supplemental feeding to ponds with full feeding, aeration and rapid rates of water turnover (Figure 1.2). Pond carrying capacities and fish stocking densities rise as the level of intensification increases. Treatment of ponds with inorganic fertilizers that provide nitrogen, phosphorus and potassium, plant composts or animal manures will enhance growth of phytoplankton and this can lead to 5- to 10-fold increases in fish production relative to unfertilized natural ponds. 'Liming' with calcium compounds is also frequently carried out to regulate water pH and alkalinity (Boyd 1995; Tucker & Hargreaves 2008). In fertilized ponds the fish are wholly dependent upon consumption of natural prey organisms to support their growth. This type of pond culture has traditionally been used for the farming of cyprinids, such as common carp (*Cyprinus carpio*), grass carp (*Ctenopharyngodon idella*) and various species of Indian major and mud carps, for example, *Labeo, Catla* and *Cirrhina* spp.

The food base of the pond may be augmented by adding supplemental feeds, usually formulated from cheap feed ingredients, to supply the fish with additional nutrients and energy. The feeds may be deficient in some vitamins, minerals and other essential nutrients that the fish can obtain by feeding on the organisms present in the pond. In the most intensive form of pond culture, the fish are provided with complete feeds formulated to meet all their nutritional requirements, there is some water renewal in the pond and supplemental aeration is applied should hypoxic conditions arise. Such intensive pond culture is used in the farming of channel catfish (*Ictalurus punctatus*) in the southern states of the USA (Tucker & Hargreaves 2004, 2008).

Tanks and raceways

Land-based culture systems usually use tanks and raceways of various sizes, connected to a water supply and drainage system. These are the rearing units within land-based flow-through (open) and recirculating (closed) culture systems (Figure 1.3; Tucker & Hargreaves 2008; Le Francois *et al.* 2010). Tanks, which may be square, rectangular or circular, are most commonly used in fish hatcheries for the rearing of larvae and juveniles, but may also be used for the on-growing of larger fish to market size. Tanks and raceways are in effect artificial ponds and streams that lack the complex biotic environment of natural systems and allow a great degree of control over the rearing environment. Flow-through systems require large quantities of water that are discharged after passing through the rearing units, whereas in a recirculating system more than 90% of the water may be recycled. In both flow-through and recirculating systems the water is pre-treated before it enters the rearing units; this includes settlement and filtration to remove particles of various sizes, treatment with ozone or UV light to kill disease organisms, heating or cooling and aeration or degassing. Effluent water from flow-through systems is usually treated prior to discharge. This often involves removal of solids such as waste feed and faeces, removal of excess dissolved nutrients and metabolic wastes and treatments to destroy potential pathogens (Figure 1.3). Treatment of effluent is mandatory in some countries where environmental regulations restrict the amounts of wastes allowed for discharge from a fish farm into the recipient water bodies (Tucker & Hargreaves 2008; Le Francois *et al.* 2010).

A raceway is a shallow longitudinal tank extended along the directional axis of the water flow. There is usually a continuous flow of water from one end to the other, adjusted to be sufficient to transport wastes and produce a self-cleaning effect. In a typical raceway, water quality degrades between input and outflow. In cross-flow raceways water is introduced along one side or both sides of the raceway and may be removed either from the opposite side or via a central drainage channel. In series and parallel raceway systems there is usually some re-use of water. The water flows into the raceways by gravity from a header pond and, after passing through the raceways, is discharged into a series of ponds. Here solid and dissolved wastes are removed and, in cases where the treated water is pumped back to the header pond for recirculation through the raceway system, aeration is carried out. The production of fish in raceway systems may be limited by dissolved oxygen and the accumulation of metabolic waste products.

Recirculating systems contain water treatment units that allow a large portion, often about 90%, of the water leaving the rearing units to be reconditioned and reused (Figure 1.3). Dissolved oxygen is the first limiting factor for production within such systems, so oxygen supplementation is required as part of the water treatment process. However, there is also the risk that metabolites and other wastes might accumulate to levels that would compromise fish growth and health. Recirculating systems often incorporate water treatment processes to control dissolved gases, feed waste, faeces and other solids, water pH, dissolved nitrogenous compounds and pathogens (Tucker & Hargreaves 2008; Le Francois *et al.* 2010).

Cages and pens

The terms 'cage' and 'pen' are often used synonymously, but a pen is sometimes defined as a system in which the base is formed by the bottom of the pond or the seabed. Pens of this type are used for the rearing of fish in several South-east Asian countries. Cages are enclosed by mesh screens on both the sides and the bottom and are usually open at the top to enable access for feeding, removal of dead fish and debris and for harvesting. Cages are open systems in contact with the surrounding water body, with water currents ensuring renewal of water and removal of metabolic wastes and faeces. Cages are relatively easy to construct and the cage culture of fish may represent a low-input farming practice with a high economic return. However, cages are vulnerable to natural hazards such as strong tides and storms and cage sites may also be vulnerable to deterioration in water quality resulting from oil spills and chemical pollution, for example (Beveridge 2004; Tucker & Hargreaves 2008).

Cage aquaculture may be extensive, semi-intensive or intensive depending upon the level of feed input. Extensive cage culture, in which the fish are reliant upon natural foods carried into the cage on currents, is generally restricted to highly productive tropical lakes, reservoirs and sewage-fed streams and rivers. This type of cage culture is used in the Philippines, China and Indonesia for farming some species of cyprinids and tilapias. Semi-intensive cage culture, in which fish are provided with low-protein feeds made from locally-available plants or agricultural by-products to supplement the intake of natural food organisms, is also largely restricted to tropical fresh waters, where it is a common method of rearing fish. Herbivorous, detritivorous, omnivorous and planktivorous tilapias and cyprinids are widely grown in this way. Intensive cage culture is the commonest method for farming high-value carnivorous species such as salmonids and a range of marine species such as the sea basses (*Dicentrarchus labrax* and *Lates calcarifer)* and sea breams and porgies (Sparidae). In intensive cage culture the fish are provided with high-protein, nutritionally complete feeds and stocking densities are generally much higher than in extensive and semi-intensive culture (Beveridge 2004; Tucker & Hargreaves 2008).

1.3 INTRODUCING THE SPOTLIGHT SPECIES

Throughout this book a small number of important culture species, or species groups, will be brought into the spotlight, with a focus on their biological characteristics and behaviour. These species have been selected as examples from the groups of fish that are reared for different purposes, including those reared directly as food for human consumption, for supplementation or conservation purposes, as ornamentals and for use in research. The selected species are introduced here, with brief presentations of their general biology and commercial importance.

1.3.1 Fish farmed for the table

Concentrating on finfish species that are produced for food in relatively high volume, the selected representatives are a cold-water and anadromous species (Atlantic salmon), a cool-water and freshwater or anadromous species (rainbow trout), a temperate and marine species (European sea bass) and a warm-water species found in fresh water (Nile tilapia).

Atlantic salmon (Salmo salar)

The Atlantic salmon is one of five representatives of the genus *Salmo* (family Salmonidae). It has its natural geographic distribution on both sides of the Atlantic Ocean in the northern hemisphere. The Atlantic salmon is usually anadromous, although there are some non-anadromous freshwater populations. Both within and among populations there are differences in the length of time spent in fresh water prior to migration to sea (following the parr–smolt transformation), in the time spent at sea, age-at-maturity and post-spawning survival (Klemetsen *et al.* 2003; Solar

2009). Atlantic salmon usually mature after one to three winters at sea, but some of the male salmon mature (as parr) without having undertaken a migration to the sea. This means that the salmon show a wide range of ages and sizes at maturity and individuals with markedly different ages at maturity may occur within the same population. Salmon spawn in fresh water during the autumn and early winter, with the sea-run maturing adults, which generally weigh 1–6 kg, entering fresh water in summer, a few months before they will spawn (Pennell & Barton 1996; Klemetsen *et al*. 2003). The eggs, which are relatively large, are laid in a series of nests (called a redd) excavated in coarse sand or gravel on the bed of a relatively swift-flowing river. The eggs incubate over winter and hatch in spring. The fish are 15–25 mm in length at hatching and have a large yolk sac that acts as a source of nourishment when they are still in the gravel redd. When most of the yolk has been used the young fish, called alevins, emerge from the gravel (swim-up phase) and start to feed on small planktonic organisms, and then they expand their diet to include insect larvae and other organisms that make up the aquatic drift (Gibson 1993).

Life in fresh water, during which the fish are called parr, can last from 1 to 8 years, after which the majority of the fish undergo the parr–smolt transformation in preparation for migration to the sea. Some male parr do not undergo the parr–smolt transformation, but mature instead, so there are more females than males amongst the fish that migrate to sea as smolt. The smolts usually migrate downstream and enter seawater during May or June. During the marine phase of their life, Atlantic salmon feed predominantly on crustaceans and small, pelagic fish. Some Atlantic salmon return to their native rivers after spending one winter at sea; these fish are known as grilse and are usually 1.5–4 kg in body weight. In some populations the majority of fish return as grilse, but most salmon return to fresh water as maturing individuals after two or three winters at sea and some may remain in the sea for up to 5 years (Pennell & Barton 1996; Klemetsen *et al*. 2003). The Atlantic salmon is a fish of considerable economic importance and introductions to Australia (Tasmania) and Chile have given rise to salmon aquaculture in these two countries. At present, salmon are farmed in northern Europe, Tasmania, Chile and North America, particularly Canada, with annual aquaculture production exceeding 1 million tonnes. Rearing methods are generally intensive and similar wherever salmon farming is practised; thus egg incubation usually takes place in trays with flowing water, start-feeding of alevins, rearing of parr, and smolt production in tanks supplied with abundant fresh water, followed by on-growing to market size (3–7 kg) in sea-cages (Pennell & Barton 1996; Stead & Laird 2002; Solar 2009; Le Fancois *et al*. 2010).

Rainbow trout (Oncorhynchus mykiss)

The Pacific salmons and trouts (genus *Oncorhynchus*, family Salmonidae) are anadromous, occasionally freshwater, fish that are naturally distributed in the North Pacific region. The natural distribution of the rainbow trout extends from Baja California through Alaska and the Aleutian Islands in the Americas, to the Kamchatka Peninsula and rivers that drain into the Okhotska Sea on the Asian side of the Pacific Ocean (Pennell & Barton 1996). Although the rainbow trout has its natural distribution in countries that border the North Pacific it has been introduced to so many other regions of the world that it is now virtually cosmopolitan (Lever 1996; Pennell & Barton 1996; Solar 2009). The successful introduction of this species to many areas outside its native range results from the fact that the rainbow trout is relatively hardy, is highly esteemed as a sport fish, is considered a good food fish and adapts well to culture. There is widespread cultivation of rainbow trout, either directly for human consumption or for stocking purposes, and it is a valuable commodity in many countries with a temperate climate.

Rainbow trout are usually considered to be freshwater fish, but many populations have some fish that are anadromous, called steelhead because they develop a silvery body colour. Steelhead trout spend 1–2 years in fresh water and then migrate to the sea where they spend 1.5–3 years before migrating back to fresh water to spawn. They do this during the spring when water temperature rises to 6–7 °C, with the eggs being deposited in gravel redds in a stream-bed. Depending upon her size, age and whether or not she is anadromous, a female rainbow trout produces 300–3000, relatively large eggs that hatch after about 40 days at 8 °C to give young that are about 15 mm in length. The young fish remain in the redd until their yolk is almost exhausted and then emerge and start to feed on small zooplanktonic organisms. As they grow the young fish broaden their diet and eat small aquatic insects, and then graduate to terrestrial insects and small fish. The fish generally mature at an age of 3 years, lifespan is 4–10 years and size may vary from 200 g to 3–5 kg, depending upon whether the fish are of the freshwater form and live in a small stream, or are of the anadromous, sea-going steelhead form. Most rainbow trout farming is carried out in fresh water in ponds, tanks and raceways, with the production of fish weighing 300–350 g and 600–750 g tending to dominate, but there is some sea-cage culture to produce larger fish weighing 2.5–3.5 kg.

The annual global production of rainbow trout is about 500 000 tonnes, with the major trout-producing countries being France, Italy, Spain, UK, Norway, Denmark, Chile, USA and Japan (Pennell & Barton 1996; Stickney 2000; Tucker & Hargreaves 2008; Le Francois *et al.* 2010).

European seabass (Dicentrarchus labrax)

The European seabass, one of six members of the family Moronidae, is primarily a marine fish, but it is sometimes found in brackish- and fresh water; its habitats include coastal waters, estuaries, lagoons and rivers. It is found in the waters in and around Europe, including the eastern Atlantic Ocean, from Norway in the north to Senegal in the south, in the Mediterranean Sea and in the Black Sea (Pickett & Pawson 1994). The European seabass is highly regarded as a food fish, particularly in Mediterranean countries, and the fish fetches high prices in international markets. The fish can tolerate a wide range of temperatures and salinities, but although it is often found in water of low salinity, spawning takes place in water of salinity close to that of full strength seawater.

