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Responses and adaptations to the environment: An introduction

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Abstract

Fishes live in diverse and highly variable environments. These environments, over evolutionary (many generations) and lifetime (within a single generation) time scales, have shaped the biochemical and physiological mechanisms that allow fish to not only survive but thrive in their environments. Fishes offer a remarkable group of study organisms in which to understand how environmental signals are transduced through the organisms to ultimately shape physiological performance through both phenotypic plasticity and evolutionary adaptations. For fish physiologists, our experimental frameworks are grounded in the comparative physiology framework where we can study closely related fishes that live across a diversity of environments to understand what physiological and biochemical mechanisms are important to live in a particular environment. In addition, by examining responses to environment over different biological scales (from the molecular to the physiological level and beyond to ecology), we can get a better understanding of all the different pieces of a complex puzzle that are necessary to live in a wide variety of aquatic environments. Our understanding of the responses and adaptations of fishes to the environment is not only important for understanding how fishes can live where they do but also is critical in our ability to predict how changes in environmental conditions, such as temperature, dissolved oxygen or dissolved carbon dioxide, will impact fish populations across the world.

Temperature

Effects of Temperature: An Introduction

Patricia M. Schulte

Effects of Climate Warming

Fredrik Jutfelt, Timothy D. Clark, Rasmus Ern, Robine H.J. Leeuwis

Measures of Thermal Tolerance

Andrea J. Morash

Temperature and Fish Biology: Insights from Metabolism

Kenneth W. Zillig

Responses and Adaptations of Cellular Metabolism to Temperature

Tony J. Hickey, Alice Harford, Jules Devaux

Case Study: The Desert Pupfish

Stanley D. Hillyard, Frank van Breukelen

Hypoxia

Oxygen in the Marine Environment

Brad A. Seibel

The Hypoxic Ventilatory Response and Oxygen Sensing in Fishes

Brittney G. Borowiec, Erin M. Leonard

Metabolic Rate Depression as a Mechanism for Surviving Hypoxia

Alexandre Goudreau, Jeffrey G. Richards, Matthew D. Regan

Anaerobic Metabolism in Fish

Yuxiang Wang, Jeffrey G. Richards

Case Study: Anoxia Tolerance in the Pacific Hagfish (*Eptatretus stoutii*)*Maria A. Yutsyshyna, Todd E. Gillis***Case Study: The Anoxia-Tolerant Crucian Carp***Sjannie Lefevre, Göran E. Nilsson***Hypercapnia****Acid-Base Regulation and Hypercapnia: An Introduction***Martin Tresguerres***Integrative Responses to Hypercapnia***Ryan B. Shartau, Daniel W. Baker***Additional chapters: Advancing the field****Multiple Stressors: Physiological Responses to Multivariate Environments***Essie M. Rodgers, Daniel E. Gomez Isaza***Epigenetic Mechanisms in Response to Environmental Change***David C.H. Metzger***Adaptation to Hydrogen Sulfide: A Case Study in Sulfide Spring Fishes***Nick Barts, Michi Tobler*

Fish are remarkable organisms. It doesn't take more than a trip to a local aquarium to see the diversity of morphologies and behaviors that fishes possess. Incredibly, their underlying biochemistry and physiology is similarly diverse and, like other phenotypic traits such as morphology and behavior, are a product of the varied environments in which these fishes live and how those environments interact with their genetic make-up, or genotype. Our ability to uncover how fishes respond to their environment through phenotypic plasticity and evolutionary adaptation takes both straightforward and creative scientific approaches. As fish physiologists, many of our experimental frameworks are grounded in the comparative approach, where we can study closely related species that live across a diversity of environments to identify unique biochemical and physiological strategies and adaptations that allow a particular species of fish to thrive in a particular environment. We can also study a diversity of species that inhabit the same habitat to uncover unifying challenges of those environments that have shaped physiological adaptations. In 1929, Danish physiologist August Krogh stated, "For a large number of problems there will be some animal of choice or a few such animals, on which it can be most conveniently studied". The August Krogh Principle continues to inspire fish physiologists as they strive to more holistically understand the diversity of biochemical and physiological strategies fishes use to respond to their environments.

It is important to recognize that fishes cannot adopt any biochemical or physiological strategy to respond to changes in their environment. Instead, all living organisms are constrained by chemical and physical laws, and through evolutionary processes they acquire phenotypic traits that are a product of how their genes respond to external conditions and obey these laws. Therefore, it is the combination of unifying and diverse 'adaptations' that teach us how organisms can solve challenges in their natural environment. As we begin to understand the biochemical and physiological adaptations of species in particular environments, it's like adding pieces to a complicated puzzle. The more pieces we have, the greater our capacity to predict the overall picture illustrated in the puzzle and this has allowed us to extend our understanding of environmental responses and adaptations to fishes we cannot study. In terms of environments, "extreme" is in the eye of the beholder. What would be considered an extreme and life threatening environment for many fishes is commonplace for others. In the chapters that follow, how fishes respond to their different environments will be uncovered with an eye to showing how our research community got to where we are today, what questions fascinate us and what is left to uncover so we can best predict the vulnerability of fish populations to anthropogenic change.

