Niche Dimensions in Fishes: An Integrative View*

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ABSTRACT

Current shifts in ecosystem composition and function emphasize the need for an understanding of the links between environmental factors and organism fitness and tolerance. The examples discussed here illustrate how recent progress in the field of comparative physiology may provide a better mechanistic understanding of the ecological concepts of the fundamental and realized niches and thus provide insights into the impacts of anthropogenic disturbance. Here we argue that, as a link between physiological and ecological indicators of organismal performance, the mechanisms shaping aerobic scope and passive tolerance set the dimensions of an animal's niche, here defined as its capacity to survive, grow, behave, and interact with other species. We demonstrate how comparative studies of cod or killifish populations in a latitudinal cline have unraveled mitochondrial mechanisms involved in establishing a species' niche, performance, and energy budget. Riverine fish exemplify how the performance windows of various developmental stages follow the dynamic regimes of both seasonal temperatures and river hydrodynamics, as synergistic challenges. Finally, studies of species in extreme environments, such as the tilapia of Lake Magadi, illustrate how on evolutionary timescales functional and morphological shifts can occur, associated with new specializations. We conclude that research on the processes and time course of adaptations suitable to overcome current niche limits is urgently needed to assess the resilience of species and ecosystems to human impact, including the challenges of global climate change.

Niche Definitions in Ecology: A Selective Overview

Human impacts on ecosystems are causing shifts in ecosystem composition and function. Climate warming (Solomon et al. 2007) alone has already affected the geographical distribution of aquatic and terrestrial animals and is associated with enhanced risk that species or even ecosystems (e.g., coral reefs) may become extinct (Parmesan and Yohe 2003; Thomas et al. 2004; Hoegh-Guldberg 2005; Perry et al. 2005). These shifts in species distribution and abundance occur because, in general, species are specialized for a limited range of environmental conditions, and as these conditions shift geographically, species ranges tend to follow. This observation reemphasizes the importance of the niche concept, which describes the specializations and limitations of species to a range of biotic and abiotic environmental factors. Although the niche concept is central to both ecology and environmental physiology, the perspectives of these disciplines differ substantially. Physiologists have typically focused on the abiotic aspects of the niche, developing a mechanistic understanding of how species respond to changing abiotic environmental conditions. Ecologists have emphasized the biotic aspects of the niche, especially species interactions, including food supply and competition. This article attempts to unite these two disparate perspectives by examining the dimensions of a species' niche, using examples from fishes.

The Hutchinsonian niche (Hutchinson 1957) provides a suitable conceptual framework to begin with when identifying the potential and role of a species within an ecosystem. It also provides a focus for an evolutionary understanding of the adaptive value of different physiological processes. The Hutchinsonian niche is the response surface of a population toward all effective environmental factors and resource dimensions. It is assessed using a single response variable and currency of success: the level of Darwinian fitness that is finally mirrored in the degree of population recruitment (e.g., Winemiller and Rose 1992; Kearney 2006).

In evolutionary ecology, analyses of the forces driving species distribution and abundance have mainly focused on resource gradients, specifically on food availability. Competitive interactions have also been considered (e.g., MacArthur 1968; Pianka 1974; Giller 1984). In environmental physiology, in contrast, the focus has been on the effect of individual environmental factors in relation to individual-level properties, such as tolerance. The latter approach relates to but does not fully match the definition of the term "fundamental niche." In the

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ecological literature, this term is used as the potential niche space that a species can occupy in the absence of competition and predation. Under conditions of competition and predation, a more restricted niche results that is termed the "realized niche" (e.g., Giller 1984). Under conditions of strong competition, a population may even shift toward suboptimal regimes of temperature, salinity, O_2, and food availability. Classical examples of such niche shifts in fish are those by Svärdson (1976) for fish communities in Scandinavian lakes and Werner (1984) for North American centrarchids. The concept of the realized niche thus most comprehensively describes the links between environmental parameters and the presence and success of a species at the ecosystem level. However, the ways in which the physiological characters of a species may relate to its realized niche have not been fully elaborated.

Although the breadth of the Hutchinsonian niche is formally derived from assessing Darwinian fitness, in practice both ecologists and physiologists typically assess niche breadth by measuring various proxies of fitness (e.g., growth, abundance, or whole-organism performance). Organismal performance can be understood as the integration of functions at the molecular, cellular, and tissue levels into those of the whole organism. As a result, tolerance windows (and thus niche widths) are narrower at the whole-organism level than at lower levels of biological organization (Pörtner 2002). Thus, traits at the organismal level are most relevant in shaping an organism's niche. From a physiological point of view, the response surface of a measured performance trait across a combined set of biotic and abiotic variables would thus represent an approximation of the niche. For the purposes of this review, we term this response surface the "functional niche" in the sense of functional capacity (in contrast to Elton's [1927] original understanding of the ecological niche as the trophic position or "function" of a species in a food web). We thus refer to the performance capacity of acclimatized populations during growth, reproduction, and behaviors, the latter including those involved in species interactions. The capacity of passive tolerance to environmental extremes is also interpreted as a functional capacity (Fig. 1). In this article, we discuss whether and how this functional niche relates to the dimensions of the realized niche.

The ultimate questions to be addressed in this review are (1) whether and to what degree the functional niche matches the dimensions of the realized niches, as defined on the basis of Darwinian fitness; (2) which are the physiological performance traits that provide the best approximation of the dimensions of the Hutchinsonian niche; and (3) how niche breadth relates to the point at which performance starts to decline and the zone of time-limited tolerance begins. Here we use examples from a variety of fish species to illustrate these points and to emphasize the importance of taking an integrative view of organismal performance and fitness. These examples are derived from the symposium "Niche Dimensions in Fish: An Integrative View," presented at the International Conference in Africa for Comparative Physiology and Biochemistry held at the Maasai Mara National Reserve in the Great Rift Valley of Kenya in July 2008. The first section ("Marine Regime Shifts: Biogeographical and Life-History Aspects") introduces relevant concepts, drawing on examples from the literature and from work by H. O. Pörtner and his group on a variety of marine fishes. It examines the Hutchinsonian niche from its physiological basis in aerobic performance capacity and in passive resistance with respect to temperature. The data presented suggest that the time limitation of tolerance sets in with the onset of a heat-induced loss in aerobic performance and that higher-level processes (at population, community, or ecosystem levels) are driven by the relationships among the physiological niches of the various species that make up a community. The second example ("Intraspecific Variation in Physiological Optima: Mechanisms of Acclimation and Adaptation"), drawn from work by P. M. Schulte and her group on intraspecific variation in performance traits across a latitudinal thermal gradient, suggests that for organisms inhabiting environments that show extreme temporal variability in environmental factors, both performance optima and passive tolerance may be important factors determining niche breadth. The third example ("Rheophilic Fishes: Ontogenetic Niche Shifts"), drawn from work by F. Schiemer and his group, focuses on water flow, temperature, and their interactions and emphasizes the importance of examining larval stages when estimating the physiological niche. The final example ("Lake Magadi Tilapia: Niche Shifts over Evolutionary Time"), drawn from work by C. M. Wood and his group, illustrates how, over evolutionary time, niche shifts can occur that allow fish to occupy extreme habitats that would be lethal to ancestral species. Our article does not intend to provide a full-scale review but uses these examples to build bridges between them and develop a unifying conceptual framework for understanding niche dimensions in fishes and beyond.

