

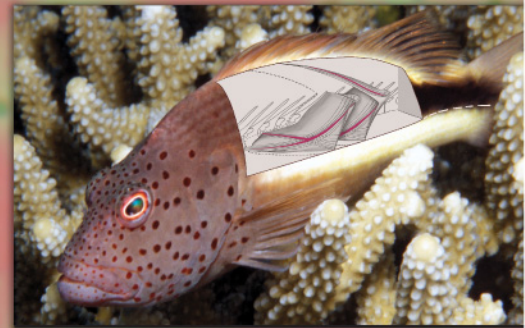
Fish Physiology
Volume 23



Shadwick
Lauder

Fish Biomechanics

Fish Biomechanics



Ever since the time of Aristotle, people have been interested in how animals work. In his wide-ranging studies of animals, Aristotle wondered specifically about how fish swim and how they function in their watery world, and he even applied basic ideas of mechanics and engineering to the study of biology. This type of research, now called biomechanics, has emerged in the past twenty years as a burgeoning enterprise that integrates approaches from engineering with studies of animal function.

With over 28,000 species, fishes are the largest clade of vertebrates and demonstrate remarkable diversity in body form, ecology, behavior, and physiology. Fishes are critical components of the earth's environment and understanding how fishes function is essential for future advances in conservation and fisheries biology, understanding major patterns in the evolution of fishes, and in the construction of new underwater robots based on principles of fish functional design.

In FISH BIOMECHANICS, leading workers in the area of biomechanics review major functional systems in fishes, and provide an overview of new approaches and techniques that are allowing long-standing questions about fish functional design to be addressed. Chapters are written to allow the non-specialist in biomechanics to understand the approaches and concepts that underlie the remarkable recent advances in our understanding of fish respiration, locomotion, prey capture, physiology, and sensing of the environment.

Coverage includes:

- Full color summary figures and explanatory diagrams
- Extensive coverage in rapidly expanding area of biomechanics research
- Comprehensive review of recent literature on fish biomechanics
- First volume in over twenty years on this subject
- Contributions by leaders in the field

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FISH BIOMECHANICS

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PREFACE

This is the first multi-authored volume on fish biomechanics to appear in over twenty years. In that time the field has grown immensely, with many new experimenters using new experimental techniques to probe questions of how fish work. Consequently, the published literature in fish biomechanics has grown rapidly, and it is time for a comprehensive review and synthesis of the important findings of recent research to update the classic *Fish Biomechanics* volume edited by Paul Webb and Danny Weihs in 1983.

This book begins at the front end of the fish with important biomechanical events that involve the head: breathing and eating. The complexity of head structure is one of the most distinctive and evolutionarily interesting aspects of fishes. The interaction of bones, joints and muscles of the head is highlighted in Chapter 1 by Brainerd and Ferry-Graham in their review of the mechanics of respiratory pumping. They discuss two-phase (suction and pressure) pumps as well as ram ventilation and air breathing. The theme of head structure as a set of muscle-powered levers and linkage bars is further elaborated in Chapters 2 and 3 which present detailed accounts of feeding mechanics, a classic illustration of an elegant form and function relationship. Westneat reviews the great diversity of skull morphologies and feeding strategies in fish groups, showing how different kinematic models have been developed, and provides clear illustrations based on high speed videography, as well as discussions of muscle activity patterns associated with feeding activities and their evolutionary relationships. Wainwright then describes how the pharyngeal jaw apparatus, a unique aspect of fish trophic biology, is designed from multiple skeletal elements modified from gill arches. He summarizes recent work on the morphology and the kinematics of pharyngeal jaws based on experimental approaches of cineradiography and sonomicrometry.