This section of the Encyclopedia starts with a focus on three specific abiotic factors (i.e., temperature, dissolved oxygen, and dissolved carbon dioxide) that can vary considerably across aquatic environments and as a result, have been areas of intense study and have revealed incredible strategies of adaptation. Throughout the chapters, following the August Krogh Principle, the fishes that have best helped us understand how fish respond to a particular environmental factor will be emphasized, with some that have been particularly instrumental in our understanding being highlighted as case studies. In addition to taking a comparative approach for understanding responses and adaptations to environments, fish physiologists also take a highly integrative approach and examine how fishes integrate environmental signals from the molecular to whole animal levels, even scaling up to ecological levels of biological organization and examining population and community level responses to environmental change. Therefore, for each of these environmental factors, response mechanisms are considered across biological scales. Furthermore, temperature, oxygen levels and carbon dioxide levels have changed considerably over the last many decades in aquatic environments. Many of the chapters are written with an eye to the importance of understanding the physiological strategies, responses and adaptations that can lead

to tolerance of environmental change for making accurate predictions about the vulnerability of fish populations to global climate change.

Temperature is considered the abiotic master factor for ectotherms, like most fishes, due to temperature's direct effect on reaction rates and macromolecular structure (**Effects of Temperature: An Introduction**). Understanding the future impacts of aquatic warming (**Effects of Climate Warming**) depends on an understanding of how fishes use a variety of strategies to mitigate the effects of temperature at the biochemical (**Responses and Adaptations of Cellular Metabolism to Temperature**) and whole animal level (**Temperature and Fish Biology: Insights from Metabolism**) to ultimately shape thermal tolerance (**Measures of Thermal Tolerance**) across different thermal environments and different time scales of temperature change. Desert pupfish species have been studied as a unique model for physiological adaptation to high temperature (**Case Study: The Desert Pupfish**). Fishes must also be able to cope with hypoxia, or low levels of dissolved oxygen, over daily and seasonal time scales. Since the first edition of the Fish Encyclopedia was published, there has been growing concern about ocean deoxygenation and how future warming and eutrophication from nutrient loading will affect oxygen availability in marine environments (**Oxygen in the Marine Environment**). Our understanding of the hypoxic ventilatory response (**The Hypoxic Ventilatory Response and Oxygen Sensing in Fishes**) as well as mechanisms to depress metabolic rate to decrease energy demand (**Metabolic Rate Depression as a Mechanism for Surviving Hypoxia**) and anaerobic metabolism (**Anaerobic Metabolism in Fish**) will be critical to predicting vulnerability to increasing hypoxia in aquatic environments in the Anthropocene. For tolerance to low levels of dissolved oxygen (hypoxia) as well as no oxygen (anoxia), there are two species that have been well studied: the Crucian carp (**Case Study: The Anoxia-tolerant Crucian Carp**) and the Pacific hagfish (**Case Study: Anoxia Tolerance in the Pacific Hagfish**). Ocean acidification (OA) and how changes in ocean pH, through absorption of atmospheric CO₂, will impact marine fishes has also been an expanding area of study over the last decade. Much of our understanding of how fishes cope with hypercapnia or elevated CO₂ levels in the water through acid-base regulation (**Acid-Base Regulation and Hypercapnia: An Introduction**) across biological scales (**Integrative Responses to Hypercapnia**) has come from many decades of productive study by fish physiologists. This foundational literature has informed not only our understanding of the potential impacts of OA but also our experimental approaches to study climate change relevant changes in CO₂ levels.

Fishes live in highly variable environments and must be able to cope with multiple changes in environmental conditions. Since the first edition of the Fish Encyclopedia, considerable effort has been taken to understand how fishes cope with multiple stressors and a chapter on our current understanding and outstanding questions is provided (**Multiple Stressors: Physiological Responses to Multivariate Environments**). Since the first edition, the scientific community has also broadened their examination of the mechanisms underlying physiological responses of fishes to environmental change across a fish's life and between generations to include epigenetic regulation (or changes in gene expression that do not involve changes in DNA sequence but can be heritable) (**Epigenetic Mechanisms in Response to Environmental Change**). Lastly, there is a remarkable group of sulfide spring fishes that show intriguing adaptations to hydrogen sulfide (**Adaptation to Hydrogen Sulfide: A Case Study in Sulfide Spring Fishes**) and are an excellent example of the power of the comparative approach in fish physiology in uncovering responses and adaptations to the environment.

After reading the articles within this section of the Encyclopedia, I hope you are encouraged to think more holistically about the diversity of fishes you see when you visit an aquarium and how the environments in which these fishes live have shaped their biochemistry and physiology over many generations. I also hope that some of you will be so inspired that you want to know more and will dig more deeply into the literature in hopes of identifying areas of study where you would like to contribute. There is still a lot to learn, and we are always looking for people interested in understanding how the diversity of fishes on Earth is shaped by the diversity of environments in which they live. Fish physiologists have an important place at the table for understanding the consequences of climate change on fishes and we need all the help with can get to address this grand challenge in biology.

See Also: Acid-base regulation and hypercapnia: An introduction; Adaptation to hydrogen sulfide: A case study in sulfide spring fishes; Anaerobic metabolism in fish; Case study: Anoxia tolerance in the pacific hagfish (*Eptatretus stoutii*); Case study: The anoxia-tolerant crucian carp; Effects of climate warming; Effects of temperature: An introduction; Epigenetic mechanisms in response to environmental change; Integrative responses to hypercapnia; Metabolic rate depression as a mechanism for surviving hypoxia; Multiple stressors- physiological responses to multivariate environments; Oxygen in the marine environment; Responses and adaptations of cellular metabolism to temperature; Temperature and fish biology: Insights from metabolism; The hypoxic ventilatory response and oxygen sensing in fishes.