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Extremophile Fishes

Ecology, Evolution, and Physiology of Teleosts in Extreme Environments

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Preface

Editing is the very edge of your knowledge forced to grow—a test you can't cheat on.—
S. Kelley Harrell

This book project grew out of our long-standing fascination with the amazing adaptive potential of many organisms, which enables them to survive some of the most extreme conditions found on Earth. For the last decade, our research has been dominated by our collaborative projects on livebearing fishes of the family Poeciliidae living in, and adapting to, extreme environmental conditions due to the presence of toxic hydrogen sulfide (H_2S) or the absence of light in subterranean habitats. Nonetheless, upon commencing the editing of this book, it became clear how little we actually knew about the biology of fishes in other types of extreme habitats, as well as about the biology of non-poeciliid fishes from sulfidic waters. Thus, editing this book became a humbling learning experience for us; something we are truly grateful for.

Extreme environments are abundant on Earth, and the scientific literature on extreme environmental conditions and how organisms deal with them have blossomed over the last few decades. In parts these efforts were driven by the desire to not only understand the limits within which life itself is possible but also to aid in our understanding of the physiological, ecological, and evolutionary responses to a more recent phenomenon that exacerbated existing and created novel extreme environments: human-induced environmental change. Teleost fishes in particular, with their high evolutionary potential (e.g., due to repeated genome duplications), are excellent models to delve into these questions, as many of them have adapted to environments usually considered inhospitable. However, books on extreme environments traditionally focused on microbes and invertebrates, while only few books to date have focused on extremophile teleosts. These books usually had more of a natural history rather than a conceptual approach to the topic (i.e., fewer habitat types were being covered and the focus was less on general evolutionary and ecological patterns). The implications of adaptation to extreme environments for the formation of new species (i.e., speciation), for example, have also not yet been covered. *Extremophile Fishes* tries to fill this gap.

However, when one of us (RR) was first approached by Springer in August of 2012 about the possibility of writing or editing a book on the adaptations of fishes to extreme environments, the first response was rather tentative. RR was just about to finish his first postdoctoral position at North Carolina State University, soon-to-be followed by a move to the University of Sheffield to begin a 3-year postdoctoral project working on chemical communication in stick insects. How much time would there really be over the coming years to devote to such an important project that focuses on fishes and not insects? Nevertheless, the opportunity was also too good to pass up on, because for the last decade we often complained (to one another as well as to other scientists) about the apparent lack of communication between scientists working in different biological specialty areas, which often seemed to result in each specialty group having to reinvent the wheel (e.g., cave biologists vs. "general" evolutionary ecologists). Since Springer was open to the option of having this become a multi-editor book, the project soon involved all three of us, and over the next few months we went to work drafting an outline for the book, and getting in touch with potential authors we considered the best choice for some of the individual chapters on fishes from specific types of extreme environments. The responses we got were so overwhelmingly positive that we decided to go ahead with this project despite some previous reservations, and so we submitted our project proposal to Springer, who officially approved the book concept by May of 2013. As a result, most authors had begun drafting their respective chapters by August of the same year.

First and foremost, we would therefore like to express our eternal gratitude and appreciation to all the authors for their excellent contributions, as well as all the external reviewers that kindly provided us with additional expert opinions and evaluations of the different chapters on top of our own assessments. All of them were a pleasure to work with, and they made our job as editors fairly easy by being very responsive to our every whim (please read: scientific enquiries, suggestions for revisions, tight deadlines, etc.), and by meeting all deadlines in a timely manner. In fact, the delays that inevitably happened during such a long-term project were usually the result of all three of us editors starting new positions during the 2 years of working on this book, rather than being the result of anything happening on the side of the authors or reviewers. It was their enthusiasm, dedication, and hard work for our project, which made the present book possible.

We also thank Ingo Schlupp (University of Oklahoma, OK, USA), who was the Ph.D. supervisor for two of us (RR and MT). He helped and guided us to find our respective scientific identities and facilitated a lot of the initial collaborative projects on poeciliids from extreme environments. Similarly, we thank Jakob Parzefall (professor emeritus and Ph.D. supervisor of MP at the University of Hamburg, Germany) for pioneering the research on the cave molly, and thus, providing a well-established starting point for our own investigations into the evolutionary ecology of the cave molly and other extremophile poeciliids. We further thank our various postdoctoral advisors who were instrumental in helping us grow as independent scientists and allowed us the freedom to pursue our own research on extremophile fishes in a collaborative fashion while being members of their research groups.

Specifically, RR would like to thank Brian Langerhans (North Carolina State University, NC, USA) and Patrik Nosil (University of Sheffield, UK), MT would like to thank Kirk Winemiller and Gil Rosenthal (both Texas A&M University, TX, USA), and MP would like to express his gratitude to Ralph Tiedemann (University of Potsdam, Germany) and Bruno Streit (JW Goethe University of Frankfurt, Germany). Furthermore, RR would like to thank Bernard Crespi (Simon Fraser University, Canada) for his valuable advice on book editing and handling contributing authors.

Moreover, we would like to thank the American Livebearers Association, the Erwin Riesch-Stiftung, the Freunde und Förderer der Goethe-Universität Frankfurt, the German Academic Exchange Service (DAAD), the German Ichthyological Society (GfI), the German Research Foundation (DFG), the Herrmann Willkomm-Stiftung, the Human Frontier Science Program (HFSP), the National Geographic Society, the National Science Foundation of the USA (NSF), and the Swiss National Science Foundation for financial support over many years. Our research was only possible due to the collaborative support and substantial help rendered by Lenin Arias-Rodriguez and Jeane R. Indy (both Villahermosa, Mexico), Francisco J. García de León (La Paz, Mexico), and Carlos Rodriguez Peña (Santo Domingo, Dominican Republic) as well as a large number of undergraduate, graduate, and postdoctoral researchers that have worked with us or circled through our labs over the years.

This book would have never reached fruition without the incredible help of the excellent people at Springer Verlag that helped, guided, and accommodated us along the way. We are grateful to Lars Koerner, who first approached us with the idea for this book, and who subsequently was of tremendous help in bringing the book from concept to reality. We are also indebted to Anette Lindqvist, the Project Coordinator for our book at Springer, in particular for her remarkable calm and accommodating responses during some of the inevitable problems we encountered during the writing and editing phases of the book. We also have to thank Murugesan Tamilselvan, our Production Editor, Sheik Mohideen, our Project Manager, and the countless others who worked behind the scenes, but who we never got to meet or interact with directly, for their tireless work and helpfulness during the design, production, advertising, and editing of the book.