Spawning takes place between December and March in the Mediterranean basin, but somewhat later (March–June) towards the northern limits of the species distribution, with spawning and egg development usually taking place at 9–15 °C. During the spawning season a large female will produce several hundred thousand small eggs that hatch after a few days to give 4–4.5 mm larvae. A few weeks after hatching young juveniles start to congregate close to shore and migrate into warm estuaries, bays, back-waters and harbours. Here they form shoals and feed on small crustaceans. As they increase in size they also include larger crustaceans, polychaetes, cephalopods and small fish in their diet. The male European sea bass may mature at 2–3 years of age, females usually one year later and most will be mature by the time they reach an age of 4–5 years (Pickett & Pawson 1994). The fish can reach an age of 30 years, and large individuals can weigh up to 10 kg.

The fish has considerable importance in Mediterranean aquaculture, with Greece, Turkey, Italy, France, Spain, Croatia and Egypt all having many European seabass hatcheries and on-growing farms. On-growing is generally carried out in sea cages, but some fish are held in lagoons and land-based culture systems are sometimes used for the intensive rearing of the species. Under farming conditions the fish are most often fed dry pellet feeds that are relatively rich in both proteins and lipids. Farmed European seabass are usually marketed at a size of 250–450 g, and the time required to reach this size is 20–24 months in the cooler regions of the western Mediterranean, but is reduced to 14–15 months in the warmer waters along the African coastline (Moretti *et al.* 1999; Theodorou 2002; Le Francois *et al.* 2010). Farmed populations often have a high percentage of males, the result of a pronounced environmental influence on sex differentiation (Chapters 2 and 10). Male-biased populations are undesirable because the males grow slower and mature earlier than do females. Under farm conditions most males mature at an age of 2 years, when they are about 300 g in weight, but some males mature during their first year of life, when they weigh no more than 50–70 g (Moretti *et al.* 1999; Theodorou 2002; Le Francois *et al.* 2010).

Nile tilapia (Oreochromis niloticus)

The Nile tilapia (family Cichlidae) is distributed throughout tropical and subtropical Africa, in the Nile River basin and in the Volta, Gambia, Senegal and Niger River watersheds of West Africa. It is also native to a number of large lakes and their feeder rivers and streams (Beveridge & McAndrew 2000; Lim & Webster 2006). Several natural populations are under threat as a result of habitat destruction, overfishing or the introduction of exotic and non-native species, such as the predatory Nile perch (*Lates niloticus*). The Nile tilapia has been introduced to many areas outside its natural range, both on the African continent and further afield; for example, it was introduced to the USA via Brazil and there have been introductions to at least 60 countries. Farming of Nile tilapia is carried out in over 50 countries, with the major producers being China, Egypt, Philippines, Indonesia, Thailand and Brazil. In some areas where it has invaded natural waters it is considered a pest (Lever 1996; Beveridge & McAndrew 2000; Lim & Webster 2006; Le Francois *et al.* 2010).

The Nile tilapia is a mouth-brooder, with the female incubating the eggs within her buccal cavity. The optimum spawning temperature is 25–30 °C. There is sexual dimorphism, with the male being larger than the female, and age and size at sexual maturation varies according to growth conditions. For example, in the large lakes of Eastern Africa the fish may mature at an age of about 1 year, and 350–450 g, but when held in farm ponds fish of the same populations may mature after 5–6 months at a size of about 200 g. Depending upon her size, a female will produce 50–2000 medium-sized eggs at each spawning, the eggs hatch after 2–3 days and remain within the buccal cavity of the female for an additional 6–8 days until the young fish have exhausted their yolk supply. This period of mouth-brooding, which lasts approximately 10 days, is followed by a short nursing period, during which the female continues to protect her offspring even though they are swimming freely and feeding. The complete reproductive cycle lasts 4–6 weeks and a female may spawn 6–11 times per year under suitable environmental conditions (Beveridge & McAndrew 2000; Lim & Webster 2006).

The Nile tilapia feeds on a wide variety of foods, including detritus and aquatic plants, plankton, small aquatic invertebrates and fish larvae. When farmed, the fish may be reliant on natural prey organisms in the farm pond or they may be provided with formulated pellet feeds. Nile tilapia are tolerant of changes in many environmental factors, including temperature, dissolved oxygen, ammonia and salinity, so they are extremely hardy and are easier to rear than other commonly-cultured fish species. Farming of Nile tilapia is carried out using a variety of methods, ranging from extensive pond culture to intensive farming in land-based, re-circulation systems. There has been some selective breeding to develop stocks that perform well under certain culture conditions; the GIFT (Genetically Improved Farmed Tilapia) programme is probably the most ambitious, and best-known example of the genetic improvement efforts (Beveridge & McAndrew 2000; Lim & Webster 2006; Le Francois *et al*. 2010).

1.3.2 Fish farmed for supplementation programmes or conservation

Several freshwater, anadromous and marine fish species are produced for supplementation purposes on a variety of scales. Some operations may be of limited proportions. For example, an individual farmer or small co-operative may produce fish for the stocking of ponds or lakes that are to be used as a source of income from fee-fishing and put-and-take fisheries and angling societies may operate hatcheries for the production of fish for stocking into lakes, canals and river reaches. These operations often involve the production of salmonids, such as rainbow trout, brown trout (*Salmo trutta*) or brook charr (*Salvelinus fontinalis*), sunfishes (*Lepomis* spp.) and basses (*Micropterus* spp.) of the family Centrarchidae, or a variety of so-called coarse fishes, such as the common carp (*Cyprinus carpio*), tench (*Tinca tinca*) and pike (*Esox lucius*). Larger-scale production may be carried out under the auspices of district or regional authorities for supplementing fish populations in regulated water-courses, or in support of local fisheries and sea-ranching operations. An example of this type of activity is the production of Pacific salmon species on the western seaboard of the USA for stocking dammed rivers and in Japan for sea-ranching. The Pacific salmons are considered in some detail throughout this book. Captive rearing may also be carried out to replenish populations that do not reproduce well in the wild, or to re-stock waters in which fish populations have been eliminated or drastically reduced in size due to severe, but transient, habitat deterioration. Finally, some species have been taken into captivity as a conservation measure in an attempt to prevent extinction of threatened local stocks, or in some cases species. The captive rearing of sturgeons is, in part, designed to fulfil this role, as is the cultivation of several species of seahorses. The seahorses are another group that will be a focus of attention throughout this book.

Pacific salmons (Oncorhynchus spp.)

Salmon with natural distributions in waters that drain into the Pacific Ocean are members of the genus *Oncorhynchus*, which also includes a number of trout species (Ruggerone *et al*. 2010). The ranges of the different species extend from the Bering Sea, southward down Asian coastal areas to Japan and Korea in the west and along the Alaskan, Canadian and US coasts to the state of California on the eastern side of the Pacific basin. Pacific salmon are an important economic resource for countries that border the North Pacific Ocean. Salmon of several species are fished in coastal waters by Canada, USA, North and South Korea, Japan and Russia and there is also a more limited high-seas fishery (Groot & Margolis 1991; Pennell & Barton 1996; Stouder *et al*. 1997; Quinn 2005). Seven species of Pacific salmon are recognized; sockeye (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*), chinook (*O. tshawytscha*), coho (*O. kisutch*), masu (*O. masou*) and amago or biwamasu (*O. rhodurus*). Natural reproduction of the first five species has been recorded on both the Asian and North American side of the Pacific Ocean, but spawning populations of the masu and amago salmon only occur in Asia.

Pacific salmon spawn in gravel beds in rivers, streams, or along lake-shores and they generally migrate to sea after a short freshwater life. Amongst the species of Pacific salmons there is considerable variation in the time spent in fresh water prior to parr–smolt transformation, and also in the length of residency in the marine environment before they mature and return to fresh water to spawn. For example, pink and chum salmon normally migrate downstream to the sea within 2–3 months after hatching, whereas young sockeye salmon may spend up to 5 years in fresh water before migrating to the sea. Pacific salmon are widely distributed in the North Pacific Ocean and Bering Sea during their marine residency and most perform extensive migrations while at sea. Upon maturation, after 1 to 7 years at sea depending upon species, the fish usually return to their natal rivers to spawn. Spawning occurs during autumn and early winter, after which the fish usually die; in other words, they are semelparous. Amago and masu may be exceptions because some fish spawn more than once. Pacific salmon are distinctive because of their semelparity and also because they produce relatively few, large eggs compared with other fish species (Groot & Margolis 1991; Pennell & Barton 1996; Quinn 2005). The number and size of eggs produced varies among species, among populations within a given species and also among females within a population, depending on their size and age, but rarely exceeds a few thousand. The young fish are generally about 20 mm in length at the time of hatching and they survive on the yolk sac for some time before starting to feed. The food eaten reflects the types and abundances of prey organisms present in particular habitats. Insects and insect larvae are the main prey of juvenile salmon in streams and rivers, zooplankton, insect larvae and small fish are eaten by lake-dwelling Pacific salmon, and large zooplanktonic organisms, fish and squid are consumed by the larger salmon when they are in the ocean (Groot & Margolis 1991; Pennell & Barton 1996; Quinn 2005).

Populations of several Pacific salmon species are under threat of extinction because of habitat loss, due to water diversion, damming and urban development, or habitat deterioration as a result of logging and the discharge of industrial and agricultural effluents. Restoration programmes have been initiated in several areas in an attempt to counteract these declines and to conserve these at-risk populations and often include a combination of watershed management and release of artificially-propagated fish (Groot & Margolis 1991; Pennell & Barton 1996; Stouder *et al*. 1997; Quinn 2005; Araki *et al*. 2008; Nielsen & Pavey 2010). As such, the vast majority of the cultivation of Pacific salmon is for supplementation of existing populations, but there is also farming of some of the species for stocking water-courses that lack natural populations, for sea-ranching, and for sea cage culture of fish for human consumption. For example, there is some sea cage culture of chinook salmon in Canada and both Chinook and coho salmon have been introduced into Chile, where they are farmed as food-fish.

Seahorses (Hippocampus spp.)

The seahorses, which along with the pipefishes make up the family Syngnathidae, are represented by almost 35 species of relatively small (3–25 cm in length, depending upon species) marine fishes within the genus *Hippocampus.* The name seahorse arises because of the equine appearance of the head. Seahorses are found in shallow tropical and temperate waters throughout the world, where they prefer to live in sheltered areas such as seagrass meadows, in amongst the submerged roots of mangroves and in the protected areas of coral reefs (Koldeway & Martin-Smith 2010; http://seahorse.fisheries.ubc.ca). Seahorses swim in an upright position using undulations of the dorsal fin. The small pectoral fins located close to the head are used for steering and in making fine positional adjustments. Seahorses are incapable of swimming rapidly and the fish often attach themselves to strands of seagrass, algae or mangrove roots by means of their flexible, prehensile tail. When attached to underwater vegetation they are well-camouflaged as a result of their grey–brown to greenish body patterns. Seahorses have elongated snouts, but very small mouths and adopt suction feeding to capture zooplankton, such as small crustaceans and fish larvae. The eyes of the seahorses can move independently, which may aid in both locating prey and the detection of predators. The males tend to remain on small home ranges, whereas the females range more widely. Prior to spawning a pair may engage in courtship for several days and then the female deposits a clutch of eggs in the brood pouch of the male. The male fertilizes the eggs as they are being transferred to his brood pouch and the fertilized eggs eventually become embedded in the pouch wall where they are held during incubation. The gestation period is generally about 2–4 weeks and the number of offspring produced by most species is 100–200 (Koldeway & Martin-Smith 2010). The small seahorses are expelled from the brood pouch by a series of quite powerful muscular contractions and after release of the offspring from the pouch the period of parental care is at an end. Some species of seahorses are bred in captivity to supply the aquarium trade and others are reared as a conservation measure. When held in captivity, the fish may be fed on live zooplankton, such as brine shrimp (*Artemia salina*), or frozen crustaceans, such as copepods (Copepoda) and mysids (Mysidacea; Koldeway & Martin-Smith, 2010; http://seahorse.fisheries.ubc.ca).

1.3.3 Fish farmed as ornamentals and for research

Many small, brightly coloured warm-water teleosts have become popular with aquarists. Most of these aquarium species are small carp-like fishes (Cypriniformes), characins (Characiformes), tooth-carps (Cyprinodontiformes) and cichlids (Cichlidae) that are displayed in tropical, freshwater aquaria in homes and work-places around the world. A few of these species, including the goldfish (*Carassius auratus*), zebrafish (*Danio rerio*) and guppy (*Poecilia reticulata*), have also been widely adopted for use in biological and medical research. These species are used for the investigation of problems relating to neurophysiology, sensory physiology, the regulation of feeding, reproductive and developmental biology, genetics and behavioural ecology. The zebrafish and guppy are two of the species spotlighted for attention in this book. The koi carp is larger than most other freshwater ornamentals and is the third freshwater fish considered here. Finally there are a few tropical marine species that are cultured for the aquarium trade; amongst these the clownfishes are the selected representatives for more detailed analysis.

