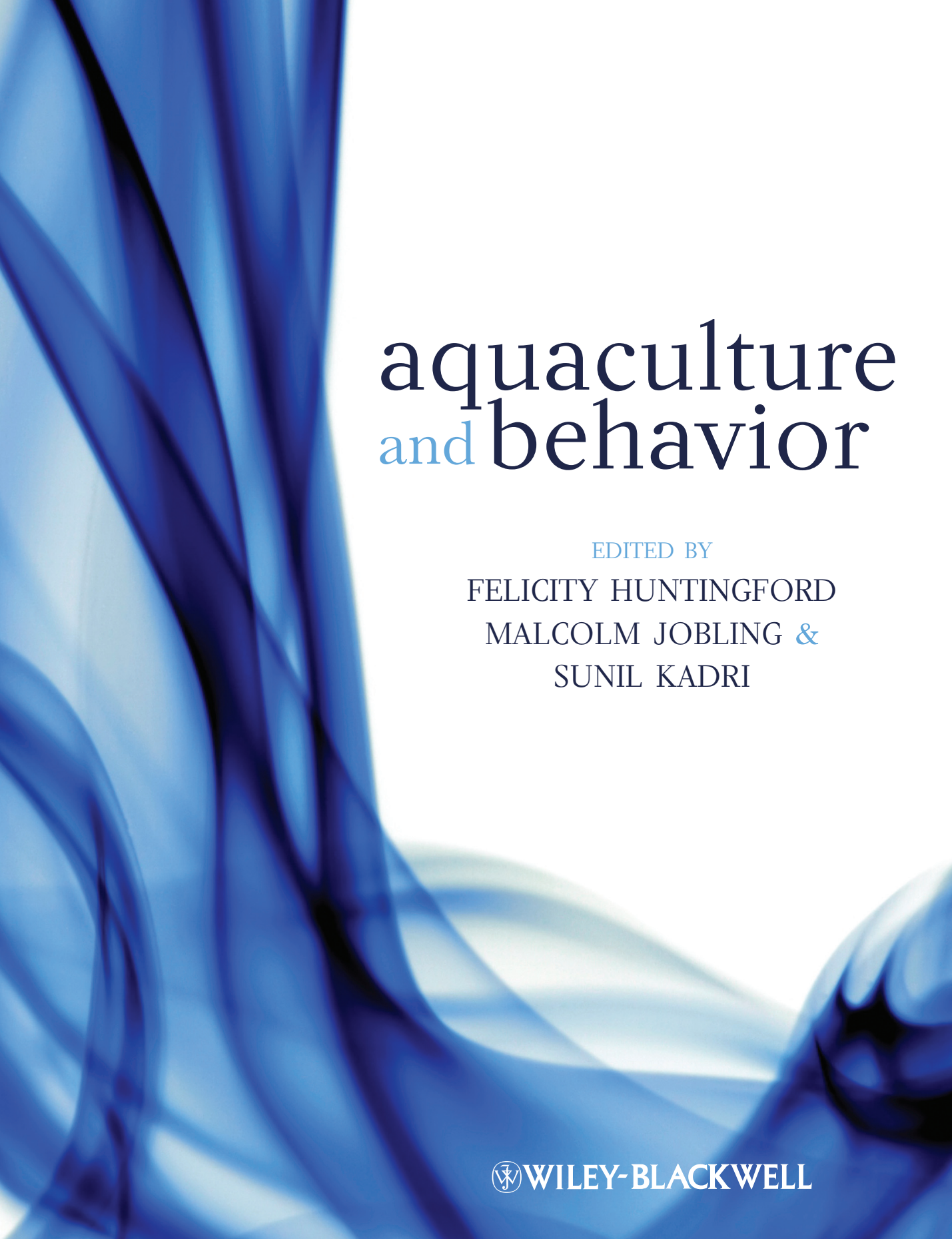


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aquaculture and behavior

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Aquaculture and Behavior

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Contents

<i>Contributors</i>	xiii
<i>Preface</i>	xiv
<i>Foreword by V.O. Crampton</i>	xvi
1 Introduction: Aquaculture and Behaviour	1
<i>Felicity Huntingford, Sunil Kadri and Malcolm Jobling</i>	
1.1 Why behaviour and aquaculture?	1
1.2 About aquaculture	2
1.2.1 What aquaculture is	2
1.2.2 Why finfish are cultured	2
1.2.3 Which finfish are cultured	3
1.2.4 Kinds of culture systems	5
1.3 Introducing the spotlight species	7
1.3.1 Fish farmed for the table	7
1.3.2 Fish farmed for supplementation programmes or conservation	10
1.3.3 Fish farmed as ornamentals and for research	11
1.4 About behaviour	14
1.4.1 What behaviour is and why biologists are interested in it	14
1.4.2 Some basic behavioural biology	14
1.4.3 How complex is fish behaviour?	19
1.5 Fish welfare	20
1.5.1 Definitions of welfare	20
1.5.2 Identifying and measuring welfare	20
1.5.3 Talking a common welfare language	24
1.6 Domestication, captive rearing and behaviour	24
1.6.1 Domestication and captive rearing	24
1.6.2 Selective breeding	25
1.6.3 Are cultured fish domesticated animals?	25
1.6.4 Behavioural responses to domestication and selective breeding	26
1.6.5 Captive rearing and fish behaviour	26
1.7 Criteria for effective and sustainable fish culture	27
1.7.1 Production criteria	27
1.7.2 Environmental criteria	27
1.7.3 Welfare criteria	29
1.7.4 Behaviour and effective, sustainable aquaculture	31
1.8 Structure and content of this book	32

2 Fish in Aquaculture Environments	36
<i>Malcolm Jobling</i>	
2.1 Introduction	36
