

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