Koi carp (Cyprinus carpio)

Koi carp is the name given to some aberrant, genetically selected forms of the common carp (*Cyprinus carpio;* family Cyprinidae). Koi is the Japanese for carp and it might be more correct to call these fish by their Japanese name *nishikigoi*. Being derived from the common carp, koi carp are larger than most other ornamental species and are usually kept in outdoor ponds in parks and gardens. The koi was originally developed from the common carp in China and was later imported into Japan, where it became popular as an ornamental species. To-day koi have a world-wide reputation and can command very high prices from devotees. Most koi are still produced in Japan, but there is increasing interest in many countries in selective breeding of these fish. A variety of colour patterns have been developed and these are classified according to a Japanese system devised for show purposes, the names often reflecting the history of the particular variety concerned or its place of origin. The different varieties combine a single body colour with superimposed patches of white, black, red, yellow, blue and orange, together with variations in scale patterns. Newer developments include the introduction of varieties with particular fin shapes and body morphology, as in veiltail and hifin koi. In order to be seen to advantage, the fish must be attracted close to the water surface, so they are usually fed on floating flake and pellet feeds, sometimes supplemented with pieces of fruit and vegetables. Koi carp are hardy, being relatively tolerant of low dissolved oxygen and a wide range of temperatures, although they thrive best at 20–25 °C. At spawning the females produce several thousand small eggs that develop a sticky outer coat and become attached to underwater plants. The eggs hatch after a few days into larvae that are about 5 mm in length and that start to feed on small planktonic organisms when they are 6–7 mm. The koi may not breed 'true', so many of the young fish and juveniles will usually be culled, because they do not develop the colour pattern considered desirable by the producer and potential purchasers. The koi carp is often long-lived and there are reports of fish that have achieved ages of 100–200 years (Purdom 1993; Billard 1999).

Zebrafish (Danio rerio)

The zebrafish or zebra danio is a small (4–5 cm), distinctive and brightly-coloured, rasbora (family Cyprinidae). It is native to the fresh waters of India and Bangladesh, where it is found in vegetation-rich, still or slow-flowing waters, such as streams, canals, ditches, ponds and rice fields. It is a popular aquarium fish and spawns readily in captivity, scattering the eggs amongst underwater vegetation. Although the fish can tolerate a wide range of temperatures, the water must be over 24 °C, and ideally 28–29 °C, for spawning to take place. Females can lay clutches of a few hundred eggs at 2–3 day intervals, the eggs hatching after 2–3 days. Zebrafish larvae are quite adept at swimming by day 4 after egg fertilization (dpf), and they readily capture prey by 5–6 dpf. In the wild, zebrafish feed on zooplankton and small insects, but in captivity they are usually given flake food or *Tubifex* worms. The fish generally have a life-span of 2–3 years. A prominent social behaviour of zebrafish is shoal formation (Chapter 8) and shoaling preferences are determined at a young age. The ease with which the zebrafish can be raised in captivity, coupled to its short generation time of 3–4 months, has led to it being adopted as a model system in a number of biological disciplines (Westerfield 2000; Detrich *et al.* 2004). The zebrafish was first used in studies of genetics and then became popular for the study of developmental biology, because the embryos and larvae are transparent until about 6 dpf, so organogenesis and tissue differentiation are easily observed. A large number of zebrafish mutants, with a wide range of phenotypes, have been isolated and described, with several of these being used for research purposes. Recently, much information about the species has been made accessible (www.zfin.org) and the zebrafish is now widely used in biomedical research, including neurophysiology, in ecotoxicology and in studies of behavioural ecology (Lieschke & Currie 2007; Spence *et al.* 2008).

Guppy (Poecilia reticulata)

The guppy, a live-bearing toothcarp, is one of about 300 species within the family Poecilidae, most of which occur in tropical and subtropical regions of the Americas. The guppy is native to Trinidad, Barbados and many other Central American islands and is also found in Venezuela, Guyana and northern Brazil. It has been introduced to many tropical and subtropical regions as a controller of the larval stages of malaria-carrying mosquitos (Lever 1996). In its native habitat it lives in fresh and brackish water and can be found in streams, ditches, small canals and drainage channels and pools. The guppy will eat a wide range of foods, including freshwater algae, insect larvae, small crustaceans and fish eggs and larvae, and it is sometimes cannibalistic. Wild male guppies, which grow to about 3 cm in length, have a dull olive-green or brown background colour with some coloured spots and the body sides shimmer with metallic greens and blues. The colour patterns of the males are highly varied, not only between populations across the species' geographic distribution range, but also within populations. This variability attracted the attention of geneticists, and made the guppy an early model species for the study of inheritance mechanisms. The guppy is still widely used in genetics research and also has a central place in studies of evolutionary ecology and fish behaviour (Purdom 1993; Magurran 2005).

The attractive appearance of the male fish, along with the ease with which the species can be reared in captivity, resulted in the guppy becoming a very popular aquarium fish following its introduction to Europe by the Reverend R.J.L. Guppy in 1866. In the intervening years aquarists have produced a wide variety of forms that differ in colour patterns and tail fin morphology and the guppy is now probably the most popular tropical aquarium fish in the world (Purdom 1993; Lever 1996). In contrast to the males, the females are rather dull in colour, being grey dorsally and lighter ventrally. Females grow to about twice the length of the males, reach sexual maturity at an age of 3–4 months and may survive for 5–6 years in well-tended aquaria. The guppy is a live-bearer and the male has the third, fourth and fifth rays of his anal fin elongated to form a copulatory organ, the gonopodium, that is used to transfer a spermatophore, a gelatinous ovoid structure that contains large numbers of sperm, to the cloaca of the female. The release of sperm from the spermatophore is slow and a female can produce several litters of offspring, often 6–8, following a single mating. The eggs are fertilized and are incubated within the ovarian cavity. After the female guppy has been inseminated a dark area near the anus increases in size and darkens to form the gravid spot. The gestation period is generally 21–35 days, litters being produced at 4–5 week intervals at 20–25 °C, but guppies prefer water temperatures of about 27 °C for reproduction. Just before birth, the eyes of the young fish may be seen through the translucent skin of the abdomen of the female. At birth the protective envelope that surrounds the embryo bursts and the young fish is released. Litters range in size from 10–100, but usually around 30 offspring are produced in a litter. The young are capable of swimming from the moment of birth and they start to feed almost immediately. They are able to feed on small waterfleas (*Daphnia* spp.), *Artemia* nauplii and finely ground flake foods.

Clownfishes (Amphiprion spp.)

The clownfishes, or anemonefishes, are a group of about 27 species of relatively small (10–18 cm in length, depending upon species) damselfishes (family Pomacentridae) of the genus *Amphiprion.* They occur on coral reefs in coastal areas of the Indo-West Pacific region. They are called clownfishes because they have a rather garish, brightly-coloured mottled appearance that resembles the dress of a circus clown, or harlequin. The fish associate with and usually live amongst the tentacles of a large sea anemone (Anthozoa, Cnidaria), which they defend, remaining with a single host throughout life and rarely moving more than a few metres away from the host (Spotte 1992; Tucker 1998). The relationship between the clownfish and the anemone (from which the fish get their alternative name) is considered a symbiotic and mutualistic one, because the fish receives protection by hiding within the stinging tentacles of the anemone and may also obtain some food by taking prey captured by the anemone. In return, the clownfish remove debris and parasites from the anemone, attack small fish that may approach the anemone to damage its tentacles and the nitrogenous excretory products of the fish may stimulate the growth of symbiotic algae in the tissues of the anemone. Anemones that have clownfishes associated with them grow faster, reproduce more frequently and suffer less damage than do anemones that lack symbionts.

Clownfishes are sequential, protandrous hermaphrodites (Chapters 2 and 10), starting life as males and later changing sex to become females. They usually live in small groups comprising two large and several small individuals. Only the two largest fish within a group are sexually mature; the largest fish is a mature female, the next largest is a mature male and all the other fish are immature males. Although the small fish may be almost as old as the two largest fish, the behavioural dominance of the mature pair prevents the immature males from growing larger and maturing. When the female dies, the mature male changes sex to become female and one of the immature males, generally the largest of these, increases in size and matures to take over the role as the mature male within the group. Female clownfish lay their eggs on the coral beneath the anemone and when the eggs hatch, some 6–10 days later, the larvae enter the plankton and drift away from the anemone inhabited by their parents. When they have grown large enough to settle out of the plankton, the young fish are attracted to reefs and anemones and by chemical signals secreted by other clownfishes, but are repelled by the scent of close relatives (Dixson *et al.* 2008; Munday *et al.* 2009).

This means that the young fish will not settle on the same anemone as family members, so the clownfishes associated with a particular anemone are not closely related to each other and inbreeding is avoided. In the wild, clownfishes feed on a mixture of algae, small molluscs and crustaceans, but in captivity are often fed on flake food, small pellets, or live or frozen zooplankton. Clownfish were the first species of ornamental marine fish to be bred in captivity and they are currently raised for the marine aquarium trade by a small number of farmers, particularly in the USA (Spotte 1992; Tucker 1998).

1.4 ABOUT BEHAVIOUR

The previous sections have dealt with the first topic in the title of this book, namely aquaculture. The descriptions of the spotlight species include information on topics such as what the fish eat, how they eat it, how much they move about and how they breed. These are aspects of the second topic in the title, namely behaviour, which is discussed in more detail in this section.

1.4.1 What behaviour is and why biologists are interested in it

The term 'behaviour' refers to what an animal does or the movements or actions it makes in response to external or internal stimuli. As discussed in Chapter 3, animal behaviour is difficult to study because it is ephemeral, usually leaving no trace once an action has been performed, because it is readily modified by past and present circumstances and because its causes and consequences are complex. Nevertheless, it is important to understand why animals behave as they do, because it is through its behaviour that an animal interacts with and adapts to its environment, providing a link between physiological and ecological events. For example, when a three-spined stickleback (*Gasterosteus aculeatus*) encounters a potential predator such as a pike, it stops feeding, raises its protective spines and starts cautiously inspecting the larger fish. Depending on circumstances, it may then move slowly away from the predator, possibly to join a group of other sticklebacks, or may escape rapidly to shelter. These responses are accompanied by striking physiological changes (Bell *et al.* 2007), but the key responses are behavioural. On a larger spatial and temporal scale, fish movements are often finely tuned to local temperature regimes. For example, European seabass move horizontally and vertically through the seas tracking water of 10 °C; this is the optimal temperature for maturation (Metcalfe *et al.* 2008), so the behavioural response to water temperature helps to determine patterns of reproduction. Understanding behaviour is also important from an applied perspective. For example, fish are very sensitive to variation in water quality and behavioural changes are among the first visible responses to adverse conditions, so monitoring fish behaviour can provide a valuable bio-indicator and early warning of, for example, water-borne pollutants. Three-spined sticklebacks form larger shoals when exposed experimentally to certain pollutants (Wibe *et al.* 2002); this may be because the pollutants impair the fishes' ability to escape, increasing their predation risk and causing them to seek safety in numbers (Chapter 8). Male three-spined sticklebacks exposed to endocrine-disrupting, oestrogenic chemicals show reduced aggression compared to control fish (Bell 2002). Both these behaviour patterns are conspicuous and relatively easy to monitor, so could provide useful bio-indicators for such pollutants.

1.4.2 Some basic behavioural biology

Researchers from a number of disciplines, including psychologists, veterinarians, anthropologists and biologists, are interested in behaviour. The modern approach to the biological study of behaviour has a number of special features highlighted by one of its Nobel Prize-winning founding fathers, Niko Tinbergen, in his book *The Study of Instinct* (1951). Tinbergen stressed the fact that as far as possible animals should be studied in natural conditions and that a complete understanding of what animals do can only be achieved when studies of the causes and development of behaviour are integrated with studies of its evolutionary history and consequences for Darwinian fitness. This section reviews briefly the picture that has emerged from this multi-faceted approach to the study of behaviour, as a background to consideration of specific behavioural systems covered in later chapters.

The causes of behaviour

One strand of research into the biology of animal behaviour involves investigating the mechanisms that control it, including the stimuli that determine whether or not a particular action is performed and how these stimuli interact with the internal state of the animal concerned.

As described in Chapter 2, fish are able to detect stimuli in a number of different modalities and their role in the control of specific behaviour patterns is considered in some detail in later chapters. In general terms, stimuli may come from the animal's non-social environment, for example water temperature and chemical and visual cues arising from potential food. Stimuli may also come from the social environment, such as the sight, sound or smell of conspecifics. Broadly speaking, such stimuli may either increase the chances that an animal will perform a particular action or they may inhibit it. Whether or not a given behaviour is performed at a given time depends on the combined action (positive and negative) of the stimuli impinging on the animal. For example, among the amino acids, cysteine stimulates feeding in many fish, whereas arginine inhibits feeding (Kasumyam & Doving 2003; Chapter 6); whether a food item containing both chemicals is eaten will depend on their relative proportions. Considering stimuli from the social environment, when two male cichlid fish (*Cichlasoma centrarchus)* fight they make sounds by grinding their pharyngeal teeth together. Short sounds with long gaps stimulate listening rivals to attack, but long, rapidly repeated sounds inhibit attack (Chapter 9). At the same time, larger males are less likely to be attacked than smaller ones. Whether a male *C. centrarchus* gets into a fight with a particular rival depends on the balance between such attack-eliciting and attack-inhibiting cues.