Marine Regime Shifts: Biogeographical and Life-History Aspects

In the marine realm, the large-scale geographical distribution of animals is shaped decisively by temperature within conditions set by geomorphology, ocean currents, water depth, and stratification or salinity. Accordingly, temperature change is a main driving force currently causing shifts in geographical distribution and in species composition of marine ecosystems (Murawski 1993; Southward et al. 1995; Kröncke et al. 1998; Perry et al. 2005; Pörtner and Knust 2007). Temperature contributes, either directly or indirectly, to shaping the relationships between climatic indexes such as the North Atlantic Oscillation (NAO) on the one hand and, on the other hand, fish stock size and recruitment. This is now clear for exploited fish species, such as cod (*Gadus morhua*; e.g., Pepin et al. 1997; Otterlei et al. 1999; von Westernhagen and Schnack 2001; Brander and Mohn 2004; Ottersen et al. 2006; Stige et al. 2006). This is also true for the seasonal timing of spawning in relation to the timing of phyto- and zooplankton production. Beyond the elaboration of statistical proof for such relationships, there is a need to understand the mechanisms involved (Jensen 2003; Parmesan and Yohe 2003; Pörtner and Knust 2007; Drinkwater et al. 2010).

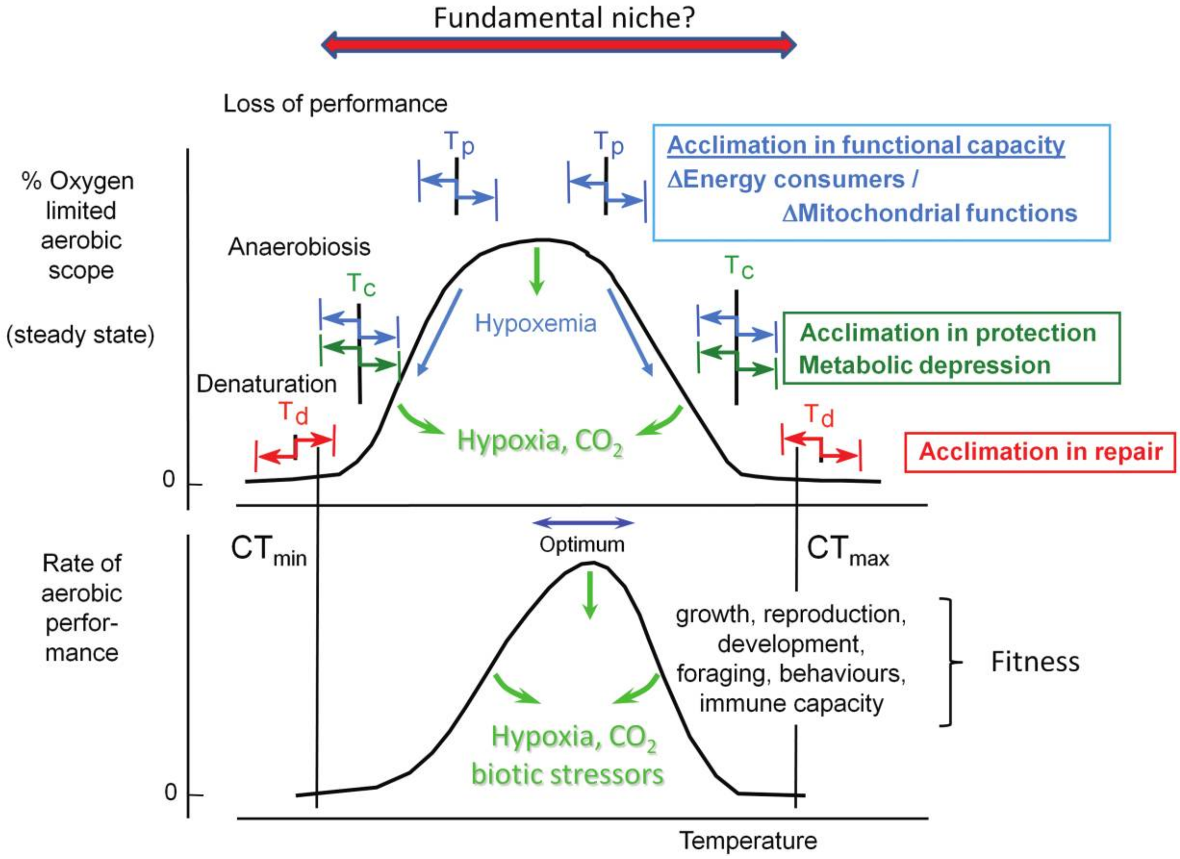


Figure 1. Conceptual model of how ocean warming, hypoxia, and acidification as interacting stressors shape the thermal window of performance of a species, based on the concept of oxygen- and capacity-limited thermal tolerance (after Pörtner 2002; Pörtner and Knust 2007). Optimized oxygen supply to tissues between low and high pejus temperatures (*top*) combined with the kinetic stimulation of performance rates by warming supports temperature-dependent performance and a functional optimum (i.e., an optimum of aerobic scope) close to the upper pejus temperature (*bottom*). This reflects functional capacity in ecosystem-level processes, such as competition, foraging, immune response, growth, and behaviors. Ambient hypoxia and elevated CO_2 levels both cause a narrowing of thermal windows and possibly lower performance optima through lower functional capacities that may involve reduced systemic oxygen tensions (*green arrows*). The illustration depicts acute performance levels and limitations in response to short-term temperature fluctuations. On longer timescales, acclimatization occurs as a shift of acute performance windows (*horizontal arrows*) within the limits of the thermal niche of a species. The traditional estimates of critical thermal maxima and minima (CT_{max} and CT_{min}) are interpreted to delineate the outermost limits of the fundamental niche where function ceases.