Finally, we would like to thank our parents and partners, as well as our extended families and friends for their lifelong support and patience with us. They put up with us storing questionable things in the home fridge, being gone for extended field trips and conference visits, or simply disappearing for days behind our computer screens whenever we were trying to meet the next grant or scholarship deadline.

Our repeated thanks to all contributors, and we hope that the reader will find this book a valuable source of information.

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Extremophile Fishes: An Introduction

Martin Plath, Michael Tobler, and Rüdiger Riesch

Abstract Extremophile organisms thrive under environmental conditions considered inhospitable for most eukaryotes due to the presence of physicochemical stressors. To cope with such stressors, extremophiles have often evolved complex adaptations. Naturally occurring extreme habitats can be regarded as evolutionary experiments that allow studying the ability of species to habituate and adapt to altered ecological conditions, which may allow generating projections about the potential of organisms to habituate and adapt to human-induced stressors as well. This introduction provides an overview of different chapters of this book, focusing on the ecology, evolution, and physiology of extremophile fishes from various extreme habitats. Chapters introduce the nature of the physicochemical stressors and the taxonomic diversity in the respective habitat type. Furthermore, each chapter reviews adaptations of fishes in terms of modification of biochemical, physiological, morphological, life-history, and/or behavioral traits. In several cases, evidence for reduced gene flow between different locally adapted populations, i.e., indications for incipient or ongoing ecological speciation, is being discussed.

1 Background

With an amazing number of more than 28,000 described species, modern bony fishes (Teleostei) are currently the most speciose clade of vertebrates (Nelson 2006; http://www.fishbase.org). The ray-finned fishes (Actinopterygii), which teleost fishes are a

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member of, seem to have derived from freshwater ancestors (Vega and Wiens 2012; see also the chapter "Hypersaline Environments" for discussion), but teleosts are nowadays found in almost any kind of aquatic habitat on Planet Earth, including shallow and deep-sea marine habitats and diverse, fast-flowing to stagnant freshwater habitats (Wootton 1991; Matthews 1998; Sebert et al. 2008). This book focuses on the ecology, evolution, and physiology of fishes living in extreme environments, so-called extremophile fishes.

The term extremophile derives from Latin *extremus* and Greek *φιλία* (*philia*) and, thus, translates to something like "loving the extreme." While this direct translation may carry a somewhat anthropomorphic connotation, the term is clearly defined in biology: extremophiles are organisms that thrive under environmental conditions considered inhospitable for most eukaryotes due to the presence of physicochemical stressors, and they exhibit complex adaptations to cope with the stressors (Begon et al. 1996; Townsend et al. 2003). The term "extremophile" frequently refers to prokaryotes (e.g., Priscu et al. 1999; Seckbach 1999; Rothschild and Mancinelli 2001; Horikoshi et al. 2011), and "extreme environment" or "extremophile" is sometimes used for invertebrates (e.g., McMullin et al. 2000; Amils Pibernat et al. 2007), but following the aforementioned definition, vertebrates also comprise a surprising number of extremophiles (e.g., Sebert et al. 2008; Gerday and Glansdorff 2009).

Some examples of extremophile fishes are widely known not only to scientists but also to laymen—like the enigmatic pale and blind cavefishes. It may come as a surprise though that teleost fishes readily occur also in waters nearly devoid of oxygen, in hot desert waters and at temperatures below freezing, at salinities far above concentrations found in sea water, or even in habitats that temporarily fall dry. While many of these habitat types are naturally extreme to teleost fishes and can only be inhabited by highly specialized forms, more and more habitats, terrestrial and aquatic, are currently becoming extreme due to novel stressors stemming from human activities. Indeed, a recent article argues that we may currently be facing the next big mass extinction (Dirzo et al. 2014), one reason being that many species cannot adapt to rapidly changing environmental conditions. Therefore, the following chapters—focusing on some major types of extreme habitats in which teleosts can be found—will provide taxonomic overviews of species and families occurring under the respective extreme conditions. This information will allow deducing what taxonomic groups may be more likely to adapt to a given (novel) stressor or combination of stressors.

What general insights can we gain from studying the ecology, evolution, and physiology of extremophile fishes? First, naturally occurring extreme habitats can be regarded as evolutionary experiments that allow studying the ability of species to habituate and adapt to altered ecological conditions, which may allow projections as to the potential of those species to habituate and adapt to human-induced stressors as well (see chapters "Pickled Fish Anyone?" and "Evolutionary Toxicology: Population Adaptation in Response to Anthropogenic Pollution", respectively). Likewise, studying the occurrence of fish in extreme habitats that have existed for prolonged periods of time allows making reasonable inferences about the limits of adaptation, which is also of central interest in light of exponentially increasing human-induced

habitat degradation. Besides that, several extremophile fishes are emerging as model organisms for general questions in disciplines as diverse as EvoDevo [e.g., eye and pigment reduction and sensory modifications in cavefish: Wilkens (1988), Protas et al. (2007), Yamamoto and Jeffery (2000), Jeffery (2008, 2009), Yamamoto et al. (2009), Soares and Niemiller (2013)], aging research [seasonal *Nothobranchius* killifishes: e.g., Genade et al. (2005), Terzibasi et al. (2007), Reichwald et al. (2009)], and especially evolutionary ecology (the focus of this book).

Extreme habitats, due to the strength of directional selection from novel, physicochemical stressors, provide some of the best cases for studying the predictability of evolution (Tobler and Plath 2011; Riesch et al. 2014). A major question in this context is whether parallel phenotypes always diversify by parallel genetic bases or if alternative genomic routes lead to the same phenotype (e.g., Wray 2002; Wood et al. 2005; Hohenlohe et al. 2010; Stapley et al. 2011; Soria-Carrasco et al. 2014), and replicated ecological gradients—e.g., of benign and extreme habitat types—may be particularly well-suited systems in which to study this set of questions [reviewed in Elmer and Meyer (2011)].