The effects of external stimuli provide just one component of the mechanism that controls behaviour, because animals do not always react identically to the same stimulus or set of stimuli. For example, depending on the time that has elapsed since its last meal, a fish may bite vigorously at or ignore identical food items; such altered responses relate to changes in internal state. At a certain level of knowledge, behavioural biologists often find it useful to explain such changes in responsiveness in terms of hypothetical entities at a behavioural level. For example, they might ascribe changes in response to food to differences in motivational state (hunger) and try to deduce the nature of such differences from behavioural evidence. In the case of feeding, many cases of altered responsiveness to food can be explained in physiological terms (Chapter 7) and the motivational concept of hunger may soon become redundant. For more complex behaviours, especially those involving other animals, much less is known about the underlying physiological processes. In the case of aggression, for example, during the course of a fight how one fish responds to the sight and sound of a rival can change dramatically, from attacking to fleeing. The nature and timing of such changes depends on many features of the two combatants, including their past history and current nutritional state, as well as on events occurring as the fight progresses. Although something is known about the neuro-endocrine processes that accompany such changes (Chapter 9), the concept of aggressive motivation is still a useful way of conceptualizing the alterations taking place inside the animals concerned. Understanding the mechanisms that control behaviour is clearly important for fish culture, telling us, for example, what makes a fish eat a particular food item at a particular time and why one fish chooses to attack its companions.

How behaviour develops

An important and challenging area of behavioural research concerns the way in which behaviour develops as the fertilized egg becomes a free-living individual that grows and matures into an adult. This involves, amongst other things, the sequential expression of the genes that an individual inherits from its parents. Under the influence of changing patterns of gene expression, sense organs, nervous system, endocrine glands and muscles develop; in other words, the young animal acquires the machinery for behaviour. Provided it lives in broadly favourable conditions, these systems develop routinely and will be at work in cases when animals show normal, species-specific behaviour without having had the opportunity of observing other animals. For example, juvenile Atlantic salmon reared from hatching on artificial feed and then offered a choice of food types show similar prey preferences in terms of colour and shape to those of their wild counterparts (Chapter 5). Male three-spined sticklebacks raised in isolation with no opportunity to interact with other fish build nests when they come into breeding condition and display species-typical aggressive behaviour when they encounter a rival male (Wootton 1984). Genetic differences between animals can alter developmental processes, resulting in individual differences in the mechanisms that underpin behaviour and in the behaviour itself. For example, interspecific crosses between goldfish, which find the amino acid proline aversive, and common carp, which show a positive preference for this substance, have revealed that the differences are inherited through the male line (Chapter 6), while genetic elements on the Y chromosome of guppies are responsible for marked differences in male aggressiveness (Chapter 9).

The term 'innate' is often used to describe behaviour that develops normally in the absence of specific environmental inputs and experiences. This is a useful term that draws attention to the fact that quite complex behaviour can be 'hardwired', but leads to problems if it is taken to mean that the behaviour concerned is not subject to any environmental modification. This is clearly not the case, because the way behaviour develops is profoundly influenced by the environment experienced by the developing animal from the point of fertilization onwards. In some cases, the influential factors are very general, as when aggressiveness in adult zebrafish depends on the amount of dissolved oxygen experienced by larval fish (Chapter 9). In other cases, behavioural changes come about through the effects of specific experiences, contingent on the results of behaviour performed in the past. In other words, both juvenile and adult fish are capable of learning. This is, defined as long-term changes in the probability of showing a particular response to a particular stimulus over successive associations between stimulus and response, sometimes depending on positive or negative reinforcement. Indeed, most of the kinds of learning of which mammals are capable have been demonstrated in fish (Table 1.1).

Differences experienced during development, from general effects of water quality through to highly specific learning opportunities, combine and interact with inherited differences to determine how juvenile and adult animals behave. For example, male three-spined sticklebacks typically chase and retrieve their fry when these first start to leave the nest. The main function of this behaviour by the male is to keep the fry safe, but the fry try to avoid their father and this has the additional consequence of giving them practice in escaping from a larger fish. Sticklebacks that have been reared by their father show better-developed escape responses when subsequently faced with a piscivorore such as a pike than do those deprived of the experience of being chased by their father. However, this is only true for fish originating from places where such predators are abundant; fish from sites lacking piscivores show poorly developed escape responses regardless of how they were reared. In this case the experience of being chased by their father interacts with inherited differences in propensity to learn from an aversive experience (Tulley & Huntingford 1987). The factors that influence how a young animal develops and how it eventually behaves may act across generations. For example, both the nutritional and hormonal state of gravid fish is known to influence the composition of their eggs and the performance of their young (Chapter 2). The eggs of stressed female coral reef fish (*Pomacentrus amboinensis*) often contain more cortisol and produce smaller offspring than do those of unstressed females (McCormick 1998, 1999). Early exposure to high levels of cortisol potentially has a number of effects on subsequent behavioural capacities in fish; for example, brown trout as ova exposed to cortisol show impaired learning abilities compared to untreated fish (Sloman 2010). As such, there would appear to be plenty of scope for cross-generational effects on the development of fish behaviour.

Understanding how such interacting genetic and environmental effects determine the way behaviour develops is important for fish culture, potentially allowing farmers to predict and control the behaviour of their stock. For example, knowing how genes generate behavioural differences may allow farmers to select stock with desirable behavioural traits, while knowing how early experience affects the way fish behave may allow them to improve the behavioural capacities of fish cultured for release into the wild.

How behaviour contributes to fitness

One reason biologists study behaviour is an interest in the link between behaviour and Darwinian fitness, defined as the relative contribution of an individual to the gene pool of the next generation(s). An important distinction to be made when considering Darwinian fitness is between naturally selected and sexually selected traits. Naturally selected traits are those that contribute to survival and/or to some aspects of reproduction, such as producing gametes in the correct season and ensuring that any resulting young survive. Sexually selected traits are those that contribute to fitness through improved competition over mates, either by increasing an animal's ability to fight off rivals or by making it particularly attractive to potential mates (Chapter 10). While sexually selected traits increase the chances of obtaining mates, they may also reduce survival, as when visually-hunting predators home in on courting fish. Natural selection and sexual selection may therefore be in conflict, although both contribute to overall Darwinian fitness and both must be considered for a full understanding of how selection has moulded the behaviour of fish, in the wild or in culture.

The subdiscipline of behavioural ecology has developed as a result of this strong interest in the link between behaviour and fitness, the aim being to identify the fitness-related consequences of behaving in a particular way. Some such consequences are beneficial; for example, by foraging in areas of high prey density, fish obtain the nutrients they need for survival, growth and, ultimately, reproduction; sticklebacks get plenty to eat if they forage on dense swarms of zooplankton that are easy to see in clear water. At the same time, there are fitness-related costs of particular actions; movement requires energy and some behaviour patterns involve a risk of physical injury or an increased risk of predation. Behavioural ecologists seek to identify and measure these costs. For example, when feeding on prey in a group, foragers must concentrate in order to follow one particular prey and have reduced ability to detect signs of danger; sticklebacks foraging on dense zooplankton swarms are less vigilant than those foraging on single prey. Animals adjust their behaviour flexibly depending on the balance between such costs and

Table 1.1. Examples of some of the different kinds of learning demonstrated by fish.

	Definition	Fish example	Reference
Habituation	Waning responsiveness after repeated exposure to an initially-effective stimulus that is not followed by positive or negative experience.	Minnows (*Phoxinus phoxinus*) cease to show fright responses to a model of a predatory fish and the less realistic the model, the more rapidly the response wanes.	Magurran & Girling 1986
Imprinting	Development of preferences for a category of animal or location through experience of that animal or location at a specific period during development.	Lake Victoria cichlids (*Mbipia* sp.) tend to mate preferentially with partners with the same colour patterns as the adults that reared them.	Verzijden & Ten Cate, 2007
		Salmon (*Salmo salar*) prefer the scent of water from the river in which they were reared around the time of smolting.	Stabell 1984
Pavlovian conditioning	Formation of an association between an initially neutral (conditioned) stimulus (CS) when repeatedly paired with a biologically-relevant (unconditioned) stimulus (US), so that the normal, unconditioned response to the US is shown to the CS.	Atlantic cod (*Gadus morhua*) held in culture conditions learn rapidly to associate a flashing light with the delivery of food after as as much as 1 minute's delay and swim towards the feeding area in anticipation of food delivery. This association is remembered for at least 3 months.	Nilsson *et al.* 2008
Operant conditioning	Increase in the probability of performing a particular behaviour when that behaviour results in a positive experience and decrease when it results in a negative experience.	Common carp (*Cyprinus carpio*) learn to press a lever if this is followed by food delivery.	Wright & Eastcott 1982
		Sticklebacks (*Gasterosteus aculeatus*) learn to avoid a previously-favoured feeding patch if they experience a simulated predatory attack in that location.	Huntingford & Wright 1992
Social learning	Acquisition of new information or learning of new behaviour patterns through observation of or interaction with social companions.	French grunts (*Haemulon flavolineatum*) in unfamiliar locations learn routes between resting sites and feeding grounds by following and copying experienced resident fish.	Helfman & Schultz 1984

benefits. For example, when undisturbed sticklebacks are offered a choice of zooplankton swarms of different density, they feed preferentially on the densest swarm. However, when foraging under a perceived risk of predation, they switch to feeding on less dense swarms and isolated individual prey. Thus they select an option that allows them feed, albeit at a reduced rate, while also watching for predators (Milinski & Heller 1978). This is almost certainly not the result of any conscious thought on the part of the animal concerned; instead it is the result of mechanisms produced by natural selection acting over evolutionary time.

Sometimes the costs and benefits of behaving in a particular way are not fixed, but depend on environmental circumstances; in the case of social behaviour, this includes how other animals behave. For example, the benefits of fighting come in the form of better access to valuable resources, whereas the costs lie in the fact that fighting is energetically expensive, imposes a risk of injury and makes the combatants vulnerable to predation (Chapter 9). Whether the benefits of fighting outweigh its costs will depend on, among other things, just how aggressive potential opponents are. When faced with many fierce opponents, the risk of getting injured may increase to the point at which this outweighs the advantages of winning a fight, so avoiding fights becomes the best option. The fitness arithmetic may be complex, but the main message is that frequency-dependent and environment-dependent costs and benefits serve to maintain adaptive behavioural variability within populations. Although such considerations seem a long way from the fish farm, an understanding of how fish adjust their behaviour to its costs and benefits can be useful. For example, holding fish in a directional current rather than in still water means that they expend more energy if they fight. Raising the cost of fighting in this way makes them less aggressive, reducing fin damage and promoting efficient growth (see below).

The phylogenetic history of behaviour

Continuing with an evolutionary theme, Tinbergen was interested in the phylogenetic history of behaviour, or how it changes over evolutionary time. This is important because the evolutionary history of an animal group determines the behavioural options open to it. Modern fish belong to an aquatic lineage and have adaptations for an aquatic lifestyle that determine how they behave. For example, water is a good medium for transmitting mechanical vibrations, fish have sensory systems for detecting vibrations (Chapter 2) and mechanosensory cues are important stimuli that influence their behaviour. The phylogenetic history of behaviour may also seem far removed from the fish farm, but understanding how behaviour has changed through evolutionary time and the genetic alterations that have accompanied such changes may in the future help in the design of targeted selective breeding programmes in fish that are cultured for specific purposes.

Behaviour does not appear in the fossil record, but in some instances its consequences may be detected in fossils. For example, feeding on planktonic as opposed to benthic prey leaves different patterns of wear on the teeth of three-spined sticklebacks and in fossil sticklebacks these can be used to reconstruct the feeding habits of fish of known geological age. Fossil fish that fed on benthic or pelagic prey usually also show the morphological traits known to be associated with these two feeding modes in living sticklebacks (Chapter 5). Evidence from the teeth of fish from one historical sequence suggests that a shift from pelagic to benthic feeding may have occurred some 100 years before any morphological changes. If correct, this provides an example of a behavioural shift (a change in feeding habit) initiating a process of rapid evolutionary change (Purnell *et al.* 2007). Such cases are rare, however, and reconstructing the phylogenetic history of behaviour mostly involves comparing equivalent behaviour in living species whose phylogenetic relationships are well known.

The advent of molecular biology has meant that genetic and genomic resources can be used to identify the chromosomal events that have been responsible for evolutionary change. To date, such studies have focused on morphological traits, but there is little doubt that the molecular changes that underlie the evolution of behavioural traits will eventually be identified. In addition, some well-studied morphological cases have clear implications for behaviour. For example, three-spined sticklebacks are named after their sharp spines, which have evolved from the rays in the dorsal and pelvic fins and protect the fish from attack by piscivorous vertebrates (Chapter 8). In a number of populations, the pelvic spines have been lost, probably as an evolved adaptation to a change in predation regime (Reimchen 1980). The genome-wide linkage map for sticklebacks shows that spine loss is linked to a specific chromosomal region containing genetic elements that are involved in the development of the hind limbs in mammals (for example, *Pitx1*) and that are also present in the ancestral, marine form of three-spined stickleback. Visualization of *Pitx1* during development shows that expression of this gene is missing in the prospective pelvic region of sticklebacks with pelvic spine loss, though it is present in other parts of the body. The same gene is associated with spine loss in sticklebacks from several different populations in which this trait has evolved. It seems that tissue-specific changes in gene expression, probably due to changes in regulatory factors near the *Pitx1* locus, were responsible for the parallel microevolution of pelvic spine loss in sticklebacks (reviewed in Kingsley & Peichel 2007). Similar studies are also elucidating, for example, the genetic mechanisms involved in the switch from pelagic feeding to benthic feeding and vice versa (Schluter *et al.* 2010).