The concept of oxygen- and capacity-limited thermal tolerance (Fig. 1; Pörtner 2001, 2002) may provide a mechanistic explanation of thermal limitation and of the transition from permanent, active survival to time-limited passive tolerance. This concept is a suitable candidate to define the borders of the niche of functional capacity of a species with respect to temperature (Pörtner 2006). The concept implies that oxygen supply to tissues is optimal and in excess of maintenance demand between the lower and upper pejus temperatures. The excess oxygen available fuels the excess performance capacity of the animal and is reflected in its aerobic scope. The kinetic stimulation of performance by warming supports a tilted performance curve with an optimum close to the upper pejus temperature. Beyond the pejus limits, oxygen supply capacity becomes limiting. Hypoxemia develops and whole-organism functional capacity (e.g., growth performance) declines. Once critical temperatures are reached, extreme hypoxemia develops over time and causes transition to anaerobic metabolism and, finally, molecular damage. On long timescales (as in growth studies), the initial onset of a performance decrement occurs at the limits of thermal acclimation capacity. A loss in fitness, mirrored in a loss of growth performance, causes reduced population abundance at the ecosystem level. For example, eelpout abundance in the Wadden Sea falls during exposure to extreme summer temperatures, in the same temperature range when growth performance decreases. Large individuals are those affected most by the heat stress as a result of the size dependence of oxygen limitation (Pörtner and Knust 2007).

These data suggest that the functional niche may relate to one unifying physiological principle in animals: the long-term availability of sufficient aerobic scope within the window of tolerance. While the concept of aerobic scope has a long-standing history in comparative physiology, it has only recently been demonstrated to underpin climate-induced ecological shifts observed in the field (Pörtner and Knust 2007; Farrell et al. 2008). The width and the tilted shape of the temperature-dependent aerobic performance curve (Fig. 1) are set by the principles of oxygen- and capacity-limited thermal tolerance. The characters of performance resulting from such mechanistic analyses meet with more empirical descriptions of performance elaborated from a large body of research in evolutionary thermal biology (for review, see Angiletta 2009).

The limited window of whole-organism performance capacity will impact the ecological success of a species directly and by influencing its interactions with other species (in predator-prey and/or competitive interactions; Pörtner and Farrell 2008). Alterations in community composition may result. The fundamental insight here is that higher-level processes (at population, community, or ecosystem levels) are driven by the relationships among the niches of the various species that make up a community.

Figure 1 also distinguishes between the temperature range associated with long-term survival, growth, and reproduction due to maintained performance (the active range) and the subsequent time-limited endurance of temperature extremes. The boundary between these two areas is defined as the pejus temperature (T_p; the temperature at which aerobic scope begins to decline). Organisms can survive but for progressively shorter periods at temperatures higher than T_p and even higher than T_c, where aerobic scope nears zero. For example, in laboratory studies, thermal tolerance limits of fishes are often determined as the onset of spasms at the critical thermal maxima (CT_{max}) and minima (CT_{min}; Lutterschmidt and Hutchison 1997*a*, 1997*b*). According to traditional views, CT_{max} and CT_{min} are the temperatures at which fish are unable to escape conditions that will ultimately lead to death (Beitinger et al. 2000) and have been suggested to delineate the limits of the fundamental niche (see above). However, CT_{max} and CT_{min} were found at more extreme temperatures than the critical limit, T_c (Zakhartsev et al. 2003), and represent temperatures at which the animal cannot survive for long periods. We suggest that the fundamental niche is more likely to be linked to either T_p or T_c rather than the CT_{max} or CT_{min} (Fig. 1). Nonetheless, during short-term exposures to environmental extremes, animals can exploit protective mechanisms—such as the capacity of anaerobic metabolism, antioxidative defense, and the heat-shock response to extend the period of passive tolerance to thermal extremes—and these processes may be under strong selection in some environments. For example, extending the range of passive tolerance could become a crucial element of the niche in highly variable environments, such as the intertidal zone.

These principles of thermal stress are also likely involved in the current northward shift of eastern Atlantic cod *Gadus morhua*, with a clear role for warming winter temperature in driving this shift (e.g., Perry et al. 2005). The sensitivity of cod to warmer winters likely mirrors the specific sensitivity of the respective life stages during the spawning period, namely adult spawners and, subsequently, egg and larval stages (Pörtner and Farrell 2008). In spawners, oxygen limitation likely sets in at a lower temperature as a result of large body size exacerbated by the up to 20% increase in body weight due to egg masses. Sensitivity to warmth may also be high in larval stages, associated with the limited capacity of the developing circulatory functions (Pörtner et al. 2006). In the winter, cold is seen as a general selective factor on the survival of fish larvae, which is also modulated by food availability and predation (Hurst and Conover 2002). While cod recruitment declines in the warming North Sea, improved recruitment results for northeastern Atlantic Cod stocks as a result of the warming-induced alleviation of cold constraints (Pörtner et al. 2001; Colosimo et al. 2003). In general, the width of the thermal niche is expected to match the temperature-dependent range of geographical distribution of a species or its genetically distinct populations. It thereby defines the long-term response to changing temperatures on either cold or warm sides of the thermal window, as in the case of Atlantic cod in the North Sea versus the Arctic Barents Sea.

Fecundity and recruitment success (number and fitness of offspring) are thus constrained to a limited thermal window or niche of a species. However, these performance indicators reflect not only the well-being of eggs and larvae but also the condition and fitness of adult fish within the spawning stock (Rothschild 1986; Kjesbu et al. 1996; Ulltang 1996; Trippel et al. 1997; Marshall et al. 1998; Pörtner and Farrell 2008). Therefore, they mirror the overall thermal niche of the species, while the niches for the various life stages over time may well differ (see above). A good example is the regime shift between colder years dominated by sardines and warmer years dominated by anchovies on the Pacific coast of Japan (Takasuka et al. 2007), reflecting thermal effects not only on growth performance but also on spawning productivity (Takasuka et al. 2008). Specialization of marine fauna on climate-related temperature windows thus causes sensitivity to temperature extremes as a result of decrements in performance, that is, the capacities to forage, migrate, grow, or reproduce.

Different thermal windows of species likely influence the quality and intensity as well as the seasonal timing of their interactions in an ecosystem (Pörtner and Farrell 2008). In general, species can coexist because their thermal windows overlap but are not necessarily identical. This may be one principal reason for changes in community composition and food web interactions. Direct effects of temperature on individual species thus lead to effects at the ecosystem level. For example, a food web analysis for cod in the southern North Sea revealed that a shift from larger *Calanus finmarchicus* to smaller *Calanus* sp. was a major reason for the decrease in the cod population (Beaugrand et al. 2003). More recently, Helaouët and Beaugrand (2007) showed that the warming trend caused this shift to the smaller copepod species, emphasizing that such direct physiological effects of temperature are key to an understanding of climate-induced changes in species interactions.

These examples strongly suggest that the thermal window of performance and thus the functional niche match the thermal dimensions of the realized niche. This is most evident where climate sensitivity is direct. In those cases where the effect is indirect, through the food chain, it is less clear whether the dimensions of the functional niche are equivalent to those of the realized niche. However, in a thought experiment, reduced food availability (see copepod example above) or enhanced competition for space or resources would demand elevated energy expenditure (e.g., for successful foraging) and/or represent less energy (food) intake. This would be equivalent to a net removal of aerobic energy from the energy budget. As a result, net aerobic scope is diminished; the functional niche is narrowed and with it the realized niche. This illustrates how biotic stressors codefine the dimensions of the niche and will be amplified below.