2 Focus of This Book

The different chapters of this book will provide an overview over the nature of the physicochemical stressors and the taxonomic diversity in the respective habitat type. Pertinent fish adaptations in terms of biochemical, physiological, morphological, life-history, and/or behavioral traits will be reviewed. Where such information is available, relevant ecological (e.g., predator–prey, host–parasite, trophic, or symbiotic interactions) and/or evolutionary patterns (e.g., phenotypic plasticity, underlying genetics, hybridization, or speciation) and coping mechanisms governing the particular systems will be discussed. As a unifying theme the following chapters—where appropriate—will discuss evidence for reduced gene flow between different locally adapted populations, i.e., indications for incipient or ongoing ecological speciation as a result of the adaptation process (see Nosil 2012; Langerhans and Riesch 2013). Due to the different backgrounds of the contributing authors and different emphases in the respective fields, the chapters of this book will have slightly different foci, some emphasizing physiological coping mechanisms and gene expression patterns, while others focus more on phylogenetic patterns or fitness costs associated with local adaptations. Also, some chapters will additionally provide information on non-teleost fishes, e.g., because sarcopterygian lungfishes (Dipnoi) are a dominant group in temporary water bodies in the tropics (see chapter "Temporary Environments" for details). While, of course, there are many more kinds of extreme aquatic habitats at least temporarily inhabited by teleosts, our book provides ten specific examples:

In the chapter "Low-Oxygen Lifestyles", Lauren J. Chapman reviews our current knowledge about teleosts experiencing ambient oxygen concentrations below 2 mg O_2 l^{-1} in their natural habitats. Low-oxygen habitats are currently

increasing on a worldwide scale as a consequence of human activities (like eutrophication and other sources), and so understanding how aquatic hypoxia affects key physiological mechanisms (e.g., oxygen uptake and transport) and morphological traits, alters ecological interactions, and acts as a selective force is of vital interest not only for evolutionary ecologists, but also from a conservation-oriented perspective. The author scrutinizes the evidence that mosaics of hypoxic and normoxic areas in larger water bodies might promote local adaptation and result in reduced gene flow between locally adapted forms.

The chapter "The Adaptive Radiation of Notothenioid Fishes in the Waters of Antarctica" by Michael Matschiner and colleagues demonstrates how teleosts have adapted to life in permanently cold Antarctic waters. Living at subzero temperatures requires adaptations to prevent freezing (i.e., intracellular ice crystallization) and leads to unique adaptations, such as antifreeze glycoproteins. The authors highlight how these key innovations appear to have initiated the adaptive radiation of notothenioid fishes, as open ecological niches became available to these fishes in the absence of competing taxa. This may be a fascinating example of sympatric speciation in marine fishes despite long-distance larval dispersal by the strong Antarctic Circumpolar Current.

In the chapter "Desert Environments" Stanley D. Hillyard and colleagues focus on fishes in arid to hyperarid environments and demonstrate how patterns of dispersal and vicariance drove evolutionary diversification and speciation of teleosts adapted to life in desert waters, where fish can experience fluctuating temperatures, hypersalinity, or dessication and isolation of the remaining water bodies. It may come as a surprise to learn that several desert regions were fairly wet only few thousand years ago. A special emphasis is put on the particularly well-studied pupfishes of the genus *Cyprinodon* from North American deserts—like the famous Devils hole pupfish (*C. diabolis*)—that have inspired a wealth of studies on the phylogeography and diversification of these hardy fishes.

Changes in ambient salinity were frequent in the evolutionary history of numerous teleost lineages due to repeated transitions between marine and freshwater environments. The chapter "Hypersaline Environments" by Gary Laverty and Erik Skadhauge focuses on physiological mechanisms employed by teleosts to cope with salinities even far above sea level. The authors outline the role of the intestinal and branchial epithelia in adapting to hypersaline conditions, as encountered, e.g., in coastal lagoons or in landlocked saline lakes. Several physiological mechanisms are similar to those seen when freshwater-habituated fish move into the sea, and include increased drinking, secretory transport of ions through the gills, as well as ion excretion via urine and through the gut.

The chapter "Life in the Fast Lane: A Review of Rheophily in Fishes" by Nathan K. Lujan and Kevin W. Conway considers adaptations to life in fast-flowing waters, including convergent specializations of body shape or attachment organs that prevent downstream drift. The authors provide a conceptual model describing longitudinal shifts at the evolutionary versus ecological scale of processes controlling the taxonomic composition of rheophilic fish assemblages from headwaters to large river rapids, while contrasting the importance of vicariance speciation in

(isolated) upland headwaters, and adaptive radiations in lowland rapids as drivers for evolutionary diversification.

Hydrogen sulfide (H_2S) is a potent respiratory toxicant often associated with geological activity or environmental pollution. In the chapter "Hydrogen Sulfide-Toxic Habitats", Rüdiger Riesch and colleagues highlight multifarious selective regimes arising not only from H_2S toxicity itself, but also from correlated abiotic stressors (like hypoxia) and altered ecological parameters. The authors show how local adaptation in key molecular (like H_2S-insensitive protein complexes and improved detoxification mechanisms), morphological, and behavioral traits repeatedly translates into the emergence of reproductive isolation in evolutionarily replicated systems due to selection against non-adapted individuals migrating between habitat types.

The chapter "Cave Environments" by Matthew L. Niemiller and Daphne Soares describes the troglomorphic fishes found in caves and other subterranean habitats, especially in karst regions. Not only does lightlessness lead to a number of convergent phenotypic changes throughout diverse groups of fishes (most strikingly, eye and pigment reduction), but the challenges of orientation and navigation, as well as finding food and mating partners in complete darkness, led to the evolution of improved nonvisual sensory systems. The authors review two long-standing topics that have fascinated generations of scientists: first, to explain what evolutionary mechanisms explain the loss of eyes and pigmentation in the absence of stabilizing selection, and second, what processes affect speciation patterns of cave faunas.

Cultural acidification of freshwaters in many parts of the world in the latter half of the twentieth century, coincident with the decline of many economically important fish species, prompted research projects on the physiological mechanisms of fishes to cope with low pH. The chapter "Pickled Fish Anyone? The Physiological Ecology of Fish from Naturally Acidic Waters" by Jay A. Nelson highlights the fact that extensive freshwater bodies, e.g., South America's Río Negro system, are inhabited by speciose fish faunas, thus raising the question of whether naturally occurring low pH over evolutionary timescales may actually be a driver of speciation processes. Acidic environments challenge fishes with net losses of essential monovalent ions especially through the gills, and mechanisms to overcome problems of ion homeostasis are being discussed.