Such research sheds light on the genetic processes that have been responsible for evolutionary change, but at present studies of the molecular genetics of behavioural evolution are at a very early stage. For this reason, questions about the phylogenetic history of behaviour are not pursued further in the specific behavioural chapters of this book. However, the possibility of using knowledge about how genetic alterations at the molecular level underpin the evolution of behaviour and related traits in targeted selective breeding programmes is considered further in Chapter 11.

1.4.3 How complex is fish behaviour?

Recently, there has been much discussion about just how complex fish behaviour is, mainly in the context of whether fish are conscious and sentient and so have the capacity for suffering. This reflects increasing concerns about the welfare of fish. The view that fish do not have the capacity for suffering, clearly articulated by Rose (2002, 2007), is based on the fact that the fish brain is small compared to that of mammals and lacks part of the cerebral cortex (the neo-cortex) that is the seat of many higher mental processes. In addition, according to this view, fish have little capacity for learning and they also have a short memory span. While they have the machinery to detect and respond to harmful stimuli and potentially dangerous events, it is considered that such responses are little more than simple reflexes with no emotional content.

Others have argued against this view (for example, Chandroo *et al.* 2004; Braithwaite & Huntingford 2006; Braithwaite, 2010), partly because of a high degree of homology and functional equivalence between the brains of fish and mammals, despite marked differences in size and in the processes of brain development in these two groups. Two parts of the forebrain (Chapter 2) are involved in generation of emotion and in learning in mammals; these are the amygdala and hippocampus, respectively. Homologues of these structures exist in the forebrain of fish; lesion of the amygdala-equivalent impairs the ability for avoidance conditioning in fish, while lesion of the hippocampus-equivalent impairs spatial learning (Rodriguez *et al.* 2006). As such, the fish brain has structures homologous to those involved in generating emotions and in complex learning processes in mammals and these also seem to serve similar functions. On this basis, it seems risky to conclude that all features of consciousness or sentience are ruled out in fish because of the nature of their central nervous system.

Considering the view that fish behaviour is simple and reflex-based, the evidence points to the contrary. For example, fish have a well developed capacity for learning (Brown *et al.* 2006), including the rapid formation of long-lasting memories of aversive events such as an attack by a predator (Chapter 8), the formation of mental maps (Chapter 4) and the ability to make complex decisions based on past social interactions with recognized individuals (Chapter 9). To give a striking example of how complex fish behaviour can be, when the prey of a Red Sea grouper (*Plectropomus pessuliferus*) escapes into a crevice, the grouper may recruit a moray eel (*Gymnothorax javanicus*) to flush the prey out. The eel is alerted by a set of specific signals and led by the grouper to the hiding place of the prey. When the prey is flushed out, the eel and grouper each catch and eat it on about 50% of these co-operative hunting sorties. It is not yet clear just how this complex interaction has developed, though a combined process of individual learning and cultural transmission through observational learning has been suggested. Such joint hunting requires complex, context-specific foraging decisions, awareness of the capacities and likely future behaviour of the other fish and coordination of behaviour based on effective communication between grouper and eel. Indeed, this example has been used to argue for ‘Machiavellian intelligence’ in fishes (Bshary 2006).

There is an extensive literature on the problems associated with identifying states of consciousness and on the different levels of consciousness that exist (reviewed by Braithwaite 2010). Access consciousness refers to the ability to generate a mental image or representation of the world, combining information from different sources and used to guide behaviour. The ability of fish to form mental maps and to predict what individual companions will do based on past experience points to the existence of this level of consciousness in fish. Phenomenological consciousness refers to the ability to experience feelings and emotions arising from events in the external world. The position here is still uncertain; however, the fact that the ability of fish to develop conditioned avoidance responses disappears when the amygdala-equivalent is destroyed (Rodriguez *et al.* 2006) suggests that the mechanisms that generate emotions in mammals also function in fish. Finally, monitoring and self-consciousness refers to the capacity for reflecting on one’s own actions and for basing decisions on considered scenarios; co-operative hunting by groupers and eels may possibly represent an example of consciousness at this level.

Clearly, there is still much to be learned about the mental and emotional life of fishes and it is likely that the capacity for consciousness in fish will be less developed than and different from our own. Nevertheless, in the opinion of the editors of this book, accumulating evidence of complex behavioural abilities and mental states in fish supports the position that fish are sufficiently complex in brain structure and behavioural function for the term "welfare" to be applicable.

1.5 FISH WELFARE

1.5.1 Definitions of welfare

The subject of fish welfare is complex and controversial, but is one that is becoming increasingly important as a result of rising public concern and of the regulations and legislation that have been introduced in response to this concern. It is clear that many aspects of fish culture, whether this be for food, supplementation and conservation, scientific research or the ornamental trade, can potentially compromise welfare, both in the fish that are cultured and in those with which they may interact (Braithwaite & Salvanes 2010). Fortunately, those who culture fish have ways of detecting when welfare is compromised and a number of strategies are available to them for mitigating any adverse effects. These topics are discussed briefly here.

Much of the controversy surrounding the welfare of cultured fish arises from the fact that there are different ways of defining welfare, placing emphasis on different aspects of the biology of the animals concerned. According to one school of thought, an animal experiences good welfare if it can adapt to its environment and is in good health, with all its biological systems functioning appropriately. According to such *function-based* definitions, animals that are in poor health have poor welfare by definition, and the converse. While most would agree that good health and proper functioning of body systems is necessary for welfare, many would feel that they are not sufficient and that welfare may be compromised in a perfectly healthy animal, for example if a social animal is housed in isolation. Such concerns can be accommodated by definitions that equate good welfare with an animal being free from negative experiences, such as pain, fear and hunger, and having access to positive experiences, such as social companionship. Such *feelings-based* definitions are based on the assumption that the animal concerned is conscious or sentient (see above) and suggest, for example, that it does not necessarily matter if an animal is thin or injured, provided that this does not generate negative feelings and emotions. For example, wild male salmon fighting to gain access to spawning females after having swum hundreds of miles up-river without feeding (Chapters 9 and 10), have markedly depleted energy reserves and may be injured. However, these are fitness costs incurred in the interest of gaining fitness benefits; the fish are highly motivated to migrate, fight and breed and their resulting poor condition should not be regarded as indicative of poor welfare.

This relates to the third way of defining welfare, namely that it requires an animal to be able to lead a natural life, expressing the same kinds of behaviour as it would in the wild and meeting what are sometimes called its 'behavioural needs'. Such a *nature-based* definition assumes that welfare is compromised if a captive animal is not able to show the full repertoire of behaviour that it would show in the wild. Most would agree, for example, that the welfare of a social animal is likely to be compromised if it is deprived of the opportunity to interact with conspecifics. It is less obvious (though not impossible) that animals in some sense need the opportunity to respond to predators, to take part in fights or to experience periods of fasting and will suffer if denied such opportunities.

None of these three approaches to animal welfare is inherently correct or incorrect; instead they emphasize different aspects of a complex topic and all throw light on a complex phenomenon. However, there is tension between the definitions. For example, on a function-based approach, a thin salmon with injuries experiences poor welfare. On a nature-based approach, if it has been fighting for breeding opportunities, it experiences good welfare. On a feelings-based approach, the fish may experience good or bad welfare depending on the sensations and emotions generated by depleted nutrient reserves and injuries. Feelings-based and nature-based definitions probably capture best the aspects of welfare that most concern the general public; functions-based definitions tend to suit veterinarians and scientists best, because these refer to aspects of animal biology that are amenable to quantitative study.

1.5.2 Identifying and measuring welfare

Welfare encompasses the comprehensive state of the animal, both bodily and mental, and requires that the animal is in good health, can adapt to its environment, is able to express the same kinds of behaviour that it would in the wild and does not have unduly negative experiences, such as pain and fear (Dawkins 2006; Branson 2008). Accordingly, welfare will vary over a continuum from good to very poor and studies of welfare will be most effective if a wide range of measures of welfare is used (Broom & Johnston 1993). The study of animal welfare therefore requires an interdisciplinary approach, bringing together, for example, physiology, veterinary science and behavioural sciences.

There are many possible indicators of poor welfare, the value of which depends on how welfare is defined (Table 1.2). These include poor physical health, which can usually be recognized relatively easily, as well as other measures that relate to poor health, such as immune suppression, that are less obvious to the casual observer and may only be revealed by advanced analytical techniques. Several physiological measures have been used in welfare assessment, including gill ventilation and heart rate and levels of hormones in the blood, especially cortisol, a major stress hormone in fish (Ashley 2007; Branson 2008). Although these are all objective, quantitative measures, they are part of the wider set of responses by which a fish responds to changes in its environment (Chapter 2) and can be difficult to interpret in welfare terms. For example, cortisol is an important mediator of salt and water balance in marine fish and is required for anadromous salmonids to complete the parr–smolt transformation. Further, mating contests will often result in plasma cortisol concentrations being elevated, but these are not necessarily a sign that the fish is in a state of poor welfare. When used as a tool for welfare assessment, physiological measures must be interpreted with reference to the environmental context in which they are collected, otherwise they may be misinterpreted. With this caveat, it is possible to use physiological measures, preferably together with other measures, to provide an assessment of welfare (Huntingford *et al*. 2006; Ashley, 2007; Branson 2008).

The behaviour of an animal can be observed directly and non-invasively and behavioural assessment of welfare has the potential advantages that it reflects ambient conditions, both internal and external, from the perspective of the animal (Dawkins 2006). Potential behavioural indicators of poor welfare include natural signals of stress or distress and the performance of abnormal behaviour and persistently repeated actions (stereotypies). For example, African catfish (*Clarias gariepinus*) held in groups in laboratory aquaria may show stereotypic behaviour in the form of continuous circling in a small area of the holding tank for minutes at a time, especially during the night when these fish are normally active (Rueda 2004). As an example of natural signs of stress and distress that can be used as welfare indicators, in salmonid fishes, the colour of the body and of the ring around the eye darken in response to various stressors and also act as social signals; for example, these patterns are typical of fish that have lost fights and serve to inhibit further attack (Chapter 9). Colour patterns can also be used as a sign of trouble by fish culturists, sometimes indirectly reflecting plasma cortisol levels in the fish concerned (Kittilsen *et al*. 2009). These are normal, adaptive responses to challenge, but abnormal behaviour can also indicate poor welfare. For example, Atlantic cod (*Gadus morhua*) that have been raised through the water column too rapidly suffer swim bladder damage, which is evident from erratic, abnormal swimming (Brown *et al*. 2010), and one response of rainbow trout to noxious stimuli applied to their mouth is to perform regular rocking movements that are not normally seen in this species (Sneddon *et al*. 2003).

A potentially fruitful approach to assessment of welfare in intensively cultured fish is to use the anticipatory response in fish that have been trained in a Pavlovian paradigm, for example to associate a flashing light in one part of a holding tank with the imminent presentation of food in another part. Various species, including Atlantic cod and Atlantic salmon for example, learn this association and towards the end of the period between the appearance of the flashing light and the delivery of food they move towards the area where the food will appear; in other words they show anticipation of the reward. When Atlantic salmon post-smolts are stressed, cortisol levels and oxygen consumption rates increase and feeding anticipation is suppressed. It takes longer for the conditioned anticipation response to reappear than it does for the other indicators to return to base line, suggesting that this behaviour is a sensitive indicator of welfare status. Conditioned anticipatory behaviour can be identified by computer analysis of video sequences of groups of fish held at high densities (Chapter 3) and so can potentially provide a practicable, non-invasive indicator of welfare in intensively farmed fish (Folkedal *et al*. 2011).

Studying behavioural choices and preferences is particularly important in the context of welfare research, since this is one of the few ways of gaining objective data about how fish respond to, and possibly feel about, particular experiences. For example, in some studies fish have been given a choice between staying, unfed, in shelter or emerging to feed in an exposed area; how they apportion their time gives information on the relative importance to the fish of security as opposed to food. It can also be used to probe more complex aspects of behaviour and welfare. For example, rainbow trout quickly learn to emerge from shelter when a light flashes to signify that food is about to be given. After application of a noxious stimulus such as bee venom to their snout, the fish tend to stay in the shelter while the light flashes rather than emerge to feed and this persists until the effects of the venom have worn off (Sneddon *et al*. 2003; Braithwaite 2010). Such results indicate that responses to noxious stimuli are not just reflexes, but include changes in behavioural priorities. Use of preference tests to study welfare is based upon the

Table 1.2. A summary of some commonly-used indicators of fish welfare, with comments on what they might potentially tell us about welfare, according to the three different ways in which this is commonly defined.