Similar observations have been made in terrestrial organisms (higher plants, insects, birds). Here, thermal effects on biogeography and biodiversity are independent from the position of the respective species in the food chain (Huntley et al. 2004), indicating constraints at the level of the individual species and organism. In conclusion, thermal performance windows are decisive elements in shaping biogeography and the realized niches of many species. Changes in thermal bioenvelopes or the respective "niche dimensions" and associated performance characters (see above; Pörtner 2006) thus have major implications for the geographical ranges of species and in species interactions (Pörtner and Farrell 2008). The beneficial nature of thermal specialization is also illustrated by the observation that temperature-dependent windows of growth performance may differ not only between species but even between populations or developmental stages of a species across thermal (i.e., latitudinal) clines (Pörtner et al. 2001, 2008).

The impact of ocean hypercapnia and acidification is also relevant in the context of climate change effects on marine ecosystems (Pörtner 2008). Increased CO_2 is expected to cause performance decrements and a narrowing of thermal windows, with implications for biogeography, species interactions, and food web structure (Pörtner and Farrell 2008). In general, realistic scenarios and thus realistic estimates of niche dimensions require integrated analyses of effects of CO_2, temperature, and oxygen deficiency, since all of these factors change concomitantly in the real world and their effects influence each other (Reynaud et al. 2003; Hoegh-Guldberg 2005; Pörtner et al. 2005; Hoegh-Guldberg et al. 2007).

Intraspecific Variation in Physiological Optima: Mechanisms of Acclimation and Adaptation

Intraspecific variation in physiological optima and tolerances can be used to provide insights into the mechanisms underlying acclimation, adaptation, and niche specialization. For example, the cod (*Gadus morhua*) of the eastern Atlantic is differentiated into several independent populations that use distinct spawning grounds and that differ genetically (Nielsen et al. 2001). Subtle differences exist between the thermal windows of growth of distinct populations of cod, indicating trade-offs in thermal adaptation associated with climate-dependent energy budgets (Pörtner et al. 2008). Energy budgets are likely shaped by climate variability, indicating, for example, lower cost of cold adaptation in stenotherms than in eurytherms (Pörtner 2006). In invertebrates living along the same cline, thermal windows change across latitudes and fluctuate with seasonal temperature variability (e.g., Wittmann et al. 2008; Pörtner et al. 2009). Changes in mitochondrial respiratory capacity and in the capacity of citric acid cycle enzymes are well-established processes associated with thermal acclimatization (Guderley 2004; for a review, see Pörtner 2006).

Similar processes have been examined in some detail in the small teleost fish *Fundulus heteroclitus* (also known as the common killifish or the mummichog), which is found in marshes and estuaries along the Atlantic coast of North America. This species exists in two physiologically and morphologically distinct forms (Morin and Able 1983; Powers et al. 1993; Scott et al. 2004) that diverged 0.5–1 million years ago (Gonzalez-Villasenor and Powers 1990; Bernardi et al. 1993). The northern form, *Fundulus heteroclitus macrolepidotus*, is found from Nova Scotia to northern New Jersey, while the southern form, *Fundulus heteroclitus heteroclitus*, is found from southern New Jersey to northern Florida. At intermediate latitudes, there is a narrow zone of admixture between these two forms, centered in New Jersey (Bernardi et al. 1993; Adams et al. 2006). Population genetic studies suggest that the contact zone between the two subspecies may have persisted for many thousands of years (Adams et al. 2006). Hybrid zones between such differentiated populations are excellent natural laboratories for the investigation of a wide variety of ecological and evolutionary questions (Barton and Hewitt 1985). According to a large body of empirical and theoretical work, hybrid zones are often located at environmental gradients (Barton 2008), providing the opportunity to utilize hybrid zones to investigate the genetic basis of differences in niche dimensions.

Because of the steep thermal cline along the Atlantic coast of North America, northern populations of *F. heteroclitus* are exposed to temperatures that are, on average, approximately 12°C lower than those experienced by their southern counterparts. There are differences in thermal tolerance (Fangue et al. 2006), thermal optima (Fangue et al. 2008), and salinity tolerance (Scott et al. 2004) between the subspecies. Southern *F. heteroclitus* have consistently higher CT_{max} and CT_{min} than do northern fish, with a difference between populations on the order of ~1.5°C (Fangue et al. 2006). Acclimation strongly affects these parameters, and both CT_{max} and CT_{min} increase by more than 10°C with acclimation from 3° to 35°C (Fangue et al. 2006). However, the difference between the subspecies persists regardless of acclimation temperature, such that when the subspecies are compared at a common acclimation temperature, the southern subspecies always has a higher CT_{max} than does the northern subspecies. The northern subspecies has higher fertilization success and larval survival in freshwater than does the southern subspecies (Able and Palmer 1988). Similarly, there are substantial differences in adult salinity tolerance. The southern subspecies experiences up to 20% mortality following freshwater transfer, while the northern subspecies experiences no significant mortality (Scott et al. 2004). In areas such as the Chesapeake Bay, the southern subspecies dominates at the coast, while the proportion of northern subspecies increases in freshwater habitats, even at latitudes well within the exclusive range of the southern subspecies when examined along the coast (Powers et al. 1993). In the future, studies on the interacting effects of temperature, salinity, and other environmental factors (such as hypoxia) on *F. heteroclitus*, are likely to provide insights into the trade-offs among competing physiological demands.

Although most work on this species has addressed tolerance limits, some studies also hint at differences in performance optima. For example, Fangue et al. (2008) showed that the optimal temperature for swimming performance differs between killifish subspecies when fish were acutely exposed to thermal challenge, with the northern subspecies having the best swimming performance at approximately 17°C and southern fish having the best performance at approximately 24°C, when acclimated to a common temperature of 18°C in the laboratory. However, when fully acclimated to the test temperature, both subspecies showed few differences in swimming performance across temperatures ranging from 7° to 30°C (Fangue et al. 2008), and there were few detectable differences in optimal temperature. These observations emphasize the importance of plasticity within the functional niche.

An important element of the oxygen- and capacity-limited thermal tolerance framework (Pörtner 2006; Fig. 1) is that, in climate zones with significant temperature variability or shifts in the seasonal temperature regime, cold-adapted or -acclimated eurytherms have wider thermal windows and greater mitochondrial capacity than do related warm-adapted or -acclimated organisms. This then generates the hypothesis that the increased mitochondrial capacity leads to a higher standard metabolic rate and results in a trade-off in the form of decreased heat tolerance as elevated oxygen demand outstrips oxygen supply capacity at lower maximum temperatures. *Fundulus heteroclitus* provides an ideal model in which to test these predictions, since the northern and southern subspecies differ in their thermal tolerance. Therefore, we can ask the question: do the northern and southern subspecies also differ in their metabolic rates and mitochondrial capacities? Figure 2 (summarized from Fangue et al. 2006, 2009) shows the thermal tolerance, metabolic rate, and mitochondrial capacity (measured as the state III, or maximum ADP-stimulated rates of oxygen consumption in vitro) of the two subspecies of *F. heteroclitus*, when acclimated to low temperatures. Consistent with the predictions of the hypothesis of oxygen- and capacity-limited thermal tolerance, the northern subspecies has greater mitochondrial capacity, higher standard metabolic rate, and lower thermal tolerance than does the southern subspecies. Thus, these data provide strong support for the existence of a trade-off between metabolic rate and thermal tolerance. Consistent with the hypothesis, these data further implicate processes at the mitochondrial level in this trade-off.