2.1.1 Fish and their behaviour	37
2.2 Locomotion and swimming ability	37
2.2.1 Body form	37
2.2.2 Swimming muscles	39
2.3 Sensing environmental stimuli	39
2.3.1 Sensory cues in the aquatic environment	39
2.3.2 Vision	39
2.3.3 Mechanosensory systems	42
2.3.4 Thermoreception	44
2.3.5 Electroreception	44
2.3.6 Chemoreception	45
2.4 Internal communication systems	47
2.4.1 Role of the neural and endocrine systems	47
2.4.2 The nervous system	47
2.4.3 The endocrine system	49
2.4.4 Cross-talk between the nervous and endocrine system	51
2.5 Coping with adverse conditions	52
2.5.1 Unpredictable environments	52
2.5.2 The stress response	53
2.6 Contrasts in life history patterns and reproductive biology	55
2.6.1 Reproductive options	55
2.6.2 Rates of development	56
2.6.3 Developmental contrasts in farmed species	57
2.7 Life history programming	58
2.7.1 Genotype–environmental interactions	58
2.7.2 Maternal contributions	58
2.7.3 Environmental factors and the development of motor systems in fish	60
2.7.4 Long-term consequences of early developmental events	60
2.8 Synopsis	61
3 Tools for Studying the Behaviour of Farmed Fish	65
<i>Marie Laure Bégout, Sunil Kadri, Felicity Huntingford and Børge Damsgård</i>	
3.1 Introduction	65
3.2 Describing and measuring behaviour	66
3.3 What we need to know about the behaviour of farmed fish	67
3.4 Indirect reconstruction of the behaviour of cultured fish	67
3.4.1 Reconstructing fish diets	67
3.4.2 Reconstructing interactions with predators and rivals	68
3.4.3 Indirect assessment of stress	69
3.5 Methods of marking and tagging fish	69
3.5.1 External marks and tags	69
3.5.2 Internal tags	70
3.5.3 Internal tags that are visible externally	71
3.6 Direct behavioural observation via video monitoring	71