Welfare indicator	Function-based definitions	Feelings-based definitions	Nature-based definitions
Physical status			
Injury & disease status	Indicative of capacity for effective functioning	Currently no clear understanding of how fish experience good or poor health	Injury & disease are natural, so their occurrence at approximately normal levels does not indicate impaired welfare
Immune status	Indicative of capacity for effective functioning	Currently no clear understanding of how fish experience altered immune status	Variable immune status is natural, so does not in itself indicate impaired welfare
Nutritional status	Indicative of capacity for effective functioning	Currently no clear understanding of how fish experience altered nutritional status	Fish make natural choices that reduce nutritional reserves, so poor nutritional status does not in itself indicate impaired welfare
Growth	Indicative of capacity for effective functioning	Currently no clear understanding of how fish experience different rates of growth	Not all wild fish grow to capacity, so poor growth does not in itself indicate impaired welfare
Reproduction	Indicative of capacity for effective functioning	Currently no clear understanding of how fish experience achieving or not achieving reproductive status	Fish are naturally selected to maximise lifetime reproductive output, so poor breeding may be unnatural and indicate poor welfare

Physiological status			
Metabolic state[1]	Indicative of capacity for effective functioning	Currently no clear understanding of how fish experience altered metabolic state, whether acute of chronic	Variable metabolic state is natural, so is not in itself indicative of poor welfare
Stress hormone production[1]	Indicative of capacity for effective functioning	Currently no clear understanding of how fish experience altered levels of cortisol or adrenaline, whether acute or chronic	Production of stress hormones is natural, so acutely elevated cortisol is not in itself indicative of poor welfare.
Brain biochemistry	Indicative of capacity for effective functioning	Bioamine systems mediate reward and punishment, so brain biochemistry may reflect what fish experience	Variable brain biochemistry is natural, so in itself is not indicative of poor welfare
Gene expression	Potentially indicative of capacity for effective functioning	Differential expression of genes (e.g. relating to brain reward and punishment systems) may reflect what fish feel	Altered patterns of gene expression are natural, so are not in themselves indicative of poor welfare
Behavioural status			
Natural signs of distress	No clear link to capacity for effective functioning	If distress responses are not just reflexes, they indicate poor welfare	Distress responses are natural acts, so not necessarily indicative of poor welfare
Stereotypical behaviour	Potentially indicative of failure of normal coping systems	If stereotypies reflect frustrated motivation, they may reflect poor welfare	Wild fish tend not to perform stereotypies, so these are unnatural and indicative of poor welfare
Full natural repertoire	No clear link to capacity for effective functioning	If fish are strongly motivated to perform specific actions, an incomplete repertoire may indicate poor welfare	By definition, inability to perform a full natural behavioural repertoire indicates poor welfare
Preferences in choice tests	No clear link between preferences and functioning	Whether or not fish choose what is good for they, they do choose what they want	Spontaneous, natural choices by fish can indicate events and circumstances that promote/impair their welfare

[1] While acute metabolic activation or secretion of stress hormones reflect effective coping and so good welfare, long-lasting activation or chronically elevated stress hormone levels probably indicate failure to cope and hence poor welfare. There is currently inadequate information about the the threshold metaboloic rate or hormone level that tips fish from good to poor welfare.

assumption that animals will choose conditions that are beneficial to their physical well-being. This may not always be the case, leading to some problems when trying to use and interpret the results of free-choice experiments in welfare measurement and assessment (Dawkins 2006).

1.5.3 Talking a common welfare language

Reaching a consensus about what constitutes good welfare is not easy, because the term means different things to different people (Dawkins 2006; Huntingford *et al.* 2006; Ashley 2007; Branson 2008). For example, farmers usually equate welfare with a healthy stock, so would argue that good welfare is a characteristic of fish that are healthy and are growing well and efficiently. On the other hand, some people would claim that criteria for good welfare are met only if the fish is able to carry out its normal behaviour patterns without undue constraint and that it is able to live a natural life (Dawkins 2006). Although there is some overlap between these two standpoints, they are not completely compatible. For example, the fact that a fish has the opportunity to perform natural behaviours need not imply that its welfare is optimal and the performance of some types of natural behaviour may be detrimental to health and growth. These may include interactions with predators that invoke emergency or escape reactions and lead to reductions in feeding and growth (Chapter 8) and damaging behaviours arising from competition and aggression (Chapter 9).

A particularly controversial issue is whether fish are sentient, conscious animals; if they are not, using a feelings-based definition for fish welfare is inappropriate. As discussed above, evidence for sentience in fish is equivocal, although it is clear that the behavioural capacities of fish are complex. In addition, some scientists hold the view that, because feelings are subjective experiences, welfare defined in terms of feelings cannot be monitored or studied objectively (Arlinghaus *et al.* 2007). Carefully designed behavioural tests can help to probe the mental states and experiences of fish (Huntingford *et al.* 2007; Braithwaite 2010), but the results may not be easy to interpret or to apply in culture conditions. The working position taken in this book is that fish have sufficiently complex mental capacities that welfare, including those aspects that relate to feelings, is an appropriate and meaningful concept, while recognizing that our understanding of this issue may well change with further research. Pragmatically, given the fact that much fish culture is at an early stage in development in which welfare and production usually go hand in hand, at this time whether welfare is defined in terms of feelings or function is unlikely to make much difference to behaviourally based recommendations for improvement.

1.6 DOMESTICATION, CAPTIVE REARING AND BEHAVIOUR

1.6.1 Domestication and captive rearing

There are many striking differences in the conditions experienced by wild fish in their natural habitat and fish reared in culture. Cultured fish are physically constrained in environments that are impoverished in many ways, they usually experience unnaturally high densities, are often provided with an abundant and predictable supply of food and are protected against predation and certain diseases. Such differences can cause the phenotypic traits of fish reared in culture, including their behavioural responses, to deviate from those of wild fish (Einum & Fleming 2001; Huntingford 2004; Jonsson & Jonsson 2006; Araki *et al.* 2008; Belk *et al.* 2008; Nielsen & Pavey 2010). As described in Section 1.4.2 in the specific context of how behaviour develops, two main forces shape the phenotypic traits of fish in culture. On the one hand there are effects arising from the programmed expression of the genes they inherit from their parents and on the other hand there are plastic responses to the environment experienced both during development (including the prenatal environment) and as adult fish. In addition, there are interactions between these two inputs, as when fish with different genotypes are differentially susceptible to environmental factors or when the effects of different genes are only expressed in particular environments. Such processes are important in aquaculture, since many desirable traits are likely to be altered by artificial culture, contributing to the process of domestication and to the tricky issue of the impact of farm escapees on native populations. From a different perspective, aquaculture offers an excellent means of studying genetic and environmental effects on development in fish and evolutionary processes in general, because of the marked changes in selective pressures (intentional and unintentional) that accompany the introduction of fish into culture.

Fish within a species and population vary considerably in morphology, physiology and behaviour and such differences are sometimes inherited. Not all fish flourish in culture systems and differential mortality of fish with different phenotypes may result in different distributions of traits in wild-reared and captive fish of the same stock after a single generation of captive rearing. Over successive generations, the same process can result in long-term inherited differences between wild and cultured stocks arising either through domestication or as a by-product of selective breeding for desirable traits such as fast growth, or both. Thus, domestication involves changes in the intensity of selection on different traits. In some cases there is a relaxation of selection that would occur in the wild, such as predation and death by starvation; selection on other traits, for example the ability to compete for resources, may be intensified. As a consequence, domesticated animals will differ from wild, ancestral stock in morphology, physiology and behaviour, perhaps to so great an extent that they will be unable to survive in the wild, in absence of husbandry and protection by humans. Effects of domestication on a given trait can, in principle, be demonstrated by rearing cultured and wild fish from the original founder population in identical conditions and then comparing them with respect to the trait(s) under investigation. Ideally, to rule out maternal effects (Chapter 2), the wild and cultured strains should be reared in captivity for at least one generation before making comparisons. This is rarely possible for long-lived species such as salmonids, but can be achieved relatively easily with short-lived species such a zebrafish. In addition to inherited effects, the strikingly different environments experienced by wild and captive reared fish during development may generate non-inherited differences in behaviour. Such effects of captive rearing can be demonstrated by rearing fish of the same stock either in the wild or in culture conditions and comparing their behaviour, with the proviso that any differences may also be due to differential mortality by behavioural phenotype during the rearing process.

1.6.2 Selective breeding

Domestication is probably an unavoidable consequence of artificial propagation, exerted by holding fish in an unnatural environment, by unintentional non-random choice of broodstock and by patterns of survival that differ from those seen in the wild. In addition, where fish can be reared in culture over their whole life cycle, farmers can influence the process of domestication by intentionally selecting for particular traits. The goals of selective breeding of animals farmed for food include altering their characteristics to give more effective and profitable production, a major goal of farm animal breeding for many decades. However, there may be negative side effects associated with this form of selection. For example, selection for fast growth, improved utilization of feed or increased resistance to disease can also have an influence upon other traits, such as reproductive capacity and aggressive behaviour (Dunham 2004; Gjedrem 2005; Bartley *et al*. 2009).

One possible way to improve production of farmed fish without embarking on long-term selective breeding is to perform interspecific hybridization (Le Francois *et al.* 2010). Hybridization has been carried out on all major groups of fish farmed for human consumption and some hybrids are the choice for commercial culture. Examples include a hybrid between Thai (*Clarias macrocephalus*) and African catfish (*Clarias gariepinus*), which combines the better eating qualities of the Thai catfish with the more rapid growth of the African species, and the sunshine bass, a hybrid cross between female white bass (*Morone chrysops*) and male striped bass (*M. saxatilis*), which is more tolerant of extremes of temperature and dissolved oxygen than either of the parental species (Lim & Webster 2006; Le Francois *et al*. 2010). Gene transfer is another possible way of circumventing the need for a long-term selective breeding programme for stock improvement and over 35 fish species have been used in different types of gene transfer studies. Potentially, genetic manipulation could be used to enhance disease resistance, alter the digestive capacity of the fish or modify metabolic pathways that influence flesh composition (Beardmore & Porter, 2003; Devlin *et al.* 2006; Hu & Zhu, 2010). To date, no transgenic fish have been adopted for the commercial production of food, although transgenic zebrafish that express green, red or yellow fluorescent proteins are being sold to aquarists under the tradename GloFish. The situation may well change soon, as permission has been sought in the United States for the use of growth-hormone transgenic salmon.

1.6.3 Are cultured fish domesticated animals?

Few of the fish species that are currently farmed have been subjected to long-term, directed genetic selection to alter and improve production traits and most selection programmes are at a very early stage (Dunham 2004; Gjedrem 2005; Shelton & Rothbard 2006; Bartley *et al*. 2009). Only a handful of fish species can be considered as being completely domesticated and the majority of farmed fish species can be classified as what Balon (2004) has called ‘exploited captives’, so there is considerable potential for improving production of farmed fish by selective breeding (Dunham 2004; Gjedrem 2005; Bartley *et al.* 2009). Such efforts are likely to benefit considerably from the application of molecular genetic technologies; for example, molecular markers that relate genotype to particular production traits could be used in pinpointing genetic loci of economic interest and allow genetic characterization of potential broodstock (Dunham, 2004; Gjedrem 2005; Liu 2007; Nielsen & Pavey 2010; Thomson *et al*. 2010).

Many stocks currently used in fish production have been derived from very small founder populations and several suffer from genetic bottleneck effects (Beveridge & McAndrew 2000; Dunham 2004; Gjedrem 2005; Bartley *et al.* 2009). Genetic deterioration may be widespread owing to extended periods of poor broodstock management, but identification of genetic lineages and estimation of the level of inbreeding are still in their infancy (Dunham 2004; Gjedrem 2005; Liu 2007; Nielsen & Pavey 2010; Thomson *et al.* 2010). In addition, knowledge about the genetic structure of natural populations of farmed fish species is extremely limited. Although such populations potentially represent genetic reservoirs that could be tapped to improve the performance of cultured fish, they are potentially at risk as a result of a reduction in genetic integrity through excessive stocking with fish raised in hatcheries for supplementation programmes (Araki *et al.* 2008; Nielsen & Pavey 2010) or through interactions with escaped fish that are farmed for food (McGinnity *et al.* 2003; Hindar *et al.* 2006).

1.6.4 Behavioural responses to domestication and selective breeding

In general, an animal that is domesticated is likely to possess character traits that facilitate adaptation to the captive environment, including traits related to behaviour, such as attenuated stress responses and increased tolerance of conspecifics (Diamond 2002; Mignon-Grasteau *et al.* 2005; Jensen 2006). When fish are bred to be companion animals, pets or ornamentals, the main selection criteria may include selection for particular colour patterns, which may affect behaviour, and a reduced reactivity to humans. Inherited effects of domestication on behaviour have been demonstrated in a number of fish species. For example, when reared under the same conditions for several generations, ruling out effects of maternal nutrition, zebrafish from domesticated strains grow faster and behave differently from fish of wild origin in several ways (Wright *et al.* 2006).

Some of the concern about the use of transgenic fish for food production relates to the potential environmental impacts should such fish escape or be inadvertently released. Part of the assessment of the risk imposed by transgenic fish involves a comparison of their characteristics with those of both the founder hatchery population and wild-type fish of the same species. Not unexpectedly, transgenic fish with enhanced growth hormone differ from the founder population and wild-type fish in a variety of characters that relate directly to feeding and growth. However, there are other differences; for example, transgenic fish of several species tend to swim higher in the water column than non-transgenic conspecifics, have poorer swimming ability and suffer higher mortality from predatory attacks (Devlin *et al.* 2006; Le Curieux-Belfond *et al.* 2009; Hu & Zhu 2010). Such differences potentially influence the capacity of the fish to survive in the wild and to interact with wild fish to the detriment of local populations. This has led to calls for stringent control of the use of transgenic fish in research, including the establishment of secure methods of containment.

