Fish Physiology
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Behaviour and Physiology of Fish

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BEHAVIOUR AND PHYSIOLOGY OF FISH

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Front Cover Photograph: The photo shows the mating position of the hamlet fish (Hypoplectrus unicolor, Serranidae) as they release gametes. The fish makes a unique mating sound while dispersing gametes (Lobel, 2002). These fish are simultaneous hermaphrodites, maintain long-term pair bonds, mate at sunset at least several times, and switch sex roles in between each mating event. Photo by P. S. Lobel, of fish located on a reef offshore of the Discovery Bay Marine Laboratory, Jamaica, West Indies.

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PREFACE

Volume 6 of the Fish Physiology series was the first to focus specifically on fish behaviour in relation to physiology. Almost thirty five years later, we are dedicating another volume of this internationally recognised series to the interrelations between behaviour and physiology in fish. Within the intervening period, several volumes had Chapters that considered fish behaviour; however, it is only in recent years that the integrative approach to fish behaviour and physiology has dramatically increased. The present volume (24) brings together these disciplines in a comprehensive review of the available literature with an additional introductory overview. The progression of Chapters focuses on different aspects in the life history of a fish, each written by scientists who are bridging the gap between behaviour and physiology in their own specialised discipline. In addition to contributing to our current knowledge on both fish behaviour and physiology, we hope that this volume will excite the future use of multidisciplinary approaches to understand the interplay between behaviour and physiology in fish.

The present Fish Physiology volume is a result of considerable effort and enthusiasm by the Chapter authors for which we are truly grateful. Without their dedication this book would not have materialised. Twenty referees, including Grant Brown, Jonathan Evans, Michael Fine, Richard Handy, Andrew Hendry, Felicity Huntingford, Masayuki Iigo, Rosemary Knapp, Jens Krause, Robin Liley, Edward Little, Carin Magnhagen, Anne Magurran, Justin Marshall, Steve McCormick, Tom Pottinger, Robert Poulin, Javier Sánchez-Vázquez, Alex Scott, and one referee who would like to remain anonymous, provided constructive guidance and have played an integral part in this project. We would also like to thank the series editors, Tony Farrell and Colin Brauner, for their never-ending support and Andrew Richford at Elsevier for publishing advice and encouragement. Our editorial association was initiated through McMaster University, Ontario where the idea for this volume was born. Our final thanks go to Chris Wood for recognising the potential for this volume.

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BEHAVIOUR AND PHYSIOLOGY OF FISH: AN INTRODUCTION

Niko Tinbergen, a pioneer of the study of animal behaviour, argued that to fully understand behaviour, research on the function of behaviour must be married with understanding the development, causation, and evolution of behaviour. Although these sentiments were presented several decades ago (see Tinbergen, 1963), interest in causation of behaviour had largely waned. Instead, most behavioural scientists have targeted questions about how behavioural mechanisms underlie an animal's relationship with its environment. Physiologists too have generally turned their back on studies examining the "regulation of behaviour" or the "mechanisms of behaviour," possibly frustrated with an apparent lack of ubiquitous principals. Today that gap between the two disciplines of behaviour and physiology is finally beginning to be filled. A renaissance of research has recently emerged, providing a much needed link between behavioural studies and physiology.

The integration of physiological laboratory studies and empirical behavioural field observations has been partly led by technical advances related to the neuroscience and molecular biology revolutions. Molecular genetic techniques such as real time PCR, gene sequencing, cellular physiology, proteomics, paternity analyses, and various new biochemical techniques to study hormone action, have literally transformed the fields of behavioural ecology and physiology. Only recently has attention been given to sequencing the whole genomes of fish species (zebrafish and two pufferfish species, medaka, salmon, and tilapia); these projects will undoubtedly shed light on the molecular mechanisms underlying many behavioural and physiological functions. The growth in neuroscience has also generated a watershed of techniques including EEG, EOG, ECG, intra and extracellular electrophysiological recordings, electromyogram biotelemetry, neuroimaging of neurochemical circuits, and gene expression levels in the brain. These techniques and tools have profoundly enabled the interplay between pure physiology and pure behavioural studies.

