Preface

Fish accomplish most of their basic behaviors by swimming. Swimming is fundamental in a vast majority of fish species for feeding, avoiding predation, finding food, mating, migrating and finding optimal physical environments. Fish exhibit a wide variety of swimming patterns and behaviors. Some fish, such as tuna, never stop swimming. Others, such as sit-and-wait predators, swim only for a relatively small proportion of time. However, even in these species, swimming performance is critical for their fitness, since it determines feeding success. Within their performance boundaries, fish choose how to swim (e.g., at what speed), and these choices have profound consequences for their energetics, feeding and vulnerability, and therefore for their overall fitness.

Fish swimming also underlies many ecological processes. At its most basic, ecology is the study of the abundance and distribution of organisms—with movement, energetics, reproduction, predator-prey relationships and migration, all contributing. Locomotion plays a major role in all of these activities. Locomotor performance plays a role in defining the boundaries of the realized niche, in terms of defining, for example, habitats with current speeds that fish can endure, given their swimming capabilities. Locomotion is also fundamental in determining the smaller realized niche, i.e., the food items that can be caught by using certain locomotor patterns or performance during feeding events. In addition, the physical properties of the environment, in terms of temperature, oxygen level and current speed, are also important determinants of fish distribution, largely through their effect on fish swimming performance.

While swimming is fundamental for the fish's ecology and behavior, historically fish swimming has been studied mainly from biomechanical and physiological perspectives (Webb, 1975; Blake, 1983; Videler, 1993). More recent work has highlighted the importance of integrating these perspectives within a holistic approach that includes ecology and behavior. The aim of this book is to look at fish swimming from behavioral and ecological perspectives. Authors from various backgrounds, all interested in fish swimming from different points of view, were invited to contribute to this book with the goal of integrating various approaches while stressing the ecological and behavioral relevance of specific aspects of fish locomotion.

The first two Chapters of the book focus on how fish deal with flow. This issue is relevant for the ecology of fish, since their ability to stabilize body posture and swimming trajectories perturbed by turbulent flows affects fish species distributions and densities, and hence fish assemblages in various habitats (Chapter 1, Webb *et al.*). Webb *et al.* introduce the subject by focusing first on the physics of fish-flow interactions, followed by a review of methods used to measure turbulence. They discuss fish swimming performance in unsteady flow, in terms of energetics and behavior, and put these issues within the context of fish assemblages in typical flow environments such as rivers, shorelines and coral reefs. Blake and Chan (Chapter 2) review the biomechanics of rheotactic behavior (defined as the orientation to flow and associated behavior), discussing morphological, biomechanical, energetic and behavioral aspects. Rheotaxis is a common phenomenon found in benthic fish that live in currents, and it allows fish to avoid displacement in a flow, thus remaining in their habitat for feeding, finding mates and protection. Adaptations for rheotaxis include morphological structures (e.g., suckers) and behavioral strategies (e.g., burying). The Chapter discusses the ecomorphology of rheotaxis while reviewing the basic physics of displacement by slipping and lift-off, and gives a simple dimensional model of the scaling of these speeds with size and in relation to current speeds. The metabolic cost of station holding is discussed in various case studies. Specific examples of interaction with a substrates are also given regarding fast starting in flatfish and the attachment behavior of remoras.

A fish's choice to swim in a certain mode and at a certain speeds, has fundamental energetic and survival consequences (Chapters 3 and 4). While flow in natural systems implies a number of adaptations in fishes, in recent years a further issue has become quite relevant, that of habitat modification in streams. This has often causes habitat fragmentation, which is a major factor contributing to reductions in biodiversity and species abundance worldwide (Chapter 3, Castro Santos and Haro). These authors discuss the ability of fish to pass barriers during both up- and downstream migrations. Fishway performance is quantified as the rate of passage past barriers, which is affected by both swimming performance and behavioral factors. Castro-Santos and Haro describe motivating and orienting cues and discuss how these can affect passage performance. The authors conclude that the challenge of fish passage is both physiological and behavioral, and neither component is sufficient on its own to produce consistent and acceptable fishway performance. In addition, fish have developed various behavioral adaptations for minimizing the cost of swimming, whether this implies holding station in a flow or swimming in still water (Chapter 4, Fish). Chapter 4 discusses a number of ways fish can minimize energy expenditure while swimming, including locomotor strategies, such as optimizing swimming speed (i.e., for minimal cost of transport), burst and coast swimming (minimizing drag during the coast phase), schooling (swimming in the wake of neighbors), hitch hiking (as in remoras), drafting (taking advantage of the wakes created by object upstream). These strategies are discussed within a biomechanical, behavioural and ecological context.