Apart from breathing and eating, one of the most important and interesting activities fishes perform is locomotion, and this is broadly the focus of the remainder of the book. Swimming and maintaining hydrostatic equilibrium go hand in hand; in Chapter 4 Coombs and van Netten discuss the structure and biomechanical features of the lateral line system as a collection of flow sensors, and how this system is used to provide information to the fish about

the hydrodynamic structure of its environment that aids locomotion and behavior. The body of a fish can be regarded as a complex mechanical structure, in which muscles generate forces and movement, while skeletal elements bear the loads and link the internal muscle action to the external resistive fluid medium. In Chapter 5 Summers and Long provide an overview of the engineering principles used to analyse both the static and dynamic mechanical properties of biological materials, and then discuss current data on the mechanical behaviour of fish skeletal tissues in the context of the various locomotor modes of fishes. A major focus of research on fish swimming has been the contractile properties of locomotor muscles, most recently advanced by use of the *in vitro* work loop technique to study power production under simulated swimming conditions. In Chapter 6 Syme provides a comprehensive review of the biomechanical properties of skeletal muscle, and shows how studies of isolated muscle have been used to understand the various strategies fish use to power swimming under different conditions. The use of muscle in undulatory swimming is further considered in Chapter 7 where Shadwick and Gemballa describe the structural organization of the lateral myomeres and their connective tissue linkages as the pathway of force transmission along the body. They also discuss body kinematics and muscle dynamics in steady swimming, noting the general trends as well as the exceptions exhibited by the highly specialized tunas and lamnid sharks. The important problem of maintaining both stability and maneuverability is discussed in detail by Webb in Chapter 8, illustrating the elegant biomechanical solutions attained by fishes, and highlighting the importance of this knowledge in biomimetic designs of underwater autonomous vehicles. Wakeling reviews the specific problem of unsteady fast-start maneuvers in Chapter 9, by considering the sequence of events that initiate muscle contraction, bend the body, and generate the hydrodynamic forces that accelerate the fish. The fast-start (c-start) escape response of fishes has been of great importance as a system for understanding the neural control of behavior, and this chapter provides a synthesis of recent advances in the biomechanics of fish escape responses.

Fish pectoral fin function during locomotion has received a great deal of attention in the past twenty years. In Chapter 10, Drucker and his colleagues review a large amount of data on pectoral fin morphology, kinematics, and hydrodynamics, and discuss the ecological implications of different pectoral fin designs. Perhaps the most noticeable feature of fish locomotion is the bending of the body; Lauder and Tytell update classical descriptions of undulatory locomotion with recent experimental data in Chapter 11, where they also discuss new hydrodynamic data from freely-swimming fishes that highlight the importance of three-dimensional effects. Finally, biomechanical approaches are moving out of the laboratory and playing an increasing role in understanding the field behavior of fishes and helping in conservation efforts.

PREFACE

xiii

In Chapter 12, Castro-Santos and Haro synthesize a large body of work on the migration and passage of fishes around dams, and describe new tagging technology and bioenergetic models that will guide future efforts in conserving fish stocks.

The editors wish to thank David Randall and Tony Farrell for help and encouragement in the formulation of this volume, Andrew Richford and Kirsten Funk at Academic Press offices in London and San Diego for shepherding this volume through the publication process. Numerous colleagues provided insightful reviews of chapter drafts, and we thank all the authors for their patience and cooperation throughout this endeavour.

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CONTENTS

CONTRIBUTORS	ix
PREFACE	xi
1. Mechanics of Respiratory Pumps <i>Elizabeth L. Brainerd and Lara A. Ferry-Graham</i>	
I. Introduction	1
II. Aquatic Respiratory Pumps	2
III. Aerial Respiratory Pumps	14
IV. Future Directions	24
References	25
2. Skull Biomechanics and Suction Feeding in Fishes <i>Mark W. Westneat</i>	
I. Introduction	29
II. Skull Morphology and Mechanisms	31
III. Biomechanical Models of Skull Function	36
IV. Suction Feeding for Prey Capture	42
V. Ecomorphology of Fish Feeding	59
VI. Phylogenetic Patterns of Feeding in Fishes	63
VII. Summary and Conclusions	68
References	68
3. Functional Morphology of the Pharyngeal Jaw Apparatus <i>Peter C. Wainwright</i>	
I. Introduction	77
II. The Pharyngeal Jaw Apparatus of Perciform Fishes	79

