

Low-Oxygen Lifestyles

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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 $2 \text{ mg O}_2 \text{ l}^{-1}$, a definition that aligns well with the mean lethal DO concentration (LC_{50}) of 206 species of aquatic organisms reviewed in Vaquer-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 $\text{mg O}_2 \text{ l}^{-1}$, $\text{ml O}_2 \text{ l}^{-1}$ ($1 \text{ mg O}_2 = 0.7 \text{ ml O}_2$), 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 $<0.5 \text{ ml l}^{-1}$ (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),

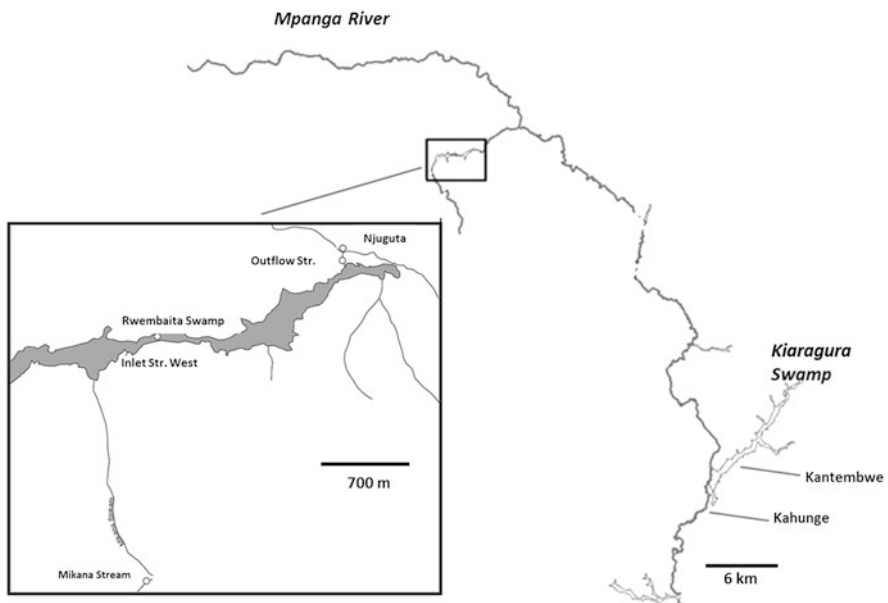


Fig. 1 Map illustrating the locations of Rwembaita Swamp and Kiaragura Swamp and their respective rivers in western Uganda. (Reprinted from Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology Volume 165, J. Joyner-Matos and L. J. Chapman, Persisting in papyrus: Size, oxidative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