Fishes are particularly useful organisms to utilise in bridging the gap between behaviour and physiology. Fish comprise the most speciose vertebrate

order with over 25,000 species and an unrivaled diversity in life history patterns, breeding systems, sensory systems, as well as environmental requirements. Hence, fish provide an almost endless test-bed for either single species studies or comparative analyses of links between behaviour and physiology. Four fish groups may be particularly useful: zebrafish, sticklebacks, cichlids, and salmonids. As a consequence of their small body size and relatively large clutches, zebrafish have emerged as the major model system to study vertebrate development and gene function. Sticklebacks and cichlids have long been the major model organisms used by evolutionary and behavioural biologists. These two fish groups have undergone recent and extreme evolutionary radiations generating a large number of distinct populations (sticklebacks) and species (cichlids) accompanied by fascinating morphological, physiological, and behavioural changes. Salmonids are another model group because of their interesting life history, ecology, and distribution, as well as the economic importance of both wild and aquaculture salmonids.

The new era of interdisciplinary research and the recent proliferation of studies linking behaviour and physiology spawned the idea for this volume on Behaviour and Physiology for the Fish Physiology series. We wanted to document the active bridging of these two often separated areas of fish biology. Our aims were to provide a comprehensive review of the available literature, highlight the need for further links between behavioural and physiological studies, and stimulate new ideas by suggesting many possible avenues for future research.

We selected 10 topics mainly organised along a lifespan/life history theme, and attempted to highlight the most active areas where fish behaviour and physiology are closely related. Each Chapter was commissioned by research experts in that specialised subdiscipline and comprises a significant contribution to our scientific knowledge on both behaviour and physiology. The first two Chapters as well as the last Chapter of this book do not fit neatly into a life-span framework. However, the effects of cognition, communication, and pollution on physiological and behavioural processes play integral roles throughout the life-span of fish, and we felt that including such chapters was imperative.

In Chapter 1, Victoria Braithwaite outlines current knowledge on cognitive processes in fishes with particular emphasis on learning and memory capacities. Although only a few studies have been published on the neural basis of cognition, these imply a strong homology between fish brains and the brains of other vertebrates, suggesting that fishes will be useful for more general studies of the evolution of cognitive processes such as memory and learning. In Chapter 2, Gil Rosenthal and Phillip Lobel review the rapidly growing field of fish communication, including visual, chemical, acoustic, and mechanosensory signaling. They show how our understanding of

communication in all modalities has been bolstered by the use of playback techniques. They also stress that fish neurobiology is in its infancy and it would be wise to pay special attention to the role of early experience and ontogeny in general when considering communication abilities in fishes.

Spending time and energy avoiding predators and parasites is a necessity in fishes and other organisms. In Chapter 3, Mark Abrahams eloquently reviews the various options available to fish when avoiding predators and describes why the "grow big fast" rule is not the only one that makes sense. Using hormonal and genetic manipulation of fish that elevate and sustain growth hormone levels, salmon have been shown to be much more willing to risk exposure to a predator in order to gain access to additional food (Du *et al.*, 1992; Devlin *et al.*, 1994). Unlike predators, parasites more often than not have only sub-lethal physiological effects on hosts but these can still impact behaviour and population regulation. In Chapter 4, Iain Barber and Hazel Wright provide in-depth coverage of how fish parasites influence the behaviour and physiology of their hosts. For example, sticklebacks infected with a particular parasite (*Schistocephalus solidus)* increase food intake rates, apparently to compensate for the nutritional demands of the parasites (Ranta, 1995).

In Chapter 5, Jörgen Johnsson, Svante Winberg, and Katherine Sloman summarise recent research on the complex interrelationships between social behaviour and physiology in fish. They discuss the many interacting physiological factors that determine social status such as energetic status, metabolic rate, growth hormone and steroid levels. They show the short and long term physiological consequences of social status (neuroendocrinological stress response) and how these might be related to fitness (via growth rates and reproduction). They also explore how both biotic and abiotic environmental variation influence social relations, and how genetics may influence these interactions and generate stress-coping phenotypes with distinct physiological and behavioural characteristics.