In addition to dealing with the physical environment, swimming is used by fish during interactions with other animals, including conspecifics, predators and prey (Chapters 5–8). A common behaviour used by most fish species to avoid being preyed upon is the escape response. In Chapter 5, Domenici reviews escape responses from the standpoint of kinematics, ecomorphology and behavior. Escape success is not only determined by swimming performance but also by behavioral variables such as readiness and directions of escape. Intra and interspecific variability in escape response is also discussed. The links between escape performance, body design and habitat types is discussed within an ecological context, focusing on of the significance of escape responses during predator-prey interactions. For most fish species, locomotion plays integral roles in the two fundamental phases of energy acquisition: searching for food and feeding (Chapter 6, Rice and Hale). These authors discuss the locomotor demands for different feeding modes. In addition to the characteristics of the predator and prey, Hale and Rice discuss the effect of the physical environment of feeding, since feeding patterns differ between structurally complex and open habitats. Various behavioral patterns of feeding are described, and the functional and ecological significance of the different locomotor patterns employed for feeding and foraging in fishes are outlined and discussed. Langerhans and Reznick (Chapter 7) put the issues raised in the preceding Chapters on predator-prey interactions and water flow within an evolutionary context. They discuss some of the major ecological factors that might have shaped the evolution of locomotor performance in fishes. Using an integrative approach, they show how morphology and swimming performance are shaped by other factors that affect fitness, such as escape from predators or reproduction. By combining analyses among species with analyses among populations within species, they show how morphology and performance can evolve as local adaptations to risk of predation, but also how the evolution of performance can also interact with or be shaped by the evolution of life histories. Swimming is an integral part of courtship of males of various fish species. Sexual selection acts on male swimming performance to modify size and shape of the body and fins. In Chapter 8 , Kodric-Brown reviews the importance of sexual selection in the elaboration of fins and courtship behavior in male fishes. The Chapter discusses how sexual selection, acting within the framework of ecological, morphological and physiological constraints, can affect swimming performance. In addition, scaling issues, such as interactions between body size, sexual size dimorphism, secondary sexual traits, courtship behavior, and metabolism also affect swimming performance.

Environmental factors such as temperature, oxygen and salinity can have a profound effect on swimming performance and , as a consequence, on all those behaviors that involve swimming (Chapters 9 and 10). Wilson *et al.* (Chapter 9) review the effect of these factors focusing on unsteady swimming manoeuvres, and discuss the potential consequences of these effects for predator-prey and mating encounters. They show that a number of environmental factors, such as hypoxia and pollutants which are present with increasing trends in coastal areas, can have profound effects on fish swimming behavior. They conclude that an integrated approach is necessary to predict impacts of both natural and anthropogenic global change on the behaviour of fish. McKenzie and Claireaux (Chapter 10) discuss the effect of environmental factors on the physiology of aerobic exercise, i.e., endurance swimming such as that used for migration and searching for food. Their Chapter shows that temperature, salinity, oxygen and pollutants can all have a significant impact on swimming performance, with important potential consequences for fish in their natural environment. Similarly, the behavioral responses to hypoxia may have major ecological implications: some species reduce their swimming activity until conditions improve, and other species may migrate away towards less hypoxic areas.