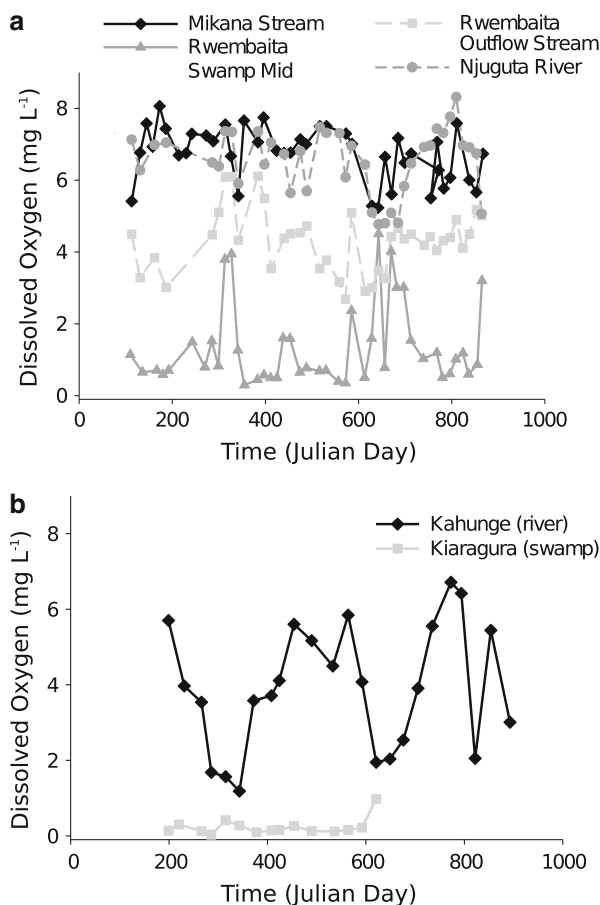


Fig. 2 Patterns in DO in two valley swamp systems in western Uganda. (a) The Rwembaita Swamp: dissolved O₂ levels (in mg O₂ l⁻¹) were taken biweekly from June 2001 to June 2003 at the Mikana Stream site (intermittent stream), Rwembaita Swamp Mid site, Rwembaita Outflow Stream, and the Njuguta River. 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 O₂ l⁻¹ in the 1993–1996 period (Chapman et al. 2000a) and 1.35 mg O₂ 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 $0.1 \text{ mg O}_2 \text{ l}^{-1}$ for the near shore areas of littoral papyrus swamps in Lake Victoria, and average values of $0.7 \text{ mg O}_2 \text{ l}^{-1}$ 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 $245,000 \text{ km}^2$ (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 $1 \text{ mg O}_2 \text{ l}^{-1}$, 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 $< 2 \text{ mg O}_2 \text{ l}^{-1}$. 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 ASR₁₀ threshold (PO₂ at which fish spend 10 % of their time at the surface) in the lower 25th percentile of the distribution and exhibited the lowest ASR₅₀ 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 nototheniid *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-O₂ blood oxygen affinity. In general, fish from hypoxic environments are characterized by high oxygen-carrying capacity, high blood O₂ 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,

Chapman et al. (2002) found that swamp-dwelling species were characterized by a lower average P_c (12.2 mm Hg) than lake-dwelling fishes (18.3 mm Hg) reflecting the high-oxygen uptake efficiency of the swamp-adapted fishes. They also observed a positive relationship between metabolic rate and P_c among the fishes in Lake Nabugabo; swamp-dwelling fishes with the lowest P_c values were also characterized by very low metabolic rates. This seems consistent with the idea that fishes of oxygen-poor areas have evolved reduced oxygen demands and improved means of extracting what oxygen is available. A low critical oxygen tension reflects other adaptations to hypoxia that facilitate oxygen extraction at low-oxygen tensions. For example, in their study of a group of closely related sculpins (Cottidae) from a range of habitats with varying levels of oxygen availability, Mandic et al. (2009) showed a phylogenetically independent correlation between hypoxia tolerance (P_c) and Hb-O₂ binding affinity.

Another strategy to deal with life in low oxygen is the use of anaerobic metabolism to bridge the difference between the aerobic capacity and metabolic demands. Many hypoxia-tolerant fishes increase oxygen-independent ATP production to maintain cellular energy balance (Land et al. 1993; Jibb and Richards 2008; Davies et al. 2011), relying more heavily on the contribution of glycolysis to produce ATP (Hochachka et al. 1996; DeKoning et al. 2004; Pollock et al. 2007). However, the yield of ATP is very low during anaerobic glycolysis relative to oxidative metabolism (Hochachka and Somero 2002); thus the use of anaerobic metabolic pathways for anything beyond small bursts of activity in fishes requires large reserves and results in accumulation of deleterious end products (Seibel 2011). Fishes living under chronic hypoxia possess a suite of adaptations (as discussed above) to facilitate aerobic survival at low DO. As such, evidence in some stable hypoxic environments suggests that anaerobic metabolism is used at most to supplement aerobic metabolism. In reviewing evidence for anaerobic metabolisms in fishes of the OMZs, Childress and Seibel (1998) concluded that in OMZs with $DO > 0.20 \text{ ml O}_2 \text{ l}^{-1}$, anaerobic metabolism is important for supporting activity above routine levels; however, the primary adaptation to zones with $DO > 0.20 \text{ ml O}_2 \text{ l}^{-1}$ is a low P_c facilitated by strategies for increasing oxygen uptake capacity at low DO. Most studies of fishes living in OMZs have found no evidence for increased anaerobic capacities in enzymatic profiles (Seibel 2011). In shallow-water systems characterized by chronic hypoxia, studies quantifying enzyme activities in natural populations are few, and results vary among study sites and species. In their study of the eurytopic cichlid *P. multicolor*, Crocker et al. (2013) reported little variation in metabolic capacities of populations from hypoxic swamps and high-oxygen sites within two drainages in Uganda. However, higher glycolytic capacity (phosphofructokinase in heart and skeletal muscle) and higher activity of liver lactate dehydrogenase were evident in the African cyprinid *B. neumayeri* from the hypoxic waters of a papyrus swamp relative to conspecifics from well-oxygenated tributary waters (Martinez et al. 2004, 2011).