3.6.1	Video technology	71
3.6.2	Limitations	71
3.6.3	Preparation before sampling	72
3.6.4	Sampling	72
3.6.5	Analysis	72
3.6.6	An example of the use of video analysis to study the behaviour of PIT tagged fish	73
3.7	Direct behavioural monitoring using electronic tags	74
3.7.1	Electronic tagging	74
3.7.2	Types of electronic tag	75
3.7.3	Scanning stations	76
3.7.4	Examples of the use of electronic tags to study the behaviour of farmed fish	77
3.8	Direct behavioural monitoring using echo integration	77
3.8.1	Echo integration	78
3.8.2	Examples of the use of echo integration to monitor the behaviour of farmed fish	78
3.9	Measuring feeding behaviour in farmed fish	78
3.9.1	X-ray detection of feed intake	78
3.9.2	Self-feeding systems for controlling and monitoring feed delivery	78
3.9.3	Examples of the use of self-feeding on-demand systems to monitor feeding in farmed fish	80
3.9.4	Feedback systems for controlling and monitoring feed delivery	81
3.9.5	Examples of the use of interactive feedback systems to monitor feeding in farmed fish	82
3.10	Synopsis	82
4	Movement and Orientation	87
	<i>Felicity Huntingford, William Hunter and Victoria Braithwaite</i>	
4.1	Introduction	87
4.1.1	Space use in wild fish	88
4.2	Mechanisms	89
4.2.1	Spatially informative cues in the aquatic environment	89
4.2.2	How fish use spatial information	91
4.2.3	Effects of hormones on migration	92
4.2.4	Summary of the causes of space use and orientation in fish	93
4.3	Development	93
4.3.1	Ontogenetic changes in movement patterns	93
4.3.2	Inherited differences in space use	94
4.3.3	Effects of experience on space use and migration	95
4.3.4	Summary of the development of space use and orientation in fish	96
4.4	Functions	96
4.4.1	Benefits of adopting particular space use patterns	96
4.4.2	The costs of adopting particular space use patterns	97
4.4.3	Integrating costs and benefits	98
4.4.4	Summary of the functions of space use in fish	100
4.5	Implications for aquaculture	100
4.5.1	How fish use space in culture system	100
4.5.2	Problems during production arising from the ways in which fish use space	101
4.5.3	Space use problems when cultivating fish for purposes other than food	106
4.5.4	Solving problems in aquaculture arising from the biology of space use in fishes	107
4.5.5	Improving the effectiveness of general husbandry practices	109
4.6	Synopsis	112

5	Feeding Biology and Foraging	121
	<i>Malcolm Jobling, Anders Alanärä, Sunil Kadri and Felicity Huntingford</i>	
5.1	Introduction to the feeding biology of fishes	121
5.2	Foraging strategies of wild fish	122
5.2.1	What fish eat	122
5.2.2	How fish acquire food	123
5.2.3	Variability in foraging within species	123
5.3	Mechanisms	124
5.3.1	The sensory cues that fish use to locate food	124
5.3.2	The structures that fish use to gather food	126
5.3.3	Mechanisms for capture and ingestion of food	128
5.3.4	Summary of foraging mechanisms in fish	128
5.4	Development	129
5.4.1	Ontogeny of foraging	129
5.4.2	Inherited differences in foraging methods	130
5.4.3	Experience and foraging methods	131
5.4.4	Summary of the development of foraging patterns in fish	132
5.5	Functions	132
5.5.1	Benefits	132
5.5.2	Costs	132
5.5.3	Trading costs against benefits	133
5.5.4	Summary of functional aspects of foraging strategy	134
5.6	Implications for aquaculture	134
5.6.1	How cultured fish are fed	134
5.6.2	Problems during production arising from natural foraging patterns	137
5.6.3	Effects of domestication and captive rearing	139
5.6.4	Solving problems arising from the natural feeding biology of cultured fish	140
5.6.5	Mitigating the effects of domestication and captive rearing	143
5.7	Synopsis	143
6	Nutrition and Diet Choice	150
	<i>David Raubenheimer, Steve Simpson, Javier Sánchez-Vázquez, Felicity Huntingford, Sunil Kadri and Malcolm Jobling</i>	
6.1	Introduction to what fish eat	150
6.1.1	What fish need from the foods they eat	151
6.1.2	What fish choose to eat	152
6.2	Mechanisms	152
6.2.1	Mechanisms for selective foraging	152
6.2.2	Sensory inputs to diet choice	153
6.2.3	Post-ingestive signals and diet choice	155
6.2.4	Modulation of diet choice	156
6.2.5	Overview of the mechanisms controlling diet choice in fish	156
6.3	Development	157
6.3.1	Ontogeny of diet choice	157
6.3.2	Inherited differences in diet choice	159
6.3.3	Experience and diet choice	160
6.3.4	Summary of the development of diet choice	161
6.4	Functions	161
6.4.1	The behavioural ecology of energy-based diet choice	161