III. Innovation in the Pharyngeal Jaw Apparatus	90
IV. Summary	98
References	99
4. The Hydrodynamics and Structural Mechanics of the Lateral Line System	
<i>Sheryl Coombs and Sietse van Netten</i>	
I. Introduction	103
II. General Function, Structure, and Organization	107
III. Hair Cell Micromechanics	111
IV. Lateral Line Mechanics and Hydrodynamics	116
V. Concluding Remarks	132
References	134
5. Skin and Bones, Sinew and Gristle: The Mechanical Behaviour of Fish Skeletal Tissues	
<i>Adam P. Summers and John H. Long, Jr.</i>	
I. Introduction	141
II. A Primer on Mechanical Behaviour	144
III. Bone	152
IV. Cartilage	155
V. Tendon	160
VI. Skin	162
VII. Whole Body Mechanics	167
VIII. Conclusions	171
References	172
6. Functional Properties of Skeletal Muscle	
<i>Douglas A. Syme</i>	
I. Introduction	179
II. Ultrastructure	181
III. Fiber Types	182
IV. Patterns of Innervation	187
V. Mechanics of Contraction	189
VI. Scaling	208
VII. Axial Variation	211

CONTENTS

vii

VIII. Effects of Temperature	218
IX. Summary	228
X. Future Directions	231
References	232
7. Structure, Kinematics, and Muscle Dynamics in Undulatory Swimming	
<i>Robert E. Shadwick and Sven Gemballa</i>	
I. Introduction	241
II. Myomere Structure and Force Transmission Pathways	243
III. Steady Swimming Kinematics	252
IV. Muscle Dynamics Along the Body in Steady Swimming	258
V. Specializations in Thunniform Swimmers	268
VI. Summary and Future Directions	273
References	274
8. Stability and Maneuverability	
<i>Paul W. Webb</i>	
I. Introduction	281
II. General principles	282
III. Stability	303
IV. Maneuvering	312
V. Future Directions	319
References	321
9. Fast-start Mechanics	
<i>James M. Wakeling</i>	
I. Introduction	333
II. Initiation of the Fast Start	335
III. Muscular Contraction Acts to Bend the Fish	338
IV. Stage 1 Body Bending Occurs with a Traveling Wave of Curvature	342
V. Muscle Power Production and Force Transmission to the Water	346
VI. Hydrodynamic Forces Accelerate the Body	350
VII. Variations in Fast-Start Performance	357
VIII. Conclusions	361
IX. Future Directions	362
References	363

10. Mechanics of Pectoral Fin Swimming in Fishes <i>Eliot G. Drucker, Jeffrey A. Walker, and Mark W. Westneat</i>	
I. Introduction	369
II. Pectoral Fin Morphology	370
III. Motor Patterns of Pectoral Fin Locomotion	375
IV. Pectoral Fin Kinematics	379
V. Fluid Dynamics	392
VI. Pectoral Fin Swimming Performance	406
VII. Ecomorphology of Pectoral Fin Propulsion	412
VIII. Summary and Areas for Future Research	416
References	417
11. Hydrodynamics of Undulatory Propulsion <i>George V. Lauder and Eric D. Tytell</i>	
I. Introduction	425
II. Classical Modes of Undulatory Propulsion	426
III. Theory of Undulatory Propulsion	430
IV. Experimental Hydrodynamics of Undulatory Propulsion	438
V. Integrating Theory and Experimental Data	460
VI. Prospectus	461
References	462
12. Biomechanics and Fisheries Conservation <i>Theodore Castro-Santos and Alex Haro</i>	
I. Introduction	469
II. Riverine Migrations	471
III. Towed Fishing Gear	492
IV. Intraspecific Diversity	494
V. Bioenergetics Modeling	498
VI. Conclusions and Recommendations	504
References	507
INDEX	525
OTHER VOLUMES IN THE SERIES	541