Reliance on anaerobic pathways is critical for persistence of fish in anoxic environments, and the best-known example is the crucian carp, a species that can persist for days to months in anoxic ice-covered water bodies. The anoxia tolerance

in this species has been well studied and reviewed by Vornanen et al. (2009). A critical factor contributing to its anoxia tolerance is its ability to produce ethanol as its major end product of anaerobic metabolism, which allows the species to endure anoxia for long periods without suffering lactic acidosis. To balance the loss of energy-rich hydrocarbons released into the water, the carp accumulates huge stores of glycogen before the winter months set in, a process induced by temperature acclimatization Vornanen et al. (2009). In addition, the crucian carp can reversibly adjust the surface of its gills (gill remodeling) to match oxygen availability (Sollid et al. 2003, 2005). Other strategies employed by crucian carp include high blood oxygen affinity (Sollid et al. 2005) and cardiovascular adjustments that extend the ability to extract oxygen from the water as ambient levels fall (Vornanen et al. 2009), and a remarkable ability to maintain brain ATP levels under anoxia by increasing brain blood flow, though activity levels of the brain are reduced and certain senses are suppressed (Johansson et al. 1997; Nilsson 2001).

4 A Cost-Benefit Approach

Fishes that persist under extreme hypoxia may incur a number of costs related to the low availability of oxygen. Hypoxia can affect growth by influencing metabolic pathways, metabolic rate, and allocation of energy resources, and growth depression is a widespread response to hypoxic stress (Wang et al. 2009). Hypoxia has also been observed to affect reproduction in fishes by altering the concentration and ratio of sex hormones, disrupting gonad formation and development, altering fertilization and spawning behavior, and impairing embryo development (e.g., Zhou et al. 2001; Wu et al. 2003; Gercken et al. 2006; Landry et al. 2007; Thomas et al. 2007; Hassell et al. 2008; reviewed in Wu 2009). For example, in the widespread mouth-brooding cichlid *P. multicolor*, populations from hypoxic environments are characterized by a smaller female size at maturity and smaller egg size than conspecifics from normoxic sites (Reardon and Chapman 2009).

Despite potential energetic constraints and reproductive costs of life in low oxygen, there may be benefits of these extreme habitats that offset physiological and/or biochemical costs such as reduced competition, predation, and/or disease. Several recent studies provide evidence for reduced predation pressure in hypoxic habitats. In the Lake Victoria basin, for example, hypoxic refugia have mitigated impacts of a large introduced piscivore, the Nile perch (*Lates niloticus*) on native fish species. The explosive speciation of haplochromine cichlid fishes in Lake Victoria is unrivaled among vertebrates; however, introduction of the predatory Nile perch and effects of eutrophication (e.g., loss of water transparency) coincided with the mass extinction of endemic cichlids (Kaufman 1992; Seehausen et al. 1997; Balirwa et al. 2003). A similar pattern of faunal collapse was observed in other lakes in the basin that host introduced Nile perch (e.g., lakes Kyoga, Nabugabo). Studies on Lake Nabugabo (historically a backwater of Lake Victoria) demonstrated that hypoxic wetlands serve as refugia for some fishes, because the