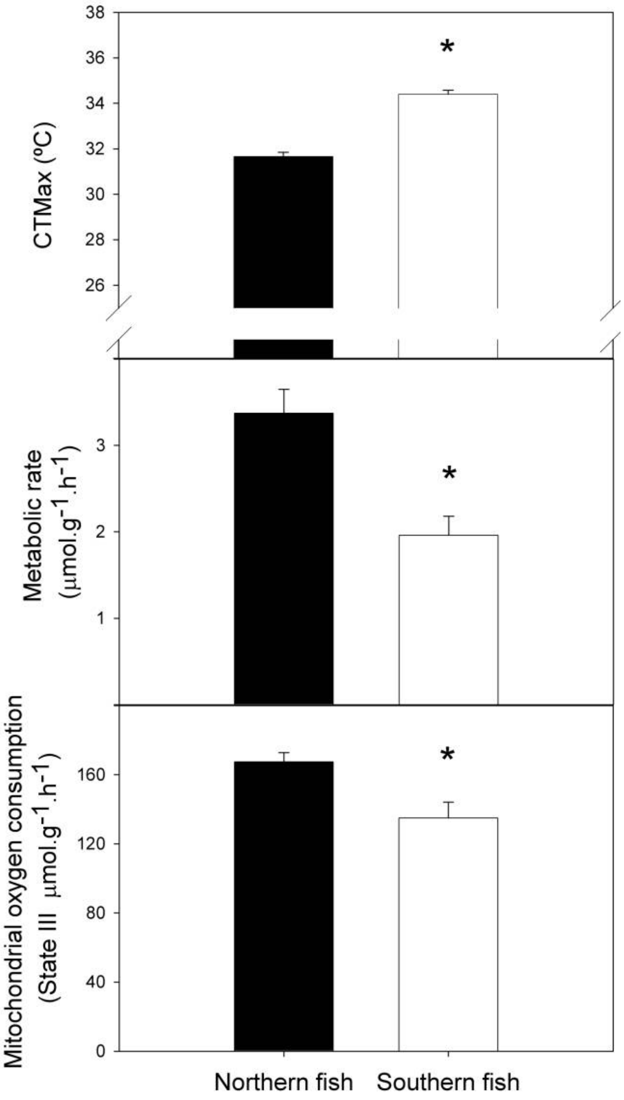


Figure 2. Relationship between maximum thermal tolerance (CT_{max}), whole-organism metabolic rate, and state III mitochondrial oxygen consumption in a northern and southern subspecies of *Fundulus heteroclitus*. Asterisks indicate significant differences between the subspecies. Data summarized from Fangue et al. (forthcoming).

Because *F. heteroclitus* can be acclimated to a wide range of temperatures, this species also provides an interesting model in which to investigate the effects of physiological plasticity on these relationships. When acclimated at high temperatures, the northern and southern subspecies differ in their thermal tolerance, as at low acclimation temperatures. Do the northern and southern subspecies also differ in metabolic rate and mitochondrial capacity under conditions of warm acclimation, as they do under conditions of cold acclimation? At warm acclimation temperatures, the northern subspecies has a higher metabolic rate than does the southern subspecies, consistent with the hypothesis that there is a trade-off between high metabolic rate and lowered thermal tolerance (Fangue et al. 2009). In contrast, there are no differences in mitochondrial capacity between the subspecies when they are acclimated to warm temperatures. Thus, these data do not support the existence of a direct link between mitochondrial capacity and whole-organism metabolic rate; other factors—such as mitochondrial density and proton and ion leak rates across mitochondrial and cellular membranes—likely complicate the picture (Pörtner 2006) and may represent targets of selection in this species.

Taken together, these data support the fundamental concept of a trade-off between metabolic rate and thermal tolerance. The observation that there are differences in the relationship between processes at multiple levels of organization depending on acclimation temperature clearly indicates the importance of physiological plasticity and complexity in setting the niche of an organism. In future studies, it will be important to examine the individual phenotypes and physiologies of hybrid individuals. This may provide an opportunity to investigate the consequences of the disruption of coadapted gene complexes (e.g., Burton et al. 1999) and yield additional insights into the genes involved in differences in thermal tolerance and physiological plasticity and those that specify the niche dimensions of this species.

Examples of adaptive niche shifts are most evident in extreme environments, as illustrated in the next two sections ("Rheophilic Fishes: Ontogenetic Niche Shifts" and "Lake Magadi Tilapia: Niche Shifts over Evolutionary Time"). In these examples, the evolution of special functions has supported the shift of the respective niche and the maintenance or adjustment of performance capacity under otherwise uninhabitable abiotic conditions. In addition, as outlined in "Rheophilic Fishes: Ontogenetic Niche Shifts," it is critical to consider the dimensions of the niche at all stages of a species' life history, since these are not necessarily constant across a lifetime.

Rheophilic Fishes: Ontogenetic Niche Shifts

Large rivers exemplify an environment controlled by the dynamic interface between hydrology and geomorphology, which poses high demands and stresses especially during the early life-history stages (Schiemer et al. 2001*b*). This may also be true for adult spawners, as seen in the case of salmon migration in warming rivers (Farrell et al. 2008). Because of allometric constraints on performance (see Wieser 1995), flowing water is especially demanding for the smallest life stages, which therefore can be considered as critical for recruitment (Miller et al. 1988). For rheophilic fish in large river systems, three environmental niche axes are particularly critical: temperature, flow velocity, and appropriate food availability. Coping with these conditions requires physiological adaptations that increase in complexity from thermal adaptations to traits of feeding and digestion. During early life history, the physiological and energetic scope is narrow, which allows us to identify niche width and location, understand match or mismatch between environmental conditions and performances, and recognize trade-offs and constraints between different elements (Wieser 1997).

Temperature is particularly important during the embryonic and larval period, when fast growth through a critical stage is decisive for survival (Houde 1989; Fuiman 2002). An interspecific comparison of the thermal niche during embryogenesis of three species representative of the longitudinal distribution of fish in central European rivers—brown trout (*Salmo trutta fario*), nase (*Chondrostoma nasus*), and roach (*Rutilus rutilus*)—shows that the niche location, defined by duration and survivorship functions, exhibit distinct differences between species characteristic of cold headwater streams (rithral) and those characteristic of warmer lowland rivers (potamal), respectively. The niche width is narrower in the rheophilic species trout and nase compared with the eurytopic roach.