Matej Polačik and Jason E. Podrabsky's chapter "Temporary Environments" focuses on fishes in temporary aquatic habitats in arid and semiarid ecosystems across the globe. Few groups have evolved the ability to persist phases of desiccation of their aquatic habitats, and different strategies include estivation as adults (e.g., in lungfishes) and survival as diapausing eggs (as seen in the famous annual killifishes in Africa and South America). The authors highlight how temporary environments offer ecological opportunities (open niches and reduced competition and predation) but require various specific adaptations to successfully exploit them.

The chapter "Evolutionary Toxicology: Population Adaptation in Response to Anthropogenic Pollution" by Elias M. Oziolor and Cole W. Matson considers recent, anthropogenic environmental changes as a source for phenotypically plastic

(i.e., habituation), epigenetic, and eventually genomic changes of fish populations. Human-induced changes that may add to naturally existing stressors include, amongst others, increased UV radiation, radionuclide or heavy metal contamination, and toxicity from novel organic compounds, like polycyclic aromatic hydrocarbons, dioxins, and polychlorinated biphenyls. Adaptive responses of Atlantic tomcod (*Microgadus tomcod*) and Atlantic killifish (*Fundulus heteroclitus*, *F. grandis*) showing reduced sensitivity to the adverse effects of those compounds are being discussed, and in several cases, the molecular mechanisms of reduced sensitivity have already been characterized.

Our book ends with a summary and discussion ["Extremophile Fishes: An Integrative Synthesis" by Michael Tobler and colleagues] in which the authors synthesize the general approaches used to investigate teleost fishes in extreme environments and highlight generalities that are evident across different study systems. The chapter concludes with a discussion of some major open questions in our understanding of the ecology and evolution of life in extreme environments.

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Low-Oxygen Lifestyles

Lauren J. Chapman

Abstract Aquatic hypoxia (low oxygen) provides a useful system for exploring ecological and evolutionary consequences of living under extreme conditions. It is also an environmental stressor of accelerating interest due to human activities that have increased the extent of hypoxic waters on a global scale. This chapter characterizes the distribution of hypoxic habitats, reviews key adaptations of fishes to extreme hypoxia, and explores the role of hypoxia as a divergent selective factor. Trade-offs in the costs and benefits of living in hypoxic and normoxic habitats may contribute to faunal diversification by creating spatially divergent selection that leads to specialized phenotypes as illustrated in studies of African fishes from hypoxic swamps and associated normoxic sites. In these systems alternative dissolved oxygen (DO) environments provide a strong predictor of intraspecific variation, particularly in traits related to oxygen uptake efficiency or oxygen limitations, but also in characteristics indirectly affected through trait correlations. Studies of fish persisting under hypoxia highlight the importance of localized extreme habitats as model systems for studying divergent natural selection and more generally for exploring effects of physicochemical stressors on ecological and evolutionary processes.

1 Introduction

In some environments organisms are challenged by adverse physicochemical conditions like extreme levels of temperature, oxygen, pH, and toxicants. Some organisms are able to cope with extreme environmental conditions via unique adaptations giving rise to specialized phenotypes and distinctive ecological communities. It has been argued that such adaptations may be costly from an evolutionary and energetics perspective. Less is known about potential benefits that trade off with these costs. However, extreme habitats are often (though not always) less

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productive than adjacent non-extreme habitats and characterized by low species diversity, which may lead to reduced competition, predation, and/or disease (Tobler et al. 2007; Tobler 2008).

Extreme habitats can occur over broad scales such as in polar regions, but can also exist at patches nested within non-extreme habitats on small spatial scales, for example, hypoxic areas of lakes and swamps, or sulfidic springs in river systems (see chapter "Hydrogen Sulfide-Toxic Habitats"). Such localized extreme habitats allow us to explore the effects of physicochemical stressors on ecological and evolutionary processes without confounding effects of larger biogeographical trends. In particular, localized extreme habitats can inform our understanding of how populations adapt to heterogeneous environments and the role of extreme habitats as drivers of divergent natural selection (Chapman 2007; Tobler et al. 2008).

Fish have colonized almost all aquatic environments on Earth including many habitats that test the limits of tolerance to physicochemical stressors—from deep oceans to sulfidic caves (see chapters "Hydrogen Sulfide-Toxic Habitats" and "Cave Environments") to hypersaline lakes (see chapter "Hypersaline Environments"), and alkaline waters. Aquatic hypoxia (low dissolved oxygen, DO) also tests the limits of fish persistence, and provides a useful system for exploring ecological and evolutionary consequences of living under extreme conditions. It is also an environmental stressor of accelerating interest due to human activities that have increased the extent of hypoxic waters on a global scale (Diaz and Rosenberg 2008). The objectives of this chapter are to (1) review key responses to hypoxic stress that have permitted fish to persist under extreme hypoxia, (2) focus on hypoxia as a modulator of ecological interactions, in particular, predator–prey relationships, and (3) explore the role of extreme hypoxia as a divergent selective factor.

2 Hypoxic Habitats

Hypoxic habitats are often characterized as waters with concentrations below 2 mg $O_2 l^{-1}$, a definition that aligns well with the mean lethal DO concentration (LC_{50}) of 206 species of aquatic organisms reviewed in Vaqyer-Sunyer and Duarte (2008). However, it has also been argued that the definition of hypoxia should reflect its impact on organisms, and include DO levels low enough to induce negative impacts on target species (Pollock et al. 2007). The oxygen profile in aquatic habitats is often reported as the DO concentration in the water, measured in mg $O_2 l^{-1}$, ml $O_2 l^{-1}$ (1 mg $O_2 = 0.7$ ml O_2), or % saturation. The amount of DO in water decreases with increases in temperature, salinity, and elevation. In fishes, oxygen from the environment is taken up at a site of gas exchange, typically (though not always) the gills. Since the rate of oxygen diffusion from water to blood is a function of the partial pressure gradient between the two media,

physiological studies often report DO as the partial pressure of oxygen in the water in units of mm Hg (the air-saturated value at sea level is about 159 mm Hg).