Nile perch is sensitive to hypoxic stress (Chapman et al. 1996, 2002, 2003; Schofield and Chapman 2000). Coincident with heavy fishing on Nile perch some species that were in retreat are reemerging in lakes Victoria, Nabugabo, and Kyoga, emphasizing the importance of hypoxic habitats in fostering resurgence of native species (Witte et al. 2000; Chapman et al. 2003). Extreme hypoxia also appears to mitigate predator–prey interactions in coral reef fishes where nocturnal hypoxia is common (Nilsson et al. 2007). Nilsson and Östlund-Nilsson (2004) reported a surprisingly high level of tolerance to hypoxia in 31 coral reef species off the coast of Australia. They suggested that the widespread tolerance in this group reflects the use of hypoxic spaces in the coral as nocturnal refugia from predators or use of isolated periodically hypoxic tide pools. In another Australian habitat, McNeil and Closs (2007) quantified hypoxia tolerance in fishes of the Ovens River floodplain where low-oxygen conditions are common in small lentic waters (billabongs). Behavioral studies indicated a high tolerance in most floodplain fish species with the exception of three species including the introduced predatory redfin perch (*Perca fluviatilis* L.), which may account for high abundance of native hypoxia-tolerant species in more deoxygenated billabongs. McKinsey and Chapman (1998) quantified fish community structure along a sharp DO gradient in a Florida spring, where they found eastern mosquitofish *Gambusia holbrooki* to be the most abundant species persisting under extreme hypoxia at spring boil where DO averaged $0.20 \text{ mg O}_2 \text{ l}^{-1}$. They suggested that the boil offers a refugium for predation and a reduced competitive environment for the mosquitofish in these springs where fish diversity (and number of piscivores) increases with distance from the boil (McKinsey and Chapman 1998). Physiological refugia are also evident in north temperate systems. The extraordinary anoxia tolerance of the crucian carp offers access to piscivore-free refugia in ice-covered shallow ponds in Northern Europe (Nilsson and Renshaw 2004; Vornanen et al. 2009). Moreover, Robb and Abrahams (2003) observed higher hypoxia tolerance of small yellow perch (*Perca flavescens*) and fathead minnows (*Pimephales promelas*), than large yellow perch, a potential predator. They suggested that prey may intentionally seek out low-oxygen habitats under risk of predation.

Robb and Abrahams (2003) proposed an ecological advantage of being small under hypoxia associated with the allometric relationship for mass-specific gill surface area (Muir 1969; Hughes 1984), and a fractal scaling relationship whereby larger fish may be limited by the fixed size of the red blood cells for gas exchange (West et al. 1997). However, relationships between fish size and hypoxia tolerance are not consistent across studies. Nilsson and Östlund-Nilsson (2008) argued that body size per se does not influence oxygen uptake ability because (1) gill surface area has a similar scaling relationship as metabolic rate, and (2) where anaerobic ATP production is required, large fish seem to benefit from a lower mass-specific metabolic rate. Interestingly, hypoxic habitats may still offer a predator or cannibalism refuge even when smaller individuals are not more tolerant: In Amazonian oscars (*Astronotus ocellatus*), Sloman et al. (2006) found evidence to suggest that juveniles are not more hypoxia tolerant than larger conspecifics, but accept a physiological cost to access hypoxic refugia. Interestingly, Everett and Crawford

(2010) reported a negative relationship between P_c and body mass in their study of seven populations of *Fundulus grandis*, suggesting that (in this species) an increase in body size is an effective strategy to mitigate effects of hypoxia. Clearly, there is a need for additional studies on the relationship between body size and hypoxia tolerance both within and across species.