The nase, *C. nasus*, is a common fish characteristic of the hyporithral and epipotamal sections of European rivers. The temperature dependence of various performances and fitness elements during the endogenous and exogenous feeding phases of larval nase was analyzed in order to identify the properties of the thermal niche (Kamler et al. 1998; Keckeis et al. 2001; Schiemer et al. 2003).

Figure 3 refers to two parameter sets: bioenergetic performances expressed as growth and transfer efficiencies, and the

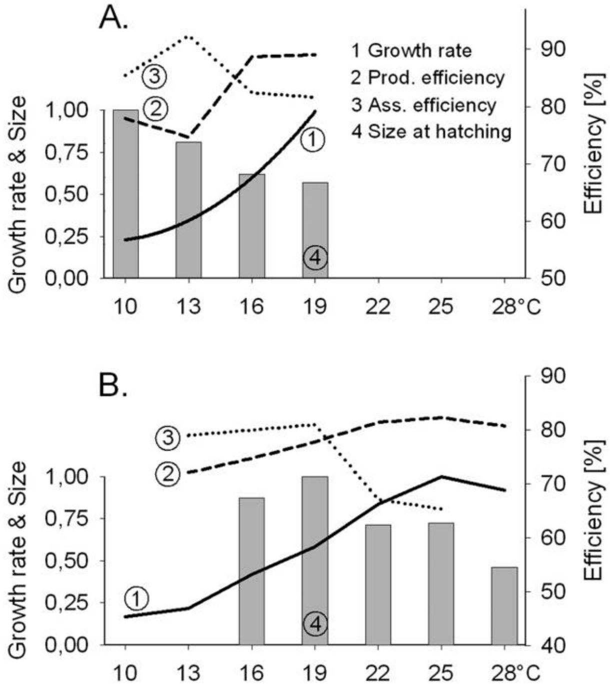


Figure 3. Temperature dependence of two fitness characteristics, energetics versus stage-specific body size of larval *Chondrostoma nasus.* The comparison of the consecutive stages embryogenesis and yolk-feeding larvae (*A*) as well as exogeneously feeding larvae (*B*) reveals similarities in warming-induced trends of increased growth and energy flux and reduced stage-specific body sizes. In both phases, assimilation efficiencies are higher at lower temperatures, while production efficiencies, reflecting the cost of growth, are increased at higher temperatures. Graphs also mirror the widening of the thermal window toward higher temperatures during the larval phase and illustrate the ontogenetic shift of thermal tolerance to higher temperature. Growth rates (*1*) and the sizes at hatching or the finite larval sizes, respectively (*4*), are expressed on a scale from 0 to 1 for easy comparison. Assimilation (*3*) and production efficiencies (*2*) are given as percentages. Experimental data were obtained at constant temperature and during the phase of exogenous feeding with an ad lib. supply of life zooplankton food (*Artemia* larvae at the beginning, followed by rations of *Daphnia* of appropriate size; Kamler et al. 1998; Keckeis et al. 2001). Note that these patterns include the effects of ongoing thermal acclimation (Fig. 1).

size attained at certain life-history events as an expression of compound developmental processes. These fitness characteristics are compared for the two consecutive stages: yolk-feeding and exogenous-feeding larvae. The thermal niche expands rapidly during the early life-history phase and shifts to higher temperatures. It lies between 10° and 19°C for embryogenesis and endogenously feeding larvae and between 13° and 28°C for exogenously feeding larvae. An ontogenetic niche shift in thermal optimum occurs by about 5°C from yolk feeding to exogenous feeding and occurs within a period of a few weeks. This can be seen as an adaptation for the seasonal temperature cycle in the inshore zones of unregulated large rivers in temperate climates.

Temperature not only determines duration but also changes the pattern of development. At a lower temperature, development is prolonged, and hatching is delayed and occurs at a larger body size associated with higher differentiation at the onset of feeding but at the expense of lower energy storage. At higher temperatures, the hatching of embryos, swimming up of larvae, and onset of exogenous feeding all occur at a distinctly smaller body size (tissue weight) at a less advanced stage of morphological differentiation but with a larger remaining yolk reserve, which provide an advantage for the critical period in the transition from endogenous to exogenous feeding (Miller et al. 1988). This strategic shift reflects trade-offs between body size, stage duration, and the conservation of energy reserves. The combined performances at the lower end of the thermal niche appear adaptive as to maintain adequate whole-organism performance. However, they may not be successful in the wild as a result of the accumulation of adverse effects in a stochastic environment. At higher temperatures, the ecological meaning of the combined performances is revealed by placing them into a temporal framework. The actual body size attained at a given age is clearly increased, however, at increased risks of mortality because of the smaller size and less advanced morphological differentiation at the start of the exogenous feeding period.

An important compound measure of niche is the energy balance of the larval organism (Kamler 1992). There are similarities in the temperature-induced trends between the two consecutive ontogenetic stages with respect to increased growth, energy flux, and transfer efficiencies. Assimilation efficiency (A/C; assimilation as a fraction of energy consumed) decreases in the upper viable temperature range. This means that the utilization of energy stored in yolk or in food is more efficient at lower temperatures—less energy is lost via defecation and excretion. Production efficiency (P/A; production as a fraction of assimilation) increases as a result of a decoupling of production and respiration in the early phase of larval fish growth. Developmental progress may well influence these patterns. For example, energy flux also fuels differentiation of muscular and sensory systems, and assimilation efficiency changes as a result of differentiation of the digestive system. Nonetheless, maximal specific growth rates in the larval phase of fish are particularly high (up to 40% per day; Kamler 1992; Kamler et al. 1998), despite the fact that feeding performances and digestive abilities are not fully developed. How is the high scope for growth achieved despite these constraints? It was suggested that the high growth rates are determined not only by a temperature-dependent increase in energy flux but also by the way assimilated energy is allocated. This is in line with the theory of Wieser (1991) and Rombough (1994) of an apparent decoupling of production in the form of growth from respiration (P : R) in the early phase of larval fish growth.

It appears that there is a trade–off, a competitive relationship between growth (energy flux) and body size at which a developmental stage or life-history event occurs. This reflects competitive selective pressures for fast growth on the one hand and for differentiation and a coordinated development of muscular and sensory systems on the other. When we look at the various processes that contribute to fitness, there is no distinct temperature optimum, but a range of viable performance combinations. This array is an expression of trade-offs between various traits.