Virtually all organisms show daily (circadian) or annual rhythms in their behaviour and metabolism. In Chapter 6, Irina Zhdanova and Stéphan Reebs describe our knowledge of fish circadian rhythms. An elaborate network of photosensitive, coexisting central and peripheral circadian oscillators has been identified in fishes, and a large number of circadian clock genes have recently been discovered in zebrafish. In fish, melatonin (secreted by the pineal gland) has long been considered the principal circadian hormone, and in most fish it is secreted only at night, as secretion is suppressed by bright light. They also discuss how other possible environmental factors (temperature, water chemistry, food availability, social interactions, and even predation risk) may act as synchronisers of the daily cycles. Migration for many fish species occurs on an annual rather than a daily cycle. In Chapter 7, a diverse team of scientists

(Scott Hinch, Steven Cooke, Michael Healey, and Tony Farrell) review current knowledge on the mechanisms underlying migration in fishes and use sockeye salmon as a model system. For example, in salmon the decision to leave the ocean seems to be closely related with the initiation of gonadal maturation (Ueda *et al.*, 2000); gonadotropin-releasing hormone (GnRH) triggering gonad growth and the onset of gonadal growth is associated with the shift from foraging to homing migration (Ueda and Yamauchi, 1995). Although a small number of fish species migrate (2.5%), the number of individuals that migrate is vast. Many of these species are important in fisheries, and migratory species seem to be at twice the risk of extinction as non-migratory species (Riede, 2004). Hence, understanding migration is crucial to successful management and conservation of many fish species.

Reproduction is the topic of the next two Chapters. In Chapter 8, Rui Oliveira reviews neuroendrocrine mechanisms of discrete within-sex reproductive variance, often called alternative reproductive tactics (ARTs). He finds broad support for the notion that like sex differentiation (male vs female), sex steroids provide the proximate control of ARTs. Brantley *et al.* (1993) found that conventional males had significantly higher levels of circulating 11-ketotestosterone (or KT, the most potent androgen in fish) compared to parasitic males. Oliveira updates the analysis, finding an even stronger association between ARTs and KT. However, differences in KT levels may in fact be a consequence, not a cause, of ARTs, as the various male morphs will have vastly different social experiences. Oliveira reviews how conventional and parasitic males differ in terms of steroid binding globulins, steroidogenic enzymes, steroid receptors, and in terms of various other neurochemical systems. In Chapter 9, Norm Stacey and Peter Sorensen review the evidence for reproductive pheromones in fishes. Pheromones are basically chemical odours or signals derived from hormones and other essential metabolites that coordinate or influence conspecific behaviour and/or physiology. Three chemical classes of reproductive pheromones have been identified in fishes; bile acids, sex steroids, and F prostaglandins. Using a number of model fish groups such as salmonids and carp, the authors show how sex steroid and prostaglandin pheromones, fairly ubiquitous among fishes, are both sensitive and specific in their behavioural and physiological effects on conspecifics.

The impact of human activities on aquatic ecosystems has unfortunately increased and intensified in recent years. In Chapter 10, Katherine Sloman and Rod Wilson explore the anthropogenic impacts upon fish behaviour and physiology; in particular they cover the effects of pollution (chemical contaminants) on fish cognition, sensory processes, predator-prey interactions, social behaviour, and reproduction of fishes. They examine the influence of inorganic chemicals (including metals) and organic contaminants on behaviour *via* physiological pathways. They show that there is likely to be

differential sensitivity to toxicants depending on the route of exposure and social status. For example, subordinate trout have higher uptake rates of waterborne copper and silver than dominant trout. However, if a toxicant is present in the diet, then a dominant fish is likely to accumulate toxicants faster as dominants may eat larger quantities of the available contaminated food. They end their Chapter with a plea for further interlinking of laboratory and field-based approaches in ecotoxicological studies that address not simply the effects of a single chemical but the cocktail of chemicals present in the aquatic environment.

Traditionally, behaviour and physiology have been considered two separate fields of enquiry with the majority of available literature focusing primarily on one or the other. The Chapters of this book underscore the fact that behaviour and physiology are inextricably linked. They advocate the need for interdisciplinary approaches to fully understand behaviour and physiology and to unravel many of the unanswered questions. New technologies and a growing recognition of the impact of physiology on life history has led behavioural ecologists to re-embrace Tinbergen's message, and the embryonic development of a more mechanistic study of behaviour has certainly begun in earnest (Ricklefs and Wikelski, 2002; Costa and Sinervo, 2004). Understanding the pattern of behaviour is no longer sufficient; there is an increased and growing interest in understanding the physiological mechanisms underlying particular behaviours. Physiologists too have increased their emphasis on field studies and recognise the need to assess the fitness implications of different physiological functions linked to behaviour. In conclusion, we hope that this book will contribute to our knowledge on both behaviour and physiology, but will more importantly highlight the increasing need for additional multidisciplinary research in this area.

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