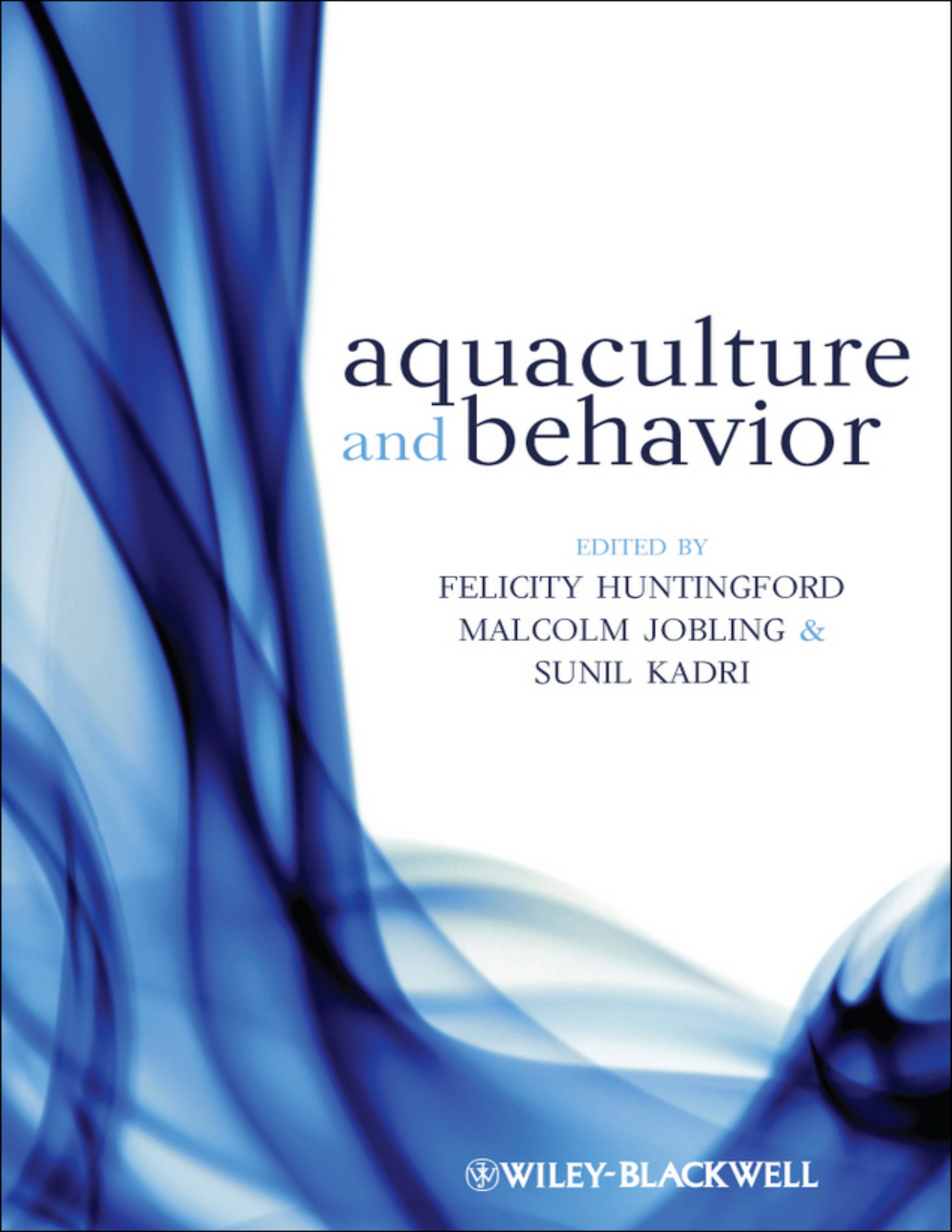


The background of the cover is an abstract, flowing blue liquid or smoke-like pattern that moves from the top left towards the bottom right, creating a sense of dynamic movement. The colors range from deep navy blue to a lighter, almost white blue.

aquaculture and behavior

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Preface

There are many problems to be overcome in aquaculture, irrespective of whether the fish are being farmed for food, cultivated for release into the wild or are being reared as pets or ornamentals or for scientific research. A number of disciplines, including engineering, veterinary science, nutrition, genetics, animal breeding and reproductive biology, have contributed to finding solutions to problems related to holding fish in captivity. This book has been written in the belief that, among these, the study of animal behaviour can make important contributions to effective, sustainable aquaculture. Many of the problems encountered when holding and rearing fish stem from the 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. The overall aims of this book are to give an account of the behavioural biology of fish, to explore its implications for fish culture and to show how knowledge of fish behaviour can be used to solve problems and promote sustainable aquaculture.