A dual approach using both field and laboratory observations of swimming speed is fundamental for our understanding of how fish swimming performance can have ecological consequences (Chapters 11 and 12). This approach is used in Chapter 11 by Fisher and Leis, in which they discuss the importance of swimming performance in the ecology of larval fishes. Evaluation of the swimming performance of various species of larval fishes reveals considerable variance. This has major consequences for their energetics and feeding ecology, their overall dispersal and connectivity patterns, and the degree to which recruitment is an active processes involving specific habitat choice and timing. Although larvae are not the passive particles they were once considered, neither are all larval fish equivalent in their behaviour and ecology, even if they may occupy a similar habitat. Fisher and Leis conclude that intraspecifc differences in larval swimming performance need to be carefully considered when developing ecological and bio-physical models involving larvae. Fulton discusses the role of swimming performance in the ecology of reef fishes in Chapter 12. It appears that one group, the labriform-swimming fishes, have emerged as the dominant occupants of coral and rocky reefs around the world. Using solely their pectoral fins to produce thrust, around 60% of reef fish taxa utilize labriform locomotion during their daily activities. Chapter 12 discusses the ecomorphological characteristics of this group using laboratory and field-based measures of swimming performance and patterns of habitat-use across micro-, meso- and macro-ecological scales. Fulton concludes that labriform swimming combines high speed performance with efficiency and flexibility to provide a highly versatile mode of swimming suited to the challenges of a reef-associated lifestyle.

The next two Chapters (Chapter 13 and Chapter 14) deal with telemetry observations of fish movements in the field. Sims (Chapter 13) discusses recent developments in the swimming behavior and energetics of sharks. The movements of sharks, their relative behavior and distribution patterns have remained largely unknown for many species. Chapter 13 discusses a new approach for analysing and interpreting the movement patterns of free-ranging sharks. Sims describes the typical generalised movement patterns of free-ranging sharks recorded using electronic tags, and how this new technology has revolutionised shark behavioural ecology. The Chapter identifies how movement types can be linked to habitat types and how foraging models can be used to test habitat selection processes in sharks. Furthermore, the Chapter discusses a new approach of analysing shark movement data that uses methods from statistical physics (Levy walk) to evaluate behavioural performance in relation to environment. Chapter 14 (Bernal *et al.*) discusses the field observations of the movement of large pelagic fishes by putting them within an ecophysiological context. This Chapter describes the species-specific swimming and movement patterns of tunas, billfishes, and large pelagic sharks derived from extensive data sets obtained using acoustic telemetry and electronic data-archiving tags. The results are then interpreted based on the current understanding of the physiological abilities of each species, while integrating these concepts with other important ecological factors such as prey movements and availability. Bernal *et al.* conclude that although groups of large pelagic predators may occupy similar geographic areas (exploited by the same fisheries), they really occupy largely separate ecosystems. This can have major implications for effective fishery management policies, resource conservation, and for the population assessments upon which they must ultimately be based. These species-specific differences also provide a wealth of opportunities for developing a fundamental understanding of the ecophysiology of these fishes.

For commercial marine fish species, swimming performance is not only important for their foraging, migration, predator-prey interactions, but also in predicting their vulnerability to fishing gears. The final Chapter (Chapter 15, He) discusses the swimming capacity of marine fishes and its role in capture by fishing gears. Swimming performance is relevant for capture processes in both active (such as trawls and purse seines) and passive (such as gillnets, longlines and traps) fishing gears. Swimming ability varies among species and sizes of the fish and can be influenced by environmental factors such as water temperature. As a result, swimming ability of fish may affect size and species selectivity of the gear and affect seasonal and spatial differences in availability and catchability, with important implications in commercial fisheries and stock assessment surveys.

This book aims at filling a gap in the literature, by adding behavioral and ecological viewpoints to the more traditional biomechanics, ecomorphology and physiological perspectives used in studies of fish swimming. The book is therefore largely integrative by its own nature, and it includes considerations related to fisheries, conservation and evolution. This book is aimed at students and researchers interested in fish swimming from any organismal background, be it biomechanics, ecomorphology, physiology, behavior or ecology.

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