All fish require oxygen for long-term survival; however, the physical properties of water make oxygen uptake a challenge even at high DO. Water holds approximately 1/30th the oxygen content of air at saturation, and oxygen diffuses about 10,000 times more slowly through water than air (Nikinmaa and Salama 1998). In addition to constraints of oxygen uptake imposed by the physical properties of water, there are many systems where water may not remain saturated with oxygen, leading to hypoxia. Oceanic oxygen minimum zones (OMZs) represent the largest areas of stable hypoxic water on the planet, and are located at intermediate depths (400–1,000 m) and low temperatures in most of the world's oceans (Childress and Seibel 1998). OMZs tend to form under areas of high surface productivity that sinks, decomposes, and consumes oxygen; and these zones are more likely to develop in areas of the ocean that lack a constant supply of well-oxygenated water such as the Arabian Sea and the eastern Pacific and Indian oceans (Kamykowski and Zentara 1990; Levin 2002; Helly and Levin 2004). In an area of the ocean containing an OMZ, upper waters are well oxygenated, but once the OMZ is entered, the DO drops very quickly, eventually stabilizing at less than 0.1 ml l^{-1}. DO may increase again in deeper waters below the OMZ; however, where these zones intersect continental margins one finds chronically hypoxic benthic habitats that are estimated to comprise approximately 1,148,000 km^2 of sea floor where DO is <0.5 ml l^{-1} (31 % in the eastern Pacific and 59 % in the Indian Ocean, Helly and Levin 2004). OMZs are unique relative to many other hypoxic habitats in that they are characterized by extreme hypoxia over very large spatial areas and over very long time periods, thus hosting an assemblage of organisms with extraordinary adaptations to hypoxia (Childress and Seibel 1998; Levin 2002; Helly and Levin 2004). In coastal marine systems, hypoxia occurs naturally in salt marsh habitats and other intertidal zones where hypoxic conditions are generated by pool isolation and/or nocturnal respiration of plants and animals (Congleton 1980; Innes and Wells 1985; Timmerman and Chapman 2004a).

Hypoxia is also characteristic of many freshwater systems with low mixing and high rates of organic decomposition, and/or inadequate light for photosynthetic production of oxygen, such as heavily vegetated swamps, flooded forests, floodplains, the deep waters of lakes and ponds, ice-covered northern lakes, and some springheads. Chronic hypoxia and extensive anoxia are characteristic of some deepwater meromictic lakes such as Lake Tanganyika and Lake Malawi in Africa, driven by strong stratification, as well as sinking and decomposition of organic matter (Spigel and Coulter 1996). In other freshwater systems, strong seasonal variation in DO is associated with seasonal fluctuations in rainfall, mixing, incident light, and water temperature. In intermittent streams, habitats may shift from fast-flowing, well-oxygenated habitats in the wetter seasons, to small isolated hypoxic pools during drier periods (Chapman and Kramer 1991). In temperate lakes, the degree of hypolimnetic oxygen depletion depends on lake depth, primary productivity, and temperature with many eutrophic lakes experiencing summer oxygen depletion. In winterkill lakes, reduced aeration due to ice cover, reduced light due to

snow cover, and a high organic matter supply relative to the amount of available DO can produce severe hypoxia or anoxia for extended periods (Kalff 2002). Nocturnal respiration in eutrophic lakes or small exposed pools often drive diel variation in DO from hyperoxia at midday to hypoxia at night (Congleton 1980; Kramer et al. 1978; Chapman and Chapman 1993), while pools characterized by little mixing under dense forest cover may be consistently hypoxic during periods of isolation (Chapman and Kramer 1991).

In tropical freshwaters, hypoxic conditions are often exacerbated by high temperatures that elevate rates of organic decomposition and reduce oxygen tension (Chapman et al. 2001). This can be particularly acute in dense tropical swamps where thick vegetation limits light and mixing, and fuels extraordinarily high rates of organic decomposition. The emergent sedge papyrus (*Cyperus papyrus*) dominates much of the permanent swamp on the African continent (Beadle 1981). In dense papyrus stands, which average 3–4 m in height (Thompson et al. 1979), the terminal brush-like umbels form a closed canopy producing dark, cool conditions. High rates of organic matter decomposition in papyrus swamps produce methane (60 %), carbon dioxide (30 %), and hydrogen (H_2, 10 %) gases (Visser 1993), and pH is slightly acidic (Chapman et al. 2001). The most striking characteristic of papyrus swamps is the very low DO, which results from high decomposition, low water flow rates, and negligible aquatic photosynthesis. In the Rwembaita Swamp, a valley papyrus swamp in the Mpanga River drainage of western Uganda (Fig. 1),

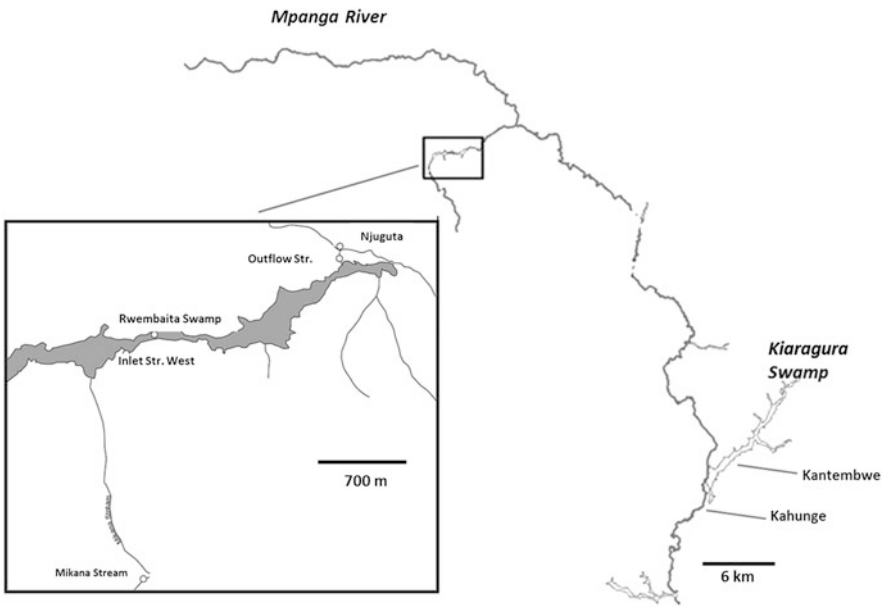

Fig. 1 Map illustrating the locations of Rwembaita Swamp and Kiaragura Swamp and their respective rivers in western Uganda. (Reprinted from Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology Volume 165, J. Joyner-Matos and L. J. Chapman, Persisting in papyrus: Size, oxidative stress, and fitness in freshwater organisms adapted to sustained hypoxia, pp. 405–416, 2013, with permission from Elsevier)