Another potential advantage of living in extreme habitats is that such habitats may serve as a refuge from parasites and disease (Tobler et al. 2007). The Atlantic molly (*Poecilia mexicana*) inhabits both surface freshwater systems and limestone caves with high concentrations of hydrogen sulfide. Tobler et al. (2007) found lower levels of parasitism by the trematode *Uvulifer* sp. in cave-dwelling mollies than in conspecifics from a non-sulfidic habitat (but see Tobler et al. 2014). Similarly, juvenile pumpkinseed sunfish (*Lepomis gibbosus*) from a periodically hypoxic wetland bay in Lac Hertel, Quebec, are characterized by a lower prevalence and load of *Uvulifer* sp. than conspecifics from well-oxygenated waters in the main lake (L. Chapman, unpublished data). In contrast, in their study of the monogenean diplozoon *Neodiplozoon polycotyleus* that parasitizes the gills of the African cyprinid *Barbus neumayeri*, Raymond et al. (2006) found that parasite occurrence was higher in the hypoxic papyrus swamp habitat than in stream and river sites in the same drainage (Raymond et al. 2006).

5 Divergent Selective Environments

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. Hypoxic habitats like papyrus swamps can occur nested within normal habitats on small spatial scales and contribute to faunal diversification by creating heterogeneous landscapes. Such localized extreme habitats and their inhabitants are especially valuable for evolutionary ecology research, because they create divergent selective environments among populations and/or closely related species, and thus can inform our understanding of a fundamental question in evolutionary biology—how populations adapt to heterogeneous environments (Schluter 2000, 2001).

Hypoxic habitats that are connected to normoxic habitats provide excellent contrasting environments for exploring the role of hypoxia in driving divergence. For example, midwater OMZs grade into waters of higher oxygen content above and below, hypoxic spring boils are often extreme habitats nested within normoxic rivers, and valley papyrus swamps in East and Central Africa represent patches of hypoxic habitat in the matrix of the larger, flowing, and generally well-oxygenated rivers. Populations of species or closely related species can be compared across divergent DO environments to inform our understanding of DO as a driver of phenotypic divergence and microevolutionary change. Studies of East African fishes from swamp and associated normoxic sites have demonstrated that alternative DO environments provide a strong predictor of intraspecific phenotypic

variation, particularly in respiratory traits (e.g., gill size), but also life-history traits, energetics, brain size, and biochemical traits. Observations comparing populations from low- and high-oxygen sites have reported larger gills in hypoxic populations of the eurytopic African cichlids *P. multicolor* (Chapman et al. 2000b, 2008; Wiens et al. 2014) and *Astatoreochromis alluaudi* (Chapman et al. 2007; Binning et al. 2010), the African cyprinid *B. neumayeri* (Chapman et al. 1999; Langerhans et al. 2007), and the African mormyrid *Petrocephalus catostoma* (Chapman and Hulén 2001). Interestingly, interdemic variation in gill size is also evident in the air-breathing African catfish *Clarias liocephalus* that exhibits a larger air-breathing organ and small gill size in a hypoxic papyrus swamp than in a connected normoxic tributary (Chapman 2007). Other traits related to maximizing oxygen uptake also differ across high- and low-oxygen populations. In the cyprinid *B. neumayeri*, swamp-dwelling populations are characterized by lower ASR thresholds (Olowo and Chapman 1996); higher hematocrit (Martinez et al. 2004; Chapman 2007), lower P_c (Chapman 2007), higher liver LDH activities, and higher glycolytic capacity (phosphofructokinase in heart and skeletal muscle) than in *B. neumayeri* from connected high-DO sites (Martinez et al. 2011; Table 1).

It is intuitive that larger gills should be advantageous under hypoxic conditions to facilitate oxygen uptake; however, there may be costs associated with gill proliferation that negatively affect performance in oxygen-rich environments. For example, because of the compact, laterally compressed head morphology characteristic of most teleosts, the production of large gills may affect surrounding morphological structures that are involved in feeding or swimming (e.g., body shape). The consequences of such functional-morphological trade-offs may limit feeding performance, swimming efficiency, or other fitness-related traits, and therefore contribute to the maintenance of specialized local phenotypes in extreme environments. Large gill size of hypoxia-adapted *B. neumayeri* correlates with a reduction in the size of key trophic muscles and lower feeding performance than in normoxia-adapted conspecifics (Schaack and Chapman 2003; Langerhans et al. 2007). Similarly, in the cichlid *A. alluaudi*, Binning et al. (2010) found a negative correlation between composite morphological variables related to the size and shape of the gill apparatus and pharyngeal jaw size. Furthermore, in a study of nine populations of *B. neumayeri*, Langerhans et al. (2007) showed that DO had an effect on body shape, but this effect was largely driven by oxygen's effects on gill size (Table 1). These studies demonstrate links between hypoxia and divergence in non-respiratory traits and suggest that an optimal trait value in one environment (large gills in hypoxia) could be indirectly associated with liability in others through trait correlation or developmental constraints.