The book has seven chapters that deal with specific behaviours relating to orientation and movement, foraging and feeding, antipredator behaviour, aggression and reproductive behaviour. For ease of comparison, the structure of these chapters has been standardised. Each chapter starts with an account of the behaviour as seen in fish in natural habitats, looking at the mechanisms that generate the behaviour, how the behaviour develops and how performing the behaviour relates to Darwinian fitness. The various ways in which these behaviours cause problems for production, for fish welfare and for the surrounding

environment are then discussed and potential solutions to such problems are suggested based on a consideration of the biology of the behaviours concerned. To put these seven chapters in context, the book begins by giving a general introduction to aquaculture and behaviour. We look at the finfish species that are cultured, the systems used to culture them and criteria for successful captive rearing. We also define behaviour and describe how biologists study it and try to explain it. Fish are very different from other farmed animals so we devote the second chapter to an overview of fish biology, concentrating on those aspects that are of particular relevance to behaviour and to performance in culture. Because the behaviour of fish is particularly difficult to study in intensive culture systems, the third chapter gives a review of the methods available for studying the behaviour of farmed fish. In the final chapter, we identify some common principles for using our understanding of fish behaviour in aquaculture, both as it is practised today and in the light of likely future developments.

This book is aimed both at undergraduate and postgraduate students interested in fish biology, animal behaviour and aquaculture and at established researchers and technical and research managers in the aquaculture industry. Our goal is to achieve an authoritative, up to date scientific content, with an accessible jargon-free style. Rather than aiming at an exhaustive academic review of all that is known about a particular aspect of behaviour, we give a broad overview illustrated by selected examples and have supplemented this by referring the reader to up to date review articles and to the primary literature.

To cover all the topics with the desired authority and clarity has required an interdisciplinary approach, and our authors bring to the book complementary expertise in many areas of fish biology and aquaculture science. They have worked in teams, coming together in different combinations

to write the various chapters. This has required a considerable amount of co-ordination and collaborative exchange among authors that, we hope, has produced a coherent end result. We would like to thank all the authors for taking part in this complicated project and the publishers for their patience in waiting for the end result. We would also like to thank Susan Linklater for setting up our electronic communication system, Lorna Kennedy for all kinds of help, including handling the copyright queries, Kirstin Harper for reviewing sections of the literature for us and Fraser Howarth for double checking some of the chapters and, with Fabio Borcato, for compiling references lists.

Felicity Huntingford, Malcolm Jobling and Sunil Kadri

Foreword

In my role as a scientist for one of the large salmon feed companies, I have worked directly with two of the editors of this book, namely Felicity Huntingford and Sunil Kadri. During the time we worked together I learnt first hand about the dedication, breath of knowledge and unbounded enthusiasm of the authors for the subject of fish behaviour. In particular, their belief that an understanding of fish behaviour can be applied to commercial fish farming practice to improve both the welfare of fish and the efficient and sustainable aquaculture production. This book is born from those qualities and beliefs.

In our work together co-supervising the work of some PhD students we came across some puzzling fish behaviour including that there were instances when, despite being offered sufficient amounts of feed, some fish chose to ignore the feed and consume almost no feed for many months; a behaviour that I found difficult to understand particularly since the feed was of such high quality.

The book is written with a clear audience in mind; anyone involved in aquaculture who would like to improve sustainable fish production. This is particularly clear from the 'Implications for Aquaculture' sections that round off each of the seven main chapters in the book. Its scope is very wide since it encompasses herbivorous to carnivorous species, extensive to intensive production, different production systems and the different purposes that aquaculture serves. They recognise that aquaculture is not just for food production but also production to supplement fish for conservation reasons and the production of ornamental species. Apart from appealing to those who aim to increase efficient and sustainable fish production, it will also interest students and teachers of aquaculture and fish

behaviour. Its style is clear and easily accessible, the authors avoiding obscure terminology and excessive citing of published work and yet it is clearly authoritative and comprehensive. The text is liberally sprinkled with interesting illustrations of behaviour such as the cooperative hunting sorties between groupers and moray eels. It shows that careful observation of fish can give clear information about welfare; for example the colour of the ring around the eye darkens in salmonids in response to various stressors and this acts as a social signal.