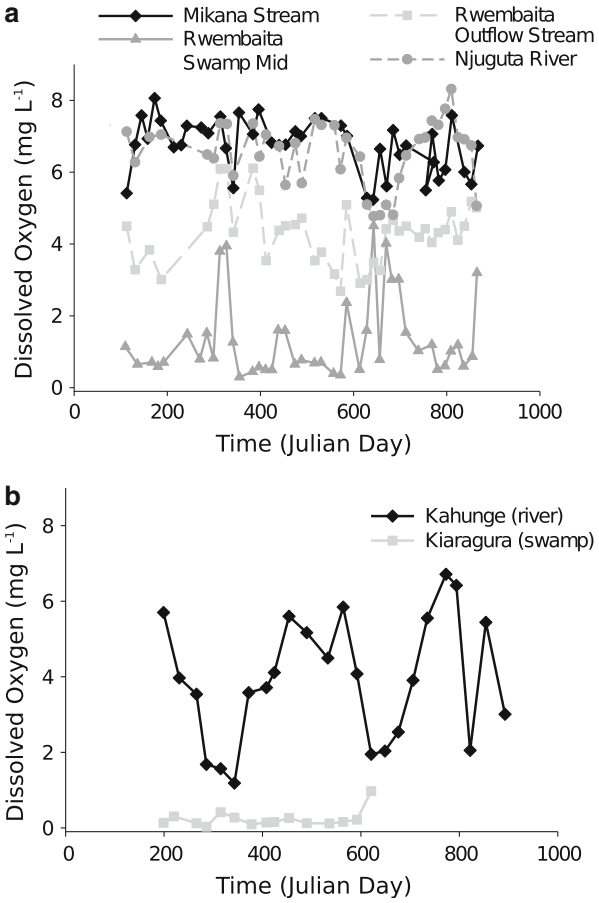

Fig. 2 Patterns in DO in two valley swamp systems in western Uganda. (**a**) The Rwembaita Swamp: dissolved O_2 levels (in mg $O_2 l^{-1}$) were taken biweekly from June 2001 to June 2003 at the Mikana Stream site (intermittent stream), Rwembaita Swamp Mid site, Rwembaita Outflow Stream, and the Njuguta River. See Fig. 1 for map of sites. Mean values were taken in the upper 20 cm of the water column, at approximately 2-week intervals at several micro-sites within each system. (**b**) The Mpanga swamp system: DO levels were taken monthly from July 2006 to December 2007 (Kantembwe site, a swamp site) and June 2008 (Kahunge site, a river site). Sampling sites are illustrated in Fig. 1. (Reprinted from Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology Volume 165, J. Joyner-Matos and L. J. Chapman, Persisting in papyrus: Size, oxidative stress, and fitness in freshwater organisms adapted to sustained hypoxia, pp. 405–416, 2013, with permission from Elsevier)

DO levels have been recorded since the early 1990s and averaged 1.5 mg $O_2 l^{-1}$ in the 1993–1996 period (Chapman et al. 2000a) and 1.35 mg $O_2 l^{-1}$ between 2001 and 2003 (range = 0.29–4.5; Fig. 2). In the Kiaragura Swamp, a more extensive valley swamp in the Mpanga River system, DO averaged only 0.29 mg l^{-1} (Fig. 2), with low seasonal variation. The chronic hypoxia in the Kiaragura Swamp likely

reflects its large size, with waters in the dense interior largely isolated from tributary influence. Interestingly, DO in the open waters of rivers into which both swamps drain declines (sometimes dramatically) during the rainy period when the swamp outflow mixes with the river water (Fig. 2). Extreme hypoxia has been documented in other papyrus swamp systems. Carter (1955) reported oxygen values averaging less than 0.1 mg $O_2 l^{-1}$ for the near shore areas of littoral papyrus swamps in Lake Victoria, and average values of 0.7 mg $O_2 l^{-1}$ in papyrus valley swamps of the Lake Victoria Basin near Jinja, Uganda.

Although hypoxic (and anoxic) environments occur naturally, human-induced environmental degradation is increasing the occurrence of hypoxia, as influxes of municipal wastes and fertilizer runoffs accelerate eutrophication and pollution of water bodies (Diaz 2001). Cultural eutrophication and associated hypoxia in freshwater systems have a long history, becoming widespread in the latter half of the twentieth century in both temperate (e.g., Lake Erie) and tropical (e.g., Lake Victoria) systems, though effective nutrient management has reversed the trend in some parts of the world (Jeppesen et al. 2005). In coastal and estuarine ecosystems, eutrophication driven primarily by anthropogenic fertilization has produced benthic hypoxia, which has led to population declines of inhabitants, mass mortality of inhabitants, and associated changes in community structure (Diaz 2001; Rabalais et al. 2002; Dybas 2005; Diaz and Rosenberg 2008). Dead zones have increased exponentially since the 1960s and are now reported for more than 400 systems that comprise an area of more than 245,000 km^2 (Diaz and Rosenberg 2008). Thus, spreading dead zones are creating extreme environments on a massive spatial scale, and the mortality that has occurred in some regions suggests that adaptive response on contemporary timescales may be limited or time lagged (Diaz and Rosenberg 1995). However, studies of adaptation to naturally occurring extreme hypoxia may provide important insights into the characteristics of organisms that may facilitate persistence and recovery.

3 Rising to the Challenge: Fish Under Extreme Hypoxia

In general, the problem of extreme aquatic hypoxia has led to one or more of the following strategies: (1) evolution of air-breathing organs, (2) movement to zones of higher DO, (3) evolution of mechanisms to maximize oxygen uptake from the water, (4) reduction of metabolic rate and/or activity to reduce oxygen requirements, and (5) use of anaerobic metabolism to bridge the difference between aerobic capacity and metabolic demands.

A number of bony fishes have evolved bimodal respiration, whereby they retain functional gills but can also gulp air at the water surface and store this in an air-breathing organ (ABO). ABOs show remarkable diversity in their structure and origins (Graham 1997), including diverticula of the branchial chambers (e.g., *Clarias*, *Ctenopoma*) and modifications of the air bladder (e.g., *Polypterus*, *Protopterus*). Air-breathing fishes combine the use of dissolved and atmospheric

oxygen; however, there is great variation in the degree of dependence on atmospheric air and in gill development. Some species like the African lungfishes (*Protopterus* spp.) are obligatory air breathers and will die without access to the surface, while other species, including the air-breathing clariid catfishes (*Clarias* spp.), have well-developed gills and can meet their oxygen requirements using water breathing at higher oxygen levels (Chapman and Chapman 1994). A large number of highly derived intertidal marine teleosts are believed to have evolved air-breathing strategies and amphibious habits independently of the freshwater air breathers, and typically use skin, gills, and branchial chambers as ABOs (Graham 1997; Graham and Lee 2004; Sayer 2005; Lam et al. 2006).