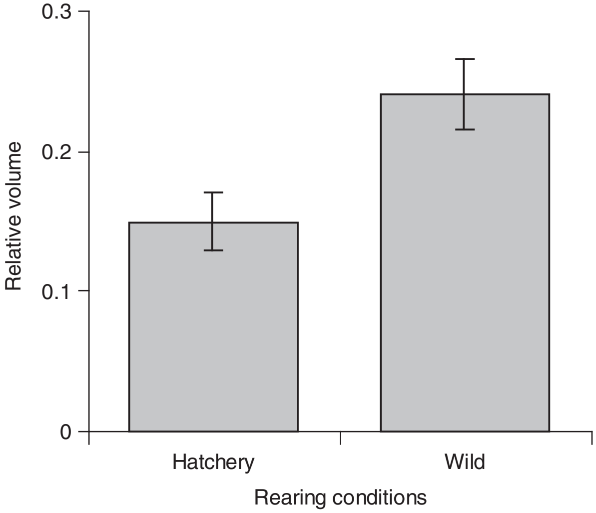

Figure 1.4. Relative volume of the telencephalon (mm^3/mass g) in Chinook salmon reared in the wild and in conventional hatchery raceways. Values are plotted as mean ± SEM. Adapted from Kihslinger *et al.* 2006.

1.6.5 Captive rearing and fish behaviour

The very different environment experienced by wild and cultured fish can have profound effects on a variety of developmental processes and so can potentially produce non-inherited differences in behaviour between wild and captive fish. Captive environments usually lack the complexity of those experienced by fish in the wild and a number of studies have shown that captive rearing alters brain development in fish. For example, the optic tectum and telencephalon of captive-reared rainbow trout (Marchetti & Nevitt 2003), Chinook salmon (Figure 1.4; Kihslinger *et al.* 2006) and guppies (Burns *et al.* 2009) are significantly smaller than those of wild fish. Although the relationship between the size of a particular brain region and its function is complex (Healy & Rowe 2007), given such striking differences it is perhaps not surprising that many behavioural differences have been reported between captive-reared and wild fish. These include differences in learning ability and in the expression of a range of behaviours, including exploration of novel surroundings and the propensity to join shoals of conspecifics (Burns *et al.* 2009; Chapman *et al.* 2010). Such differences are explored in more detail in the relevant later chapters.

1.7 CRITERIA FOR EFFECTIVE AND SUSTAINABLE FISH CULTURE

Effective, sustainable fish culture requires the economic production of a product that meets consumer expectation, with the minimum of negative impacts on the welfare of the fish and the environment (Tucker & Hargreaves 2008; Le Francois *et al.* 2010). For whatever purpose fish are being cultured there is a set of common requirements for sustainable culture. How fish behave is just one of many factors to be taken into account, but it is an important factor.

1.7.1 Production criteria

First, for effective and economically-viable culture the fish must survive, which means keeping them free from injury and disease. The fish should grow well and efficiently. When being produced as food for human consumption, fish must also be of an acceptable quality both nutritionally and aesthetically. Fish reared for other reasons must be of an appropriate size, in good health and fulfil the purpose for which they were reared in other respects. Key points that must be considered are responsible use of land and water resources and the cost-effectiveness of the rearing methods. It is also necessary that the end product is affordable and in regular supply, so the sustainability of the farming operation in terms of use of raw materials and energy is also an important consideration (Wedemeyer 2001; Tucker & Hargreaves 2008; Le Francois *et al.* 2010).

1.7.2 Environmental criteria

Concern over the environmental impacts of aquaculture is relatively recent, increasing in step with the industrialization of fish farming, and it has attracted attention from environmentalists and conservationists, as well as regulatory authorities and the general public. Criticism has been directed against fish farming because of perceived environmental impacts that involve destruction of wetland habitats, excessive use of water resources, pollution by farm effluents and the potential impacts of farm escapees on native faunas. Potential environmental effects depend upon the species being farmed, the type of culture system and production intensity and the extent to which the farming operation directly impacts the landscape (Naylor *et al.* 2005; Tucker & Hargreaves 2008; Le Francois *et al.* 2010).

Land resources

Land resources are under pressure from many different human activities. As far as aquaculture is concerned, sites that are suitable for land-based fish farming are limited by desirable combinations of climate, topography, water availability and access to other resources such as a labour force, power supplies and transport facilities (Stickney 2000; Wedemeyer 2001; Tucker & Hargreaves 2008). Most of the problems associated with land use for fish farming relate to the value of alternative uses, leading to potential conflicts. This is especially the case in coastal regions, where land area is limited, where sensitive and environmentally valuable habitats exist and where land is used for a wide variety of other purposes. For example, the clearing of mangrove forests to provide space for the construction of ponds for fish and shrimp farming has been a contentious land use issue in several tropical and sub-tropical countries in recent years. Mangrove forests protect coastlines from erosion and flooding, provide habitats for a wide variety of species, including acting as nursery grounds for commercially important fish, and act as an important interface between marine and freshwater environments.

Water resources

Both fresh waters and coastal ecosystems are under pressure from many different human activities. Fresh water is a scarce resource, but it is an obvious and essential resource for the farming of fish and no single factor influences success or failure more than access to adequate supplies of good quality water (Tucker & Hargreaves 2008; Le Francois *et al.* 2010). Fish farms must compete with other users for finite water supplies, especially in arid regions or where most of the fresh water comes from groundwater resources. Some water sources that receive agricultural, industrial or domestic discharges may not be suitable for use in fish farming or must be subjected to prior treatment to remove physical, chemical and biological hazards. Fish production systems produce wastes to an extent depending upon the type of production and the degree to which the units are open to surrounding waters. Well-managed ponds will generally release very little waste to nearby waters and when fish are reared in land-based tanks or raceways, the effluent can be treated to remove solids, some dissolved nutrients and wastes and to destroy pathogens (Wedemeyer 2001; Tucker & Hargreaves 2008). On the other hand, when there is direct contact between the rearing units and surrounding waters, as is the case with cage systems, the control of effluent release is extremely difficult. The major sources of fish farm wastes are uneaten food and the excreta produced by the fish; effluent release from open systems can be reduced by a combination of good feeding routines and use of the correct types of feed (Le Francois *et al.* 2010. Chapters 5–7).

Feed resources

Fish meals and oils extracted from marine fish have been important feed ingredients throughout the years of expansion of intensive fish culture. These ingredients have been major components in the pellets fed to high-value carnivorous species such as salmonids, sea basses and sea breams and marine flatfishes, because both fish meals and marine fish oils are excellent sources of several essential nutrients (Chapter 6) and they have been available on the international market at reasonable price (Dabrowski & Hardy 2010; Le Francois *et al.* 2010). Fish meals are rich in protein, have a good balance of amino acids, are a good source of certain vitamins and essential minerals and have taste properties that make them attractive feed ingredients for many species of farmed fish. Marine fish oils are esteemed as feed ingredients because they are a good source of essential fatty acids and some fat-soluble vitamins. Both fish meals and marine fish oils have increased in price and are in shorter supply than previously, so are being increasingly replaced by alternative ingredients. In particular, there is increased replacement of fish meals with terrestrial plant proteins and there is also an increase in the use of plant oils to partially replace marine fish oils in the pellet feeds given to farmed fish (Le Francois *et al.* 2010. Chapter 6).

Living resources

A major cause for public concern about the environmental impact of fish culture and an important aspect of the management of fish in aquaculture systems centres on potential threats to wild fish populations. Such threats might be removal of natural prey through capture of fish for the manufacture of fish meals and fish oils, or might relate to transmission of parasites and diseases. In addition, major environmental concern is centred on the threats to wild populations through release of cultured fish, which can occur either deliberately or unintentionally. Intentional releases are usually carried out in an attempt to mitigate the effects of over-exploitation, habitat alteration and destruction on wild populations, but these attempts at restoration have met with mixed success (Stouder *et al.* 1997; Araki *et al.* 2008). Fish are also released in supplementation and sea ranching programmes to increase the resources that can be harvested. The fish may be released at all life stages, but the release of captive-bred, hatchery-reared juveniles is most usual. Unintentional releases occur when juvenile and adult fish escape from hatcheries and fish farms, or when fish held in cages mature, reproduce and release fertilized eggs and larvae into surrounding waters. For example, many farmed Atlantic cod (*Gadus morhua)* mature before they reach harvest size and some spawn in sea cages and produce fertilized eggs. In some cases 20–25% of larval and juvenile cod in the vicinity of a farm may derive from fish that spawn in nearby sea cages (Kah *et al.* 2010).

Irrespective of whether releases are intentional or unintentional, the fish of cultivated origin will generally intermingle with naturally-occurring populations of the same species, exploiting the same feeding areas and possibly interbreeding with wild fish (Araki *et al.* 2008; Tucker & Hargreaves 2008; Le Curieux-Belfond *et al.* 2009; Nielsen & Pavey 2010; Chapter 10). Interbreeding between cultured and wild fish could alter the genetic structure of wild populations through outbreeding depression, homogenization or a reduction in effective population size. For example, interbreeding between wild and cultured fish could result in changes in allele frequencies in wild populations and the genetic profiles of wild populations could be altered by the introduction of rare alleles selected for in the cultured fish on the basis of performance criteria. As discussed above, fish that have been held in captivity for several generations generally differ markedly in several characteristics from fish of wild local stocks. Population sizes could decrease if cultured fish replace wild fish and then have low reproductive success. The effects of cultured fish on the genetic profiles of wild populations are expected to be least when local, wild fish are used as broodstock in restoration, enhancement and sea ranching programmes (Araki *et al.* 2008; Nielsen & Pavey 2010).

Many fish species have been transplanted to areas outside of their natural distributional range for farming and other purposes and several of these have established self-sustaining populations in the wild, following either intentional release or escape from captivity (Lever 1996; Shelton & Rothbard 2006). This can be illustrated by the rather curious case of the establishment of populations of some tropical aquarium species in a number of localities within the British Isles. For example, following the discard of pet-shop stock into a canal in north-west England a breeding population of the guppy (*Poecilia reticulata*) established itself; this was possible because the reach of the canal into which the fish were released received warm-water effluent from a nearby factory (Lever 1996). A number of the species that have been naturalized into non-native areas are now considered pests with detrimental effects on native faunas and habitats (Lever 1996; Tucker & Hargreaves 2008).

The only sure way to prevent the establishment of feral populations and to hinder interbreeding between cultured and wild fish is to ensure that any fish released into the wild are infertile. Interspecific hybrids are usually infertile, so the farming or stocking with hybrids is one way to circumvent both the establishment of self-sustaining populations and interbreeding with local wild fish. Sterile fish can also be produced by genetic manipulations involving the induction of polyploidy, particularly triploidy. Triploid fish have three sets of chromosomes, two from the female and one from the male and are produced by application of thermal or pressure treatments shortly after egg fertilization. Because triploid fish have an extra set of chromosomes, the germ cells cannot undergo all the meiotic divisions needed to produce viable eggs or sperm, so the fish are usually functionally sterile (Kah *et al.* 2010; Le Francois *et al.* 2010). Triploid fish are not considered genetically modified organisms according to European regulations (EU, Directive 90/220/CEE), but are perceived negatively by fish farmers, traders and consumers and few efforts have been made to develop the technique for mass use. Triploid rainbow trout are produced when large fish are in demand, such as for smoking, and triploid rainbow trout and other salmonids are raised for the reproductive containment of fish released by angling associations in several European countries. The introduction of exotic fish species such as grass carp (*Ctenopharyngodon idella*) in United States for the purpose of weed control in ponds requires that the fish are sterile triploids to reduce the threat of uncontrolled reproduction in the wild (Piferrer *et al.* 2009).

Although the production of sterile farmed stock might eliminate problems related to genetic impacts of intentionally-released fish or farm escapees on natural populations, it would not serve to eliminate all forms of interaction. Released fish could be members of non-native or introduced species, highly-selected stocks or hybrids with a range of characteristics that could impact wild populations in a number of different ways. The released fish could act as either predators or prey, could be vectors of parasites or disease organisms and could compete for food or other habitat resources resulting in displacement or exclusion of native species and natural populations. In all likelihood several of these interactions would act simultaneously. Given these considerations, and the low success rates of many supplementation programmes, the culture of fish for this purpose is questioned by some environmentalists and fisheries managers (Devlin *et al.* 2006; Jonsson & Jonsson 2006; Tucker & Hargreaves 2008; Le Curieux-Belfond *et al.* 2009; Le Francois *et al.* 2010). This book discusses how the culture of fish for supplementation or reintroduction could be made more effective through consideration of the behavioural traits of cultured fish, in cases where it has been decided that this is appropriate and advisable.