6.4.2	The nutritional ecology of diet choice	163
6.4.3	Summary of functional approaches to diet choice	166
6.5	Implications for aquaculture	166
6.5.1	The kinds of diet that cultured fish receive	166
6.5.2	Problems arising from the nutritional needs of cultured fish	169
6.5.3	Problems arising from natural dietary choices in cultured fish	169
6.5.4	Problems arising from domestication and captive rearing	171
6.5.5	Solutions to nutritional and behavioural problems relating to diet choice in cultured fish	171
6.5.6	Using nutritional ecology to solve problems in aquaculture	174
6.6	Synopsis	176
7	Appetite and Feed Intake	183
	<i>Malcolm Jobling, Anders Alanärä, Chris Noble, Javier Sánchez-Vázquez, Sunil Kadri and Felicity Huntingford</i>	
7.1	Introduction	183
7.1.1	Irregular changes in appetite	184
7.1.2	Regular changes in appetite: feeding rhythms	185
7.1.3	Feeding in relation to life history events	187
7.1.4	Feeding by diseased fish	188
7.2	Mechanisms	189
7.2.1	Mechanisms underlying meal-based changes in appetite	189
7.2.2	Mechanisms that control circadian rhythms	192
7.2.3	Mechanisms underlying circannual changes in appetite	194
7.2.4	Mechanisms underlying appetite changes in relation to life history events	194
7.2.5	Summary of the mechanisms underlying appetite changes in fish	195
7.3	Development	195
7.3.1	Ontogeny of appetite patterns	196
7.3.2	Genetic effects on appetite	197
7.3.3	Effects of experience on appetite	197
7.3.4	Summary of the development of appetite patterns	198
7.4	Functions	198
7.4.1	Costs and benefits of feeding at a particular rate	198
7.4.2	Costs and benefits of feeding at a particular time	199
7.4.3	Summary of the costs and benefits of appetite patterns	200
7.5	Implications for aquaculture	200
7.5.1	Patterns of feed delivery in fish culture	200
7.5.2	Problems for fish culture arising from natural appetite variation in fish	202
7.5.3	The effects of under-feeding	202
7.5.4	The effects of over-feeding	204
7.5.5	Failure to match feed delivery to natural appetite patterns	204
7.5.6	Solutions to problems for fish culture arising from natural appetite variation in fish	206
7.5.7	Domestication and captive rearing	208
7.6	Synopsis	209
8	Avoiding Predators	220
	<i>Felicity Huntingford, Susan Coyle and William Hunter</i>	
8.1	Introduction	220
8.1.1	How fish avoid being eaten by predators	220
8.1.2	Individual variation in risk taking	223