For the practising fish farmer there are helpful ways in which an understanding of fish behaviour can be used to improve production and welfare. A few examples that caught my attention are given here. In Chapter 4 the authors explain that growth and feed efficiency can be improved by optimising the swimming speed and since this is often a function of body length it pays to site farms for smaller fish in slower moving waters compared to larger fish. Similarly, the carefully considered placement of underwater lights will allow reduced stress. Fish have a clear pattern of behaviour such as preferred swimming depth and trajectories and these vary with, for instance, time of day and hunger level. Hence, lights should be placed at depths that allow them to express this natural preference but also to avoid creating excessively high densities. The provision of cover allows the reduction in cannibalism in a variety of species and similarly the provision of cover for wrasse and spatial information or landmarks allow salmon to seek the attention of these cleaner fish when they are co-habited to control lice numbers. The need to give fish sufficient opportunity to consume feed during a meal is well known but from chapter nine it is clear that even where increasing feeding opportunity further gives no increase in growth or efficiency, there can still be a benefit in reduced aggression

and thus less damage and a resultant improvement in health and value.

As for those odd-behaving salmon that did not consume any of my high quality feed for so many months, the answer lies within the book, so whether you simply wish to gain a better understanding of fish behaviour or are a fish farmer aiming to increase sustainable production, this book is for you.

V.O. Crampton, EWOS Innovation

1

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; captive rearing; consciousness; conservation; culture systems;

domestication; environmental protection; fish in research; food fish; ornamental fish; production; selective breeding; supplementation; sustainability; welfare.

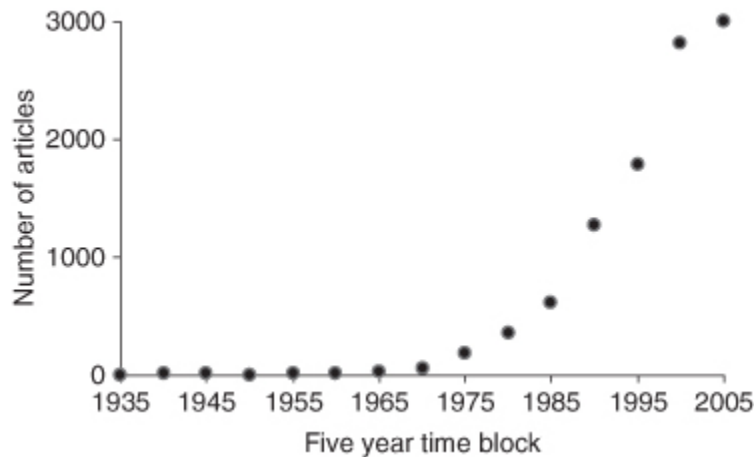
1.1 WHY BEHAVIOUR AND AQUACULTURE?

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 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.

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.



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 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.

Box 1.1 Further details of some cultured groups of Ostariophys

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 (*Aristichthys 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.

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, Paralichthyidae, 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

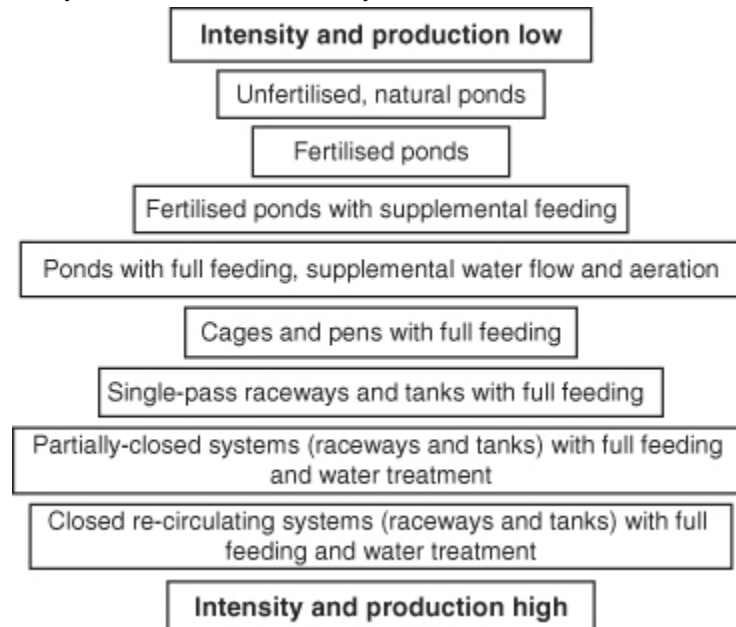
Extensive and intensive fish culture

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.

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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.