1.7.3 Welfare criteria

Why welfare matters in fish culture

The culture of fish for whatever purpose raises a number of welfare issues, both for fish that are reared in captivity and sometimes for wild fish (Huntingford *et al.* 2006; Ashley 2007; Branson 2008). A wide variety of factors, both biotic and abiotic, have the potential to create welfare problems for cultured fish. Such problems can arise early in life; for example, unfavourable temperatures during larval development may give rise to deformities in the soft tissues, including abnormalities in the heart and swim-bladder. Unfavourable temperatures may also interfere with development of skeletal tissues, causing, for example, malformed gill covers and jaws (Branson 2008; Chapter 2). Deformities may also arise if the fish experience unfavourable conditions at a later stage in development; for example, provision of nutrient-deficient live prey and formulated feeds at first feeding can cause spinal deformation (Branson 2008; Dabrowski & Hardy 2010). Abnormal development in both hard and soft tissues interferes with swimming and hence compromises many aspects of behaviour. In addition, malformed gill covers cause breathing problems and may make the fish vulnerable to gill infections, while malformed jaws are likely to interfere with feeding. Such general and specific effects all lead to poor welfare, but they also compromise production, since deformed fish survive and grow less well than normal fish and have a lower market price. In addition to such dramatic effects on physical condition, many unavoidable aspects of routine husbandry can potentially compromise fish welfare; these include confinement, housing at high densities, grading, disease treatment, transport and harvest (Huntingford *et al.* 2006; Ashley 2007; Branson 2008).

Since intensive aquaculture is a relatively new enterprise in which rearing conditions have often not been optimized, good welfare and good production often go hand in hand, with interventions that promote welfare also improving production. For example, when fish are allowed to feed according to their natural appetite rhythms (Chapter 7), their welfare improves, according to various indicators, including reduced fin damage, as does feed conversion

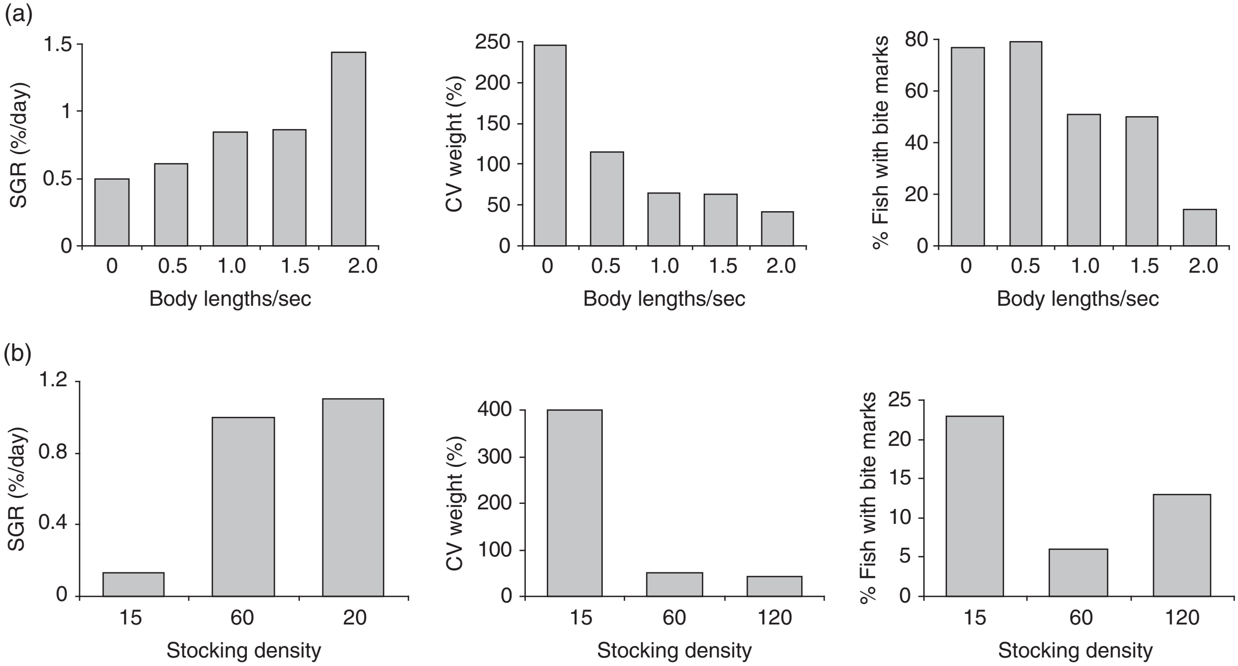

Figure 1.5. Detecting and improving the welfare of farmed fish. Specific growth rate (SGR %/day), coefficient of variation in weight (CV weight %) and percentage of fish with bite marks in Arctic charr held (a) at different current speeds (body lengths/sec) and (b) at different stocking densities (Kg/m^3). Adapted from Jobling *et al.* 1993; Jobling 1995.

efficiency (Noble *et al.* 2007). This is one reason why, over and above having a responsible attitude to their stock, good fish farmers are concerned about the welfare of the fish in their care. Another reason is that public pressure has resulted in regulations and legislation with which farmers must comply. In addition, there are various schemes through which farmers can charge a premium for fish that have been reared in conditions that promote welfare, the Royal Society for the Protection of Animals (RSPCA)'s freedom food label for farmed salmon being a case in point(http:/www.rspca.or.uk/science group/farm animals/standards/salmon).

The response of Arctic charr (*Salvelinus alpinus*) to early culture efforts illustrates well some of the problems that can arise when fish are being farmed. When trials aimed at commercial development of Arctic charr culture were initiated in the mid 1970s, rainbow trout and Atlantic salmon farming were already well established. Hatchery and husbandry techniques had been developed, tanks and other equipment were readily available and cage culture was well-established (Le Francois *et al.* 2010). When Arctic charr were reared in fresh water at similar stocking densities and with similar feeding routines to those used for farming rainbow trout and salmon, a number of problems arose, with implications for both production and welfare. In the first place, growth was uneven, with some fish growing rapidly and others growing very slowly. Behavioural observations showed that at low stocking densities and in shallow water with low current speed, many of the charr were relatively inactive, remaining close to the bottom and sides of the tank. These fish were often small and dark and tended to feed in midwater and on the tank bottom rather than at the surface. In contrast, a few pale-coloured charr, usually the largest, swam almost continuously in the water column, frequently chased and delivered nips to other fish and fed either in midwater or close to the water surface. The high levels of attacks and fin-nipping delivered by the large charr resulted in many of the smaller fish having bite marks on their fins and bodies (Figure 1.5; Jobling *et al.* 1993; Jobling 1995). A further indication that rearing conditions were suboptimal came from the fact that some of the charr showed a reduced ability to regulate gas within the swim bladder. These fish experienced difficulty in maintaining neutral buoyancy and swam on their sides or belly-up, often at the water surface, though they were still able to feed and grow. Thus, many of the early farmed charr showed several indicators of poor welfare, including slow growth, dark colouration, damaged fins, restricted space use and abnormal swimming.

Strategies for improving the welfare of cultured fish

Having identified welfare problems, two broad approaches to mitigation are available; these are not mutually exclusive. One possible strategy is to make a careful choice of which fish to culture, since some species and strains of fish are more amenable to being held in captivity than others. For example, some species and strains are less aggressive than others (Chapter 9) and welfare problems arising from aggression among cultured fish could be mitigated by culturing these species or strains. In a number of lakes, two forms of Arctic charr exist, one that feeds selectively on large, benthic invertebrates and one that specializes on zooplankton (Chapter 5). The pelagic form is less aggressive than the benthic form (Chapter 9) and so might be more suitable for culture.

A second mitigation strategy is to design culture facilities, equipment, husbandry practices and management systems that promote welfare. In the early farming of Arctic charr it proved possible to mitigate the adverse effects on welfare by some fairly simple and practicable steps. Increasing the depth of water, subjecting the fish to flowing water and increasing stocking density helped to solve several welfare problems. When charr were exposed to flowing water, they exhibited schooling behaviour, distributed themselves evenly in the water column, fed in midwater or close to the surface and showed reduced levels of aggression; the net result was fewer fish with bitemarks, higher rates of growth and reduced size heterogeneity (Figure 1.5a). In addition, a smaller number of fish showed signs of stress or exhibited problems related to buoyancy regulation. Similar effects, including the induction of schooling, reduced chasing and fin-nipping and improved growth, were achieved by rearing the fish at higher stocking density (Figure 1.5b; Jobling *et al.* 1993, 1998; Jobling 1995). The effects of the two interventions (increased stocking density and exposure to flowing water), which were independent of each other, can be explained in terms of the behavioural biology of aggression (Chapter 9).

1.7.4 Behaviour and effective, sustainable aquaculture

Behaviour can influence the effectiveness and sustainability of aquaculture in the period during which fish are being grown to a useable size. For example, how fish feed in culture systems can affect how much food is wasted, as well as whether fish survive and how well they grow (Chapters 5–7) and whether and how much fish fight can affect how fast they grow, their physical condition, their welfare and how efficiently they convert food into flesh (Chapter 9). Thus behaviour during the culture process determines the effectiveness of production and the condition and health status of the fish, regardless of the reason why the fish are being farmed.

Over and above this, the purpose for which the fish are being cultured determines what is required of their behaviour. For example, the attractive traits for which ornamental fish are cultured are best appreciated if they behave in an appropriate way. Fish that emerge from cover and can readily be seen, especially if they display bright colours and elaborate fins, are more rewarding that those that consistently hide. In addition, for many people simply watching the behaviour of their fish is a key part of the rewards of maintaining an aquarium. For all these reasons, the value of cultured ornamental fish depends on their showing many of the behaviour patterns that are normal for their species. Where fish are reared for scientific purposes, how they behave is also important if they are used to study neurobiology or behaviour; if their behaviour and the mechanisms that generate it are abnormal, the generality of any research conclusions may be limited.

The success of programmes in which fish are cultured for release into the wild clearly depends on how well they survive, grow and in some cases reproduce after being released. Their behaviour is important here, because how efficiently fish feed, compete with conspecifics and avoid predators are all determinants of post-release survival and growth. As discussed in later chapters, there is evidence that captive-reared fish differ from wild fish in foraging ability, in predator avoidance and in agonistic behaviour towards conspecifics (Einum & Fleming 2001; Jonsson & Jonsson 2006; Araki *et al.* 2008; Nielsen & Pavey, 2010). It is therefore important that cohorts of cultured fish and individuals within the cohorts show a natural spectrum of species-typical behaviour. Where the aim is simply to generate a population of fish for subsequent angling, the spectrum of behaviour in individuals and populations is important, as the fish need to survive long enough to service an angling use and to behave sufficiently naturally to be an interesting catch. Exactly how such traits develop is not critical. If the aim of a supplementation programme is to generate or augment self-sustaining wild populations for conservation, then clearly both the ability to reproduce and the inherited behavioural profiles of the released fish are important (Fleming & Petersson 2001; Jonsson & Jonsson 2006; Araki *et al.* 2008; Chapter 10).

1.8 STRUCTURE AND CONTENT OF THIS BOOK

The aim of this book is to familiarize the reader with the fundamentals of behavioural biology of fish and to show how this is relevant to fish culture. Understanding fish behaviour requires knowledge of some other aspects of their biology, such as their sensory capabilities and how they process and respond to sensory information. Early developmental processes are also important in governing the physiological and behavioural responses shown by fish later in life and the environment experienced by a fish during the earliest stages of its life can have long-lasting effects on how it will react under a given set of circumstances. A brief overview of these topics is presented in Chapter 2, by way of preparation for the material presented in later chapters.

The behaviour of aquatic animals is difficult to study because the environment in which they live is often inaccessible to human observers. Studying the behaviour of fish in aquaculture systems is additionally challenging because huge numbers of fish are often held together in conditions that are not conducive to direct observation. This has required development of special techniques for collecting scientific data on the behaviour of cultured fish and these are described in Chapter 3.

The remaining chapters take specific aspects of behaviour in turn, first presenting fundamental information about their causes, development and consequences for fitness, illustrated wherever possible using examples from cultured species, and then discussing the implications for aquaculture. This includes an account of how the behaviour concerned is expressed in cultured fish, the problems for production arising from its expression and the effects of domestication and captive rearing on the behaviour concerned. Solutions to these problems are also described, looking at how behavioural knowledge can be used, among other things, to devise husbandry systems that promote production, welfare and environmental protection and to mitigate the effects of captive rearing.

The most studied aspects of behavioural biology that are relevant to fish culture relate to finding, selecting and consuming food, closely followed by studies of reproductive behaviour. More recently the topics of orientation and movement, aggressive interactions and antipredator behaviour have been introduced into the aquaculture literature. All of these are covered in this book, starting with orientation in and movement through space, which could be important given that cultured fish are unable move as freely as they would in nature (Chapter 4). Knowledge about feeding and nutrition is critical for effective fish culture and much is known about the nutritional biochemistry and physiology and the growth biology that underpins effective production of some species. However, behavioural aspects of feeding are also important, including how fish acquire and process food (covered in Chapter 5), their dietary preferences (covered in Chapter 6) and the factors that determine how much fish eat and when (covered in Chapter 7). Farmed fish are usually protected from predators, but they do sometimes experience predatory attack and even when this is not the case anti-predator behaviour may be elicited by husbandry practices. Knowledge about antipredator behaviour is therefore important for effective culture and this is described in Chapter 8. Cultured fish very often live in close proximity to many other individuals of the same species and this can affect social relationships and how frequently fighting occurs, topics covered in Chapter 9. Finally, behavioural traits associated with life history events, including reproduction, are very important in culture; reproduction must be controlled and often prevented during on-growing, but must be promoted in broodstock to produce the next generation to be farmed. The life history patterns and reproductive behaviours of fish and their implications for fish culture are covered in Chapter 10. The final chapter considers common themes relating to the expression and importance of fish behaviour in aquaculture, both as it is currently practiced and in the light of developments that may take place in the future.

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