8.2	Mechanisms	224
8.2.1	External stimuli	224
8.2.2	The internal dynamics of fish schools	224
8.2.3	Some internal factors that control and mediate antipredator behaviour	224
8.2.4	Summary of the mechanisms that control predator avoidance in fish	225
8.3	Development	225
8.3.1	The ontogeny of predator avoidance	226
8.3.2	Genetic influences on antipredator behaviour in fish	227
8.3.3	Environmental effects	228
8.3.4	Summary of the development of predator avoidance	229
8.4	Functions	229
8.4.1	Benefits of antipredator behaviour	229
8.4.2	Costs of antipredator behaviour	230
8.4.3	Integrating costs and benefits	231
8.4.4	Summary of the functions of antipredator behaviour	231
8.5	Implications for aquaculture	232
8.5.1	The incidence of antipredator behaviour in culture systems	232
8.5.2	Adverse effects of antipredator behaviour in culture systems	233
8.5.3	Effects of domestication and captive rearing	234
8.5.4	Solutions to the problems arising from antipredator behaviour in fish culture	236
8.5.5	Using predators and antipredator behaviour in fish culture	237
8.5.6	Mitigating the effects of domestication and captive rearing	238
8.6	Synopsis	240
9	Fighting and Aggression	248
	<i>Børge Damsgård and Felicity Huntingford</i>	
9.1	Introduction	248
9.1.1	What aggression is	248
9.1.2	Aggression in the lives of fish	249
9.1.3	Territoriality and dominance	249
9.1.4	Individual variation in aggressiveness	250
9.2	Mechanisms	251
9.2.1	Stimuli from potential opponents	251
9.2.2	Effects of environmental factors	252
9.2.3	Internal factors	252
9.2.4	Effects of aggression on the neuroendocrine system	254
9.2.5	Summary of the mechanisms of aggression in fish	255
9.3	Development	256
9.3.1	Ontogeny of aggression	256
9.3.2	Genes and aggression	257
9.3.3	Environmental effects	258
9.3.4	Summary of the development of aggression	260
9.4	Functions	260
9.4.1	Benefits of winning fights	260
9.4.2	Costs of fighting	260
9.4.3	Integrating benefits and costs	261
9.4.4	Summary of the functions of aggression	263
9.5	Implications for aquaculture	263
9.5.1	The incidence of aggression in culture systems	264

9.5.2	Problematic consequences of aggression in aquaculture	265
9.5.3	Effects of domestication and captive rearing on aggressive behaviour in cultured fish	268
9.5.4	Solutions: controlling aggression during fish culture	270
9.5.5	Solutions: mitigating the effects of domestication and captive rearing	277
9.6	Synopsis	277
10	Reproductive Behaviour	286
	<i>Ian A. Fleming and Felicity Huntingford</i>	
10.1	Introduction	286
10.1.1	The reproductive biology of wild fish	287
10.1.2	The reproductive behaviour of wild fish	288
10.2	Mechanisms	291
10.2.1	The control of maturation in fish	291
10.2.2	The control of reproductive behaviour: external stimuli	292
10.2.3	The control of reproductive behaviour: neuroendocrine processes	293
10.2.4	Summary of the mechanisms that control the reproductive behaviour of fish	294
10.3	Development	295
10.3.1	Ontogenetic process	295
10.3.2	Genetic effects	295
10.3.3	Environmental effects	296
10.3.4	Summary of the development of reproductive behaviour in fish	297
10.4	Functions	297
10.4.1	Natural selection, sexual selection and reproduction	297
10.4.2	Differential selection on males and females	297
10.4.3	Functional aspects of the timing of life history events	298
10.4.4	Functional aspects of courtship	299
10.4.5	Functional aspects of parental care	301
10.4.6	Summary of the functions of reproductive behaviour in fish	301
10.5	Implications for aquaculture	302
10.5.1	Management of reproduction in cultured fish	302
10.5.2	Problems in production arising from the behavioural biology of fish reproduction	305
10.5.3	Problems arising from domestication and captive rearing	308
10.6	Solutions	310
10.6.1	Research into the natural breeding behaviour of cultured and candidate species	311
10.6.2	Providing the right physical environment for spawning	311
10.6.3	Providing the right social environment for spawning	311
10.6.4	Avoiding domestication	313
10.6.5	Mitigating the effects of captive rearing	313
10.7	Synopsis	314
11	Conclusions: Aquaculture and Behaviour	322
	<i>Felicity Huntingford, Malcolm Jobling and Sunil Kadri</i>	
11.1	The relevance of behaviour in current aquaculture systems	322
11.1.1	Aquaculture and its aims	322
11.1.2	The behaviour of fish in nature and in culture	323
11.1.3	Problems in fish culture arising from the natural behaviour of fish	323
11.1.4	Behavioural solutions to behavioural problems	325
11.1.5	Behavioural solutions to non-behavioural problems	326
11.1.6	A disclaimer	327