After the hatching and swimming-up of the larvae, water current velocity becomes a very important niche dimension of rheophilic fish. It determines larval distribution, acts as a stress and mortality factor beyond certain threshold values, and also provides food to drift-feeding stages. There is a good deal of work on the energetics of microhabitat use of larger-sized drift-feeding fish (e.g., Fausch 1984; Hughes and Dill 1990; Hill and Grossman 1993). Niche dimensions of larval fish will be dependent on the development of swimming and sensory performances and digestive abilities. Figure 4 summarizes results of experimental studies by Flore (1999), Flore and Keckeis (1998), and Flore et al. (2001; L. Flore, H. Keckeis, and F. Schiemer, unpublished data). Essential survival functions such as swimming performances and escape reactions are scaled with size; that is, they increase linearly with fish length (Fig. 4).

A central element in performance capacity is the relationship between food availability and food acquisition, since low food rations result in reduced growth and fitness. Successful foraging depends on visual and swimming performance, supported by morphological conditions such as mouth gaping and feeding apparatus as well as digestive capacity. Figure 4*A* explores the relationship between high and low availability of optimal-particle-size food and energy gain based on prey attack rates and capture success by drift-feeding larvae and juveniles of nase, depending on body size and water velocity. Higher water velocities increase the drift rate but also the respiratory costs for swimming and reduce the costs of foraging (Kaufmann 1990). A specific performance window results in optima of energy return and thresholds skewed toward higher water velocities. This window resembles the one for temperature (Fig. 1). At limiting food densities, the window of energetic benefit is narrowed, with an optimum emerging at higher velocities and food advection. Both optima and limits shift to higher velocities with increasing body size. Figure 4*B* shows the continuous niche expansion with larval size. The shaded areas indicate the current velocity ranges that provide high energy return at high (*light gray*) and low (*dark gray*) food availability. The data predict that at lower food densities fish have to spend more time feeding and take higher risks in higher current velocities. This will

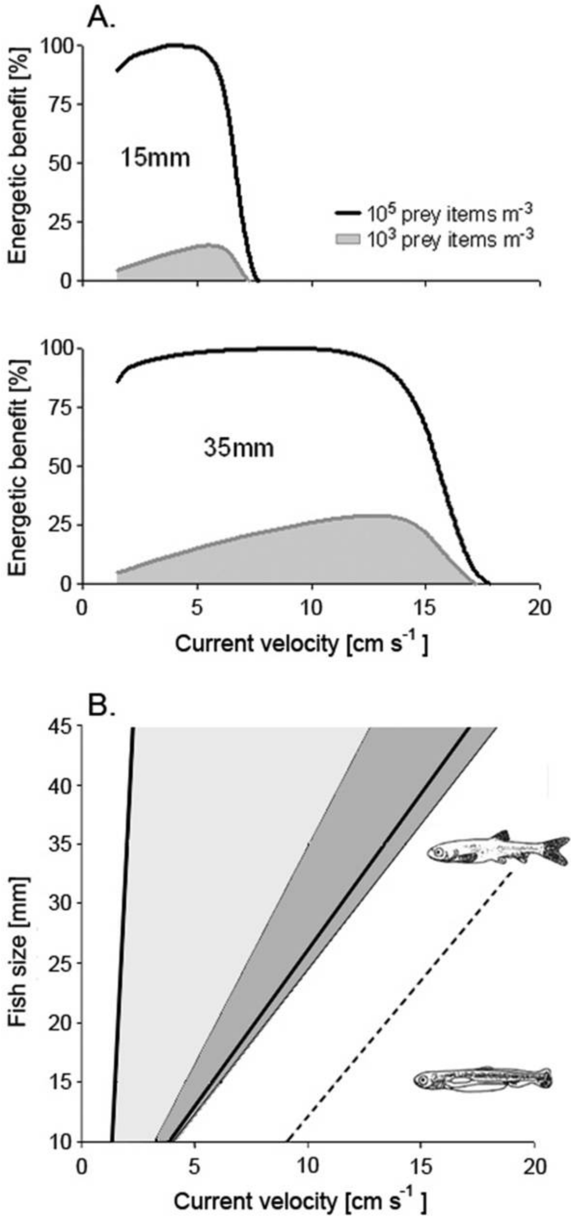


Figure 4. Compound action of food availability and water velocity on drift-feeding larvae and juveniles of *Chondrostoma nasus* of various body lengths (experimental studies by Flore and Keckeis 1998; Flore 1999; Flore et al. 2001; L. Flore, H. Keckeis, and F. Schiemer, unpublished data). Studies on swimming performances and on prey detection and acquisition capacities depending on body size were carried out under tight control of water currents, temperature (16°C), and food availability (optimized particle sizes depending on fish size). *A*, Functional response curves (*top*), that is, the relationship between current velocity and energetic net gain calculated from feeding rates and respiratory costs for two food densities (*thick line*, high; *shaded area*, low) and for two size classes of fish (15 and 35 mm total length). Feeding rates were calculated from experimental observations of prey detection and handling by video recordings. The response surfaces are given as percentages of maximal values for each size class to allow for immediate comparison. *B*, Summary of the ontogenetic niche shift and niche expansion regarding the two significant parameters current velocity and food density according to body size. Shaded areas indicate the current velocity range that provides a high energy return (more than 90% of the respective maximum shown in *A*) at high (*light gray*) and low (*dark gray*) food availability. The dashed line shows critical water velocities (maximum swimming speed sustained for a period of 30 s) in relation to body size (length) as essential for survival. Note the narrow range between maximal swimming performances and optimal current velocities.

contribute to higher cumulative costs of transport at the expense of growth. By shaping performance capacity and energy budget, the seasonality of food occurrence will thus alter survival and population recruitment.

How do these niche dimensions match with the conditions larval fish encounter in the field? In order to answer this question, we have to assess the relevant environmental conditions in the inshore zones of rivers (inshore retention concept; Schiemer et al. 2001*a*). Considering the stochastic nature of microhabitat conditions with regard to water velocity, continuous disturbances, and the heterogeneous food supply, we can conclude that larval fish live at high risk with low energetic scope and buffer capacity. Similar to limitations at the edges of the thermal window (Fig. 1), this limits their capacity to successfully respond to further challenges. Detailed studies of early larval growth in the inshore location of large rivers show that suboptimal conditions (cumulative effects of suboptimal temperature and high swimming costs at low food) are responsible for low growth rates in the field, leading to prolonged risks in a stochastic environment. Performance windows during the larval period are particularly narrow and need to closely match the environmental conditions of temperature, water velocity, and food availability according to the original dimensions of their niche. Spatial heterogeneity has been considerably affected by river engineering. In contrast to the warming trend, average river temperatures in central Europe have declined during spring and summer as a result of faster runoff. River regulation has thus disrupted the species-specific tuning between physiological requirements and field conditions, leading to a decline of formerly abundant species. In rivers entering the North Pacific, heat stress has increased, bringing salmon on spawning migrations to the limits of their thermal window of aerobic performance (Farrell et al. 2008). At present, there is a pressing need for river restoration in order to maintain ecological services and species diversity. Detailed understanding of niche dimensions at critical life stages is essential to derive quantitative guidelines for restoration measures.