Air breathing should, in theory, be more energetically efficient than water breathing for fishes, because air is so much richer in oxygen and requires much less effort to ventilate (Kramer 1983a, 1987; Graham 1997). However, air-breathing fishes comprise only 2 % of known fish species (Graham 1997), and most fishes that persist in extremely hypoxic waters are non-air breathers. For example, the majority of the fish species in dense papyrus and *Miscanthidium*-dominated wetlands in Africa are water breathers from a diversity of lineages including cichlids, cyprinids, mormyrids, and killifishes (Joyner-Matos and Chapman 2013). Thus, there must be significant physiological and ecological costs to air breathing, which likely include energetic costs and increased risk of predation associated with travel to the surface (Kramer 1983a, 1987; Kramer et al. 1983; Bevan and Kramer 1986).

Behavioral responses provide additional flexibility to deal with variation in DO that can occur temporally or spatially in extreme environments through diel or seasonal movements, decreases in activity, or use of aquatic surface respiration (ASR). Extreme hypoxia can induce changes in spontaneous swimming activity—either a reduction in activity or an increase in activity, depending upon the species and the context, with the former viewed as an energy-saving response and latter viewed as an avoidance response (reviewed in Chapman and McKenzie 2009). For example, one of the energy-saving strategies used by crucian carp (*Carassius carassius*) is to reduce spontaneous activity by 50 %, providing an estimated saving of 35 % of overall energy requirements in anoxia (Nilsson et al. 1993).

Habitat shifts or avoidance behavior in response to hypoxia has been observed in several studies (reviewed in Pollock et al. 2007). For example, Wannamaker and Rice (2000) characterized the hypoxia avoidance response in several species of estuarine fishes, and found that all species could detect and avoid waters of 1 mg $O_2\,l^{-1}$, the lowest concentration in their choice tests. In their study of pelagic fish distributions in the seasonally hypoxic coastal waters of the northern Gulf of Mexico, Zhang et al. (2009) found that fish avoided waters <2 mg $O_2\,l^{-1}$. They did so by moving vertically or horizontally to the edges of hypoxic areas, and spatial overlap between fish biomass and mesozooplankton biomass was reduced during years of severe hypoxia. Diel migrations are common in myctophid (lantern) fishes that encounter OMZs during the daytime and ascend to warmer and better-oxygenated surface waters during the night (Lopes et al. 2013). Interestingly, an anticipated challenge for organisms migrating from OMZs is the production of

reactive oxygen species (ROS) driven by the transition between extreme hypoxia and reoxygenation states, as well as higher oxygen consumption demands driven by warmer temperatures. In their study of heat-shock responses and antioxidant enzyme activities of myctophids in the Eastern Pacific Ocean, Lopes et al. (2013) observed an increase in heat-shock protein levels under elevated temperatures, likely to prevent oxidative stress.

In shallow water systems that experience hypoxia, a widespread behavioral response is the use of ASR, whereby fish rise to the surface and ventilate their gills with the layer of water in contact with air, which is richer in DO than the underlying water (Lewis 1970; Gee et al. 1978; Kramer and McClure 1982; Kramer and Mehegan 1981; Kramer 1983b; Gee and Gee 1995; McNeil and Closs 2007). Aquatic surface respiration is more efficient than simply increasing ventilation under extreme hypoxia (Kramer and Mehegan 1981; Kramer 1983a, b). In addition, some fishes increase the efficiency of oxygen extraction during ASR by swimming continuously across the surface (Chapman et al. 1994, 1995; Rosenberger and Chapman 2000) or through the use of buccal bubble holding that may serve as a buoyancy compensation mechanism and/or to increase the oxygen content of the water passing over the bubble (Burggren 1982; Gee and Gee 1991). A number of species have morphological features, such as upturned mouths and flattened heads that seem to increase the efficiency of ASR (Lewis 1970; Cech et al. 1985), or dermal lip protuberances that facilitate access to water from the surface film (Winemiller 1989). ASR can, however, incur costs in terms of energy and predator risk, which may account for very low ASR initiation thresholds in many species, levels that are often close to the critical oxygen tension (reviewed in Chapman and McKenzie 2009). In a recent study, compared the ASR threshold of the cichlid *P. multicolor* from a chronically hypoxic swamp in Uganda to a literature review of ASR thresholds (81 values, Chapman and McKenzie 2009). *P. multicolor* was characterized by an average ASR_{10} threshold (PO_2 at which fish spend 10 % of their time at the surface) in the lower 25th percentile of the distribution and exhibited the lowest ASR_{50} threshold of all fish examined, indicating far-reaching adaptation to extreme hypoxia in this species.

Fishes relying on aquatic respiration in chronically hypoxic habitats use many strategies to increase oxygen transfer from the environment to their tissues and/or to evade problems associated with hypoxia. One mechanism to meet routine metabolic requirements under hypoxia is to increase oxygen uptake through an enlarged gas exchange surface. Several studies comparing populations of the same species from hypoxic swamp and high-oxygen environments in East Africa have demonstrated larger total gill size (surface area and/or total gill filament length) in swamp-dwelling populations including, as examples, the cyprinid *Barbus neumayeri* (Chapman et al. 1999; Langerhans et al. 2007) and the cichlid *Pseudocrenilabrus multicolor victoriae* (Chapman et al. 2000b; Wiens et al. 2014). In the poeciliid fishes *Poecilia mexicana* and *P. sulphuraria*, populations from sulfidic, hypoxic springs exhibit larger gills than populations from adjacent non-sulfidic habitats (Tobler et al. 2011; see chapter “Hydrogen Sulfide-Toxic Habitats”). Large gill surface area is also characteristic of some species of demersal fishes from oxygen

minimum zones: Friedman et al. (2012) found that the OMZ-dwelling flatfish *Microstomus pacificus* had a larger gill surface area than comparably sized flatfishes from higher-oxygen waters outside the OMZ in Monterey Canyon, California. Similarly, in their comparison of two rattail (gadiform) species, *Nezumia liolepis* from the OMZ exhibited a larger gill surface area than *Corphaenoides acrolepis*, a species living below the OMZ in waters of higher oxygen content. In addition to interspecific and interdemic patterns in gill surface area, some fishes can alter their gill surface area by remodeling their gill morphology. Gill remodeling was first observed in crucian carp and goldfish (*Carassius auratus auratus*) (see review in Nilsson et al. 2012) and involves either the expansion or reduction of the cell mass between the lamellae on the gill filaments referred to as the interlamellar cell mass (ILCM). In response to increased oxygen uptake demands, the ILCM is reduced through apoptosis exposing the respiratory epithelium to water and increasing oxygen uptake capacity (Sollid and Nilsson 2006; Nilsson 2007; Tzaneva et al. 2011; Nilsson et al. 2012).