Phenotypic variation across DO gradients may reflect genetic and/or phenotypically plastic adaptation to local selective pressures. The cichlid *P. multicolor*, a species that persists under both extreme hypoxia and normoxia and exhibits high levels of phenotypic plasticity in several morpho-physiological traits, has provided a valuable tool for exploring the potentially diverse roles of plasticity in the process of adaptation and evolutionary change. Lab-rearing experiments with *P. multicolor* have demonstrated a high degree of developmental plasticity in its gill size, brain

Table 1 Studies illustrating trait variation between populations of the African cyprinid *Barbus neumayeri* from high-DO and low-DO field sites, between fish held in cages in high-DO or low-DO field sites (acclimatization experiment), between fish held for short periods in high-DO and low-DO aquaria in the lab (acclimation experiment), or between fish reared under high-DO or low-DO conditions in the lab

Trait	High DO	Low DO	Study design	Reference
Gill filament length	↓	↑	Field populations	Chapman et al. (1999), Langerhans et al. (2007)
Gill filament length	↓	↑	Lab rearing under low vs high DO	Chapman (unpublished)
Aquatic surface respiration thresholds	↑	↓	Field populations	Olowo and Chapman (1996)
Critical oxygen tension	↑	↓	Field populations	Chapman (2007)
Hematocrit	↓	↑	Field populations	Martinez et al. (2004)
Lactate dehydrogenase (liver)	↓	↑	Field populations	Martinez et al. (2004, 2011)
Aerobic enzyme CCO (heart)	↑	↓	Field acclimatization	Martinez et al. (2011)
Glycolytic enzyme PFK (heart/muscle)	↓	↑	Field acclimatization	Martinez et al. (2011)
Growth rate	↑	↓	Field acclimatization	Martinez et al. (2011)
Body condition	↑	↓	Lab acclimation	Barrow and Chapman (2006)
Parasite frequency [Afrodiplozoon Polycotyleus (Monogenea)]	↓	↑	Field populations	Raymond et al. (2006)
Head size	↓	↑	Field populations	Schaack and Chapman (2003), Langerhans et al. (2007)
Body depth	↓	↑	Field populations	Schaack and Chapman (2003), Langerhans et al. (2007)
Geniohyoideus length; sternohyoideus height	↑	↓	Field populations	Schaack and Chapman (2003)
Feeding rate	↑	↓	Lab acclimation	Barrow and Chapman (2006)
Feeding performance	↑	↓	Field populations	Schaack and Chapman (2003)

Arrows indicate that the trait value is higher or lower

size, and body shape in response to growth of full sibs under either low DO or high DO, suggesting that selection against dispersers may be weak. However, population level differences were also detected in some traits (e.g., brain mass), suggesting