11.2	The relevance of behaviour in future aquaculture systems	327
11.2.1	Likely developments in aquaculture	327
11.2.2	Diversification of cultured species	327
11.2.3	Intensification of technology-based aquaculture	327
11.2.4	Molecular technology and selective breeding	328
11.2.5	Increased emphasis on environmental protection and fish welfare	328
11.2.6	Blurring distinction between aquaculture and commercial fisheries	329
11.2.7	Increased emphasis on aquaculture in conservation programmes	330
<i>Index</i>		333

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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

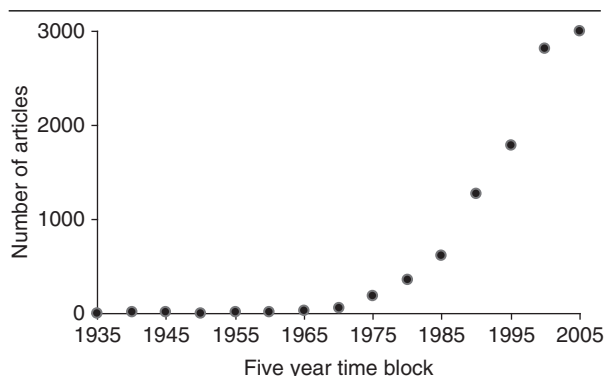


Figure 1.1. The number of papers on behaviour and aquaculture published in each 5 year period since 1935. Based on a Web of Science search using the key words behaviour (British and American spelling) and aquaculture.

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 stur-

geons, 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 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.

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 Scopthalmidae, 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

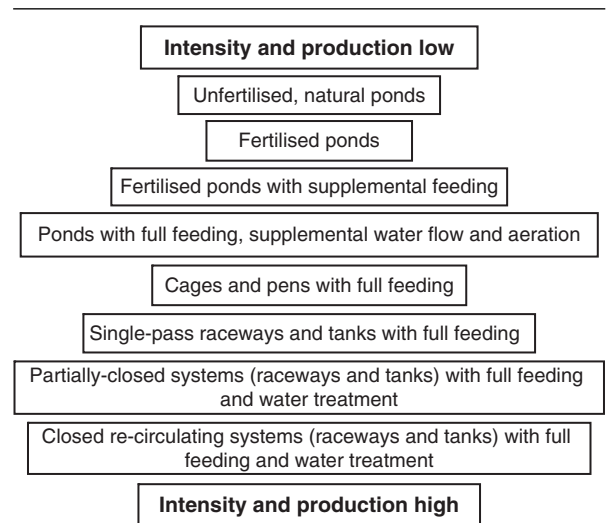


Figure 1.2. Schematic depiction of culture systems used for producing fish, classified in terms of intensity. Reproduced with permission from Le Francois *et al.* 2010.

failure is increased and the margin of error reduced compared to low-technology systems.

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

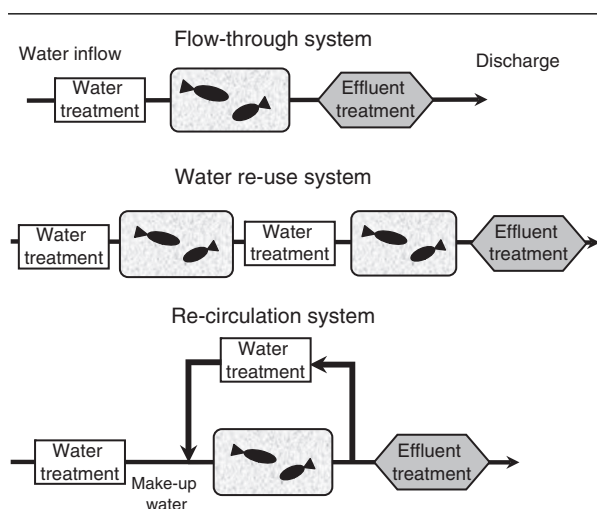


Figure 1.3. Schematic depiction of three water management systems used for producing fish. Reproduced with permission from Le Francois *et al.* 2010.

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 Fançois *et al.* 2010).

Rainbow trout (*Oncorhynchus mykiss*)

The Pacific salmon 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 salmonids 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 salmonids (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 salmonids 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 Poeciliidae, 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