There is great diversity in blood oxygen transport traits of fishes that appear to have evolved in response to both functional hypoxia driven by metabolic demands and environmental hypoxia. Blood oxygen transport in most teleosts is dependent upon the protein hemoglobin and is increased by adjusting the affinity of hemoglobin for oxygen, increasing the number of erythrocytes in circulation, and/or increasing hemoglobin concentration [Hb] (Hughes 1973; Johansen et al. 1978; Jensen 1991; Brauner and Val 2006; Wells 2009). Wells (2009) suggested that the evolutionary success of teleost fishes may be due, in part, to an oxygen secretion mechanism involving Root effect hemoglobins, which are unique to teleosts. Short-term increases in Hct (volume percentage of red blood cells in blood) and [Hb] in response to seasonal or acclimation-induced hypoxia have been reported in several non-air-breathing and air-breathing fishes including, as examples, increased Hct in the characid *Prochilodus cf. nigricans* (Val et al. 1992), increased [Hb] in the characid *Piabucinae festae* (Graham 1985) and the loricariid catfishes *Hypostomus plecostomus* and *Ancistrus chagresi* (Graham 1985), and increased Hct and [Hb] in the notothenid *Pagothenia borchgrevinki* (Wells et al. 1989) and the poeciliid *Poecilia latipinna* (Timmerman and Chapman 2004b). However, these blood capacity changes are often modest, and some studies have detected no change at all (Marinsky et al. 1990).

Oxygen-binding properties of hemoglobin are also critical in meeting the challenges of environmental hypoxia. These properties are routinely described by the relationship between the partial pressure of oxygen and the fraction of the oxygen-bound Hb, referred to as the oxygen equilibrium curve (OEC). The shape of the relationship is quantified by Hill's coefficient that varies from 1 when hyperbolic to approximately 3 when the relationship is sigmoidal (see Fig. 1 in Wells 2009). The P_{50} is an important diagnostic trait that represents the PO_2 at which 50 % of the hemoglobin is oxygenated. Increases in blood oxygen affinity of hemoglobin are frequently observed in response to hypoxia, and are mediated by increased pH (Bohr effect), decreased erythrocytic concentration of organic phosphates (adenosine and guanosine triphosphates, ATP and GTP, respectively),

or variation in the organic phosphate ratio (e.g., Bartlett 1978; Monteiro et al. 1986; Val et al. 1992; Rutjes et al. 2007). The organic phosphates bind to specific sites on the Hb tetramer, and a decrease in phosphates results in increased hemoglobin oxygen affinity (Wells 2009). The synthesis of ATP and GTP proceeds via an aerobic pathway; thus hypoxia that drives a shift from aerobic to anaerobic metabolism can reduce ATP and GTP and therefore increase blood oxygen affinity (Val 2000; Wells 2009). Teleosts also often have complex hemoglobin systems, which can be important in determining hypoxia tolerance (Fyhn et al. 1979; Riggs et al. 1979; Perry and McDonald 1993; Perez et al. 1995). In their study of adaptations to lifelong hypoxia in the East African cichlid *Haplochromis ishmaeli* from Lake Victoria, Rutjes et al. (2007) reared offspring under normoxic and hypoxic conditions. They found that hypoxia-reared fish exhibited a different iso-Hb pattern compared to normoxia-reared sibs, which correlated with a higher Hb-O_2 blood oxygen affinity. In general, fish from hypoxic environments are characterized by high oxygen-carrying capacity, high blood O_2 affinities, low Hill coefficients, and a hemoglobin function that is modulated by both GTP and ATP (Wells 2009). This pattern is seen both among species and populations inhabiting low- and high-oxygen sites. For example, in their study of hypoxic swamps surrounding Lake Nabugabo in Uganda, Chapman et al. (2002) found that swamp-dwelling fish species were characterized by higher Hct and [Hb] than lake-dwelling species, and Graham (1985) reported a negative relationship between [Hb] and the DO content of the habitat among three populations of the catfish *Hypostomus plecostomus*.

Another approach to persisting under extreme hypoxia is to reduce metabolic demands. A lower metabolic rate under hypoxia may offset energetic constraints of high blood viscosity driven by high [Hb], but has the disadvantage of reducing aerobic metabolism and the amount of energy available for many biochemical processes. Nonetheless, a relatively low metabolic rate seems to be characteristic of several fishes that inhabit chronically hypoxic waters. Examples include the mormyrid *Petrocephalus catostoma* (Chapman and Chapman 1998) and the cichlid *P. multicolor* (Rosenberger and Chapman 2000) from hypoxic swamps in Uganda, and the sailfin molly (*P. latipinna*) from periodically hypoxic saltmarsh habitat in Florida. Low metabolic demands are also characteristic of some fish species inhabiting OMZs (Childress et al. 1990); however, Childress and Seibel (1998) argue that these low metabolic rates have not evolved in response to low DO, because pelagic taxa living at comparable depths outside of OMZs have comparably low rates. Nonetheless low metabolic rates in these fishes are functionally adaptive for their aerobic survival under the extreme hypoxic characteristic of OMZs.

Very low critical oxygen tensions are characteristic of many hypoxia-tolerant fishes. The majority of fish species can be described as metabolic oxygen regulators, i.e., they are capable of maintaining a constant metabolic rate over a range of DO. The minimum oxygen level required to maintain a constant metabolic rate is defined as critical tension (P_c), below which metabolism decreases linearly with oxygen tension. In their study on interior swamps in the Lake Victoria basin,