genetic components to trait divergence (Chapman et al. 2008; Crispo and Chapman 2010a, 2011). Mitochondrial DNA and microsatellite studies provided evidence for high gene flow among *P. multicolor* populations from divergent DO environments in the Mpanga and Nabugabo River drainages of Uganda (Crispo and Chapman 2008, 2010b). Thus, in this system, evolutionary divergence in ecologically important traits seems to occur despite high levels of gene flow. The cyprinid *B. neumayeri* displays similar differences in behavioural, morphological, and biochemical traits between high- and low-DO sites (Olowo and Chapman 1996; Schaack and Chapman 2003; Martinez et al. 2004, 2011; Langerhans et al. 2007; Table 1). However, a combination of long-term acclimation and allozyme studies suggest the possibility of genetic differentiation between oxygen regimes over small spatial scales (Chapman et al. 1999; Martinez et al. 2004). Harniman et al. (2013) used nuclear introns to examine whether populations of *B. neumayeri* within swamp/river systems of western Uganda are genetically structured by DO regime (hypoxia or normoxia), physical barriers such as geographical distance, or both oxygen regime and geography. They found that over a large scale (between drainages), geographical distance affected the genetic structure of *B. neumayeri* populations; however, within the Rwembaita-Njuguta system (Fig. 1), gene flow was high between locations of similar DO regimes, but low between areas of divergent oxygen regimes, suggesting that DO can act as a selective force limiting gene flow among populations of some fish species. These findings are supported by earlier studies on the biochemistry of *B. neumayeri* in this system that detected differences between DO regimes, and demonstrated that these differences were maintained under long-term acclimation, conclusions consistent with some degree of genetic isolation between low- and high-oxygen populations (Martinez et al. 2004, 2011; Table 1). Together these studies 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.

6 Conclusions and Outlook

Hypoxia habitats are useful systems for exploring ecological and evolutionary consequences of living under extreme conditions. Hypoxia occurs naturally in habitats characterized by low mixing and/or light limitation, such as heavily vegetated swamps, flooded forests, floodplain lakes and ponds, ephemeral pools, spring boils, tidal pools, coral reef crevices, and profundal zones of deep lakes. Oceanic oxygen minimum zones (OMZs) represent the largest areas of stable hypoxic water on the planet characterized by extreme hypoxia over very large spatial areas and over very long time periods, thus hosting an assemblage or organisms with extraordinary adaptations to hypoxia. In tropical freshwaters, hypoxic conditions are often exacerbated by high temperatures, and hypoxia can be both chronic and severe in dense tropical swamps where thick vegetation limits

light and mixing and fuels extraordinarily high rates of organic decomposition. Human-induced environmental degradation is increasing the occurrence of hypoxia to the point where hypoxia is now recognized as an environmental issue of global importance to fresh and coastal waters. Spreading dead zones are creating extreme environments on a massive spatial scale, and mass mortality of fishes and other organisms characteristic of some recent eutrophication-induced hypoxic events suggests that adaptive response on contemporary timescales is challenging in these systems.

Fishes have evolved a variety of solutions to hypoxic stress, including morphological adaptations, physiological adjustments, and biochemical and molecular defenses. Behavioral responses provide additional flexibility to deal with variation in DO that can occur temporally or spatially in extreme environment. In general, fishes persisting under extreme hypoxia use 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. Future studies that fully integrate the molecular basis for hypoxia adaption will ultimately be critical to understanding the extraordinary abilities of many non-air-breathing fish species to colonize and persist in naturally occurring extreme hypoxia (see reviews by Nikinmaa and Rees 2005; Richards 2009).

Despite potential energetic constraints and reproductive costs of life in low oxygen, there may be benefits of these extreme habitats that offset physiological and/or biochemical costs; these include reduced competition, predation, and/or disease. Several recent studies provide compelling evidence for reduced predation pressure in hypoxic habitats and the significance of hypoxic refugia for hypoxia-tolerant species in the face of piscine predators. However, there is much need for additional studies of parasite communities in extreme environments (Tobler et al. 2006). 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 East African fishes from swamps and associated normoxic sites. In these systems alternative DO environments provide a strong predictor of intraspecific variation, particularly in traits related to oxygen uptake efficiency or oxygen limitations (e.g., gill size, brain mass), but also in traits that are indirectly affected through trait correlations (e.g., body shape, trophic muscles). The integration of rearing experiments, field studies, and population genetics tools in a modest number of extremophilic fishes demonstrates that phenotypic variation across DO gradients reflects genetic and/or plastic adaptation to local selective pressures with trait-specific variation in plasticity. Together these studies highlight the importance of localized extreme habitats as model systems for studying divergent natural selection and more generally for exploring effects of physiochemical stressors on ecological and evolutionary processes.

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