Lake Magadi Tilapia: Niche Shifts over Evolutionary Time

An environment in which only one species of fish can and does exist, and which is so severe as to kill even closely related species within a matter of minutes (Wood et al. 1989; Wright et al. 1990), should provide an adequate practical example of a niche and also of a niche shift over evolutionary time. Lake Magadi, in the southern Rift Valley of Kenya, is arguably the most extreme aquatic environment on earth to support fish life. As first documented in the classic monograph of Coe (1966), the Magadi tilapia (*Alcolapia grahami*, formerly *Oreochromis al-*

calicus grahami, formerly *Sarotherodon alcalicus grahami*, formerly *Tilapia grahami*) thrives in this extremity: water pH 10, alkalinity >300 mmol L^{-1}, osmolality 525 mOsm kg^{-1} with high $[Na^+]$ and low $[Cl^-]$, temperatures as high as 42°C, daytime hyperoxia, severe nighttime hypoxia, substantial ultraviolet radiation, a monoculture diet of N-fixing cyanobacteria (*Arthrospira platensis*, formerly *Spirulina platensis*), and intense avian predation. Its physiology and behavior have been studied intensively by some of the most eminent comparative physiologists of the twentieth century (e.g., Johansen et al. 1975; Maloiy et al. 1978; Eddy et al. 1981; Randall et al. 1989; Johnston et al. 1994; Laurent et al. 1995).

The picture that has emerged is one of unique adaptation to "life on the edge" in this very small cichlid (adult size typically 1–5 g). All N-waste is excreted as urea at a rate equal to that of a small mammal via a facilitated diffusion-type urea carrier (UT-A) in the gills (Randall et al. 1989; Wood et al. 1989, 1994; Walsh et al. 2001). Diffusive excretion of ammonia would appear to be impossible into this highly buffered alkaline water, and indeed, none occurs, making the Magadi tilapia the only 100% ureotelic teleost fish. Expression of the Krebs ornithine urea cycle throughout the white muscle mass and liver accounts for 100% ureotelism (Randall et al. 1989; Walsh et al. 1993; Lindley et al. 1999) and can serve also to detoxify exogenous ammonia-N to urea-N (Wood et al. 1989, 1994). Other adaptations include exceptionally high extracellular and intracellular pH (Johansen et al. 1975; Wood et al. 1994); a high-affinity blood O_2 curve apparently insensitive to pH in the physiological range (Lykkeboe et al. 1975; Narahara et al. 1996); a very high gill O_2 diffusing capacity (Maina et al. 1996); an exceptionally high metabolic rate with a Q_{10} relationship adaptive to the diurnal temperature and O_2 cycle, as well as a capacity for facultative air breathing via a physostomous air bladder (Franklin et al. 1995; Maina et al. 1995; Narahara et al. 1996); and a unique drinking system that allows alkaline lake water to bypass an acidic stomach (Bergman et al. 2003). Interestingly, these animals retain the ability to live in circumneutral freshwater, where urea production and drinking continue (Wood et al. 2002*a*, 2002*b*; Bergman et al. 2003). This suggests that these adaptations are now part of inflexible physiological programs.

The species provides a clear example of how the evolution of special physiological performance characteristics can overcome severe environmental constraints. For one such characteristic—the evolution of 100% ureotelism—the pathway is likely a very simple one, the retention of an embryonic characteristic. When ureotelism was first discovered in the Magadi tilapia (Randall et al. 1989), it was widely believed that the genes for the ornithine urea cycle had been silenced or deleted in teleost fish. We now know this is not the case and that the early life stages of teleosts in general express the enzymes of the ornithine urea cycle and urea transporters as a way of detoxifying and excreting nitrogenous wastes before the gills come on line to excrete ammonia (Wright and Fyhn 2001). It is not difficult to imagine that natural selection would favor retention of these characteristics into adult life as the environment became progressively more alkaline and more highly buffered through changes in hydrology and climate, while simultaneously favoring the growth of a monoculture of an N-rich cyanobacterial food source.

The Magadi tilapia also provides a clear indication of the timescale over which physiological adaptation to such a challenging niche can occur. There are in fact two lines of evidence, geological and molecular, and both concur that it is <10,000 yr. The geological record indicates that the whole area of Lake Magadi plus much larger Lake Natron to the south were covered by Paleolake Orolongo at the end of the Pleistocene, approximately 10,000–12,000 yr BP (Butzer et al. 1972; Goetz and Hillaire-Marcel 1992). The lake level was 50–60 m above the current surface of Lake Magadi, and fossil tilapia, very similar in morphology to but much larger in size than present-day *A. grahami*, have been found in deposits approximately 20–40 m above the current surface (Coe 1966; Tichy and Seegers 1999). At this time, the water chemistry was much less alkaline and less salty, but the Younger Dryas event then occurred, a period of intense climate change that resulted in progressive drying in this part of Africa as a result of a reduction in ocean to land moisture flux (Roberts et al. 1993). Separation of Paleolake Orolonga into smaller Lakes Natron and Magadi, as well as an additional small Lake Little Magadi to the north, ensued and was probably complete by 7,000 BP (Butzer et al 1972; Tichy and Seegers 1999). Increasing contraction of Lake Magadi has occurred since then, and today the majority of the surface is covered with a thick layer of floating "trona" (precipitated sodium carbonate salts). *Alcolapia grahami* populations persist only in isolated small areas of open water around the edges of the lake, where volcanic hot springs run in (Coe 1966; Wilson et al. 2004).

The molecular evidence is based on two recent analyses of mitochondrial DNA sequence haplotypes, one focusing mainly on animals collected from Lake Natron (Seegers and Tichy 1999; Seegers et al. 1999) and the other mainly on animals collected from Lakes Magadi and Little Magadi (Wilson et al. 2000, 2004). In total, 18 haplotypes were identified by Seegers et al. (1999) and 13 by Wilson et al. (2000, 2004). The two studies concur that there is a single haplotype common to all populations, termed *A1* by Seegers et al. (1999) and *B* by Wilson et al. (2000, 2004), and a dominant Magadi specific haplotype, termed *A17* (most frequent of five) by Seegers et al. (1999) and *A* (most frequent of seven) by Wilson et al. (2000, 2004). Both studies concluded that the single common haplotype was present in the ancestor to all populations, likely a cichlid species resident in Paleolake Orolonga with basic similarity to present-day *Alcolapia alcalicus* of Lake Natron. Thereafter, an "explosive radiation" occurred, resulting in several other distinct *Alcopia* species now considered to represent the youngest species flock known among the cichlids of East Africa (Seegers et al. 1999; Tichy and Seegers 1999). By making conservative assumptions about the generation time (60 d; Coe 1966) and using a base substitution rate for the mitochondrial DNA control region of 1.65×10^{-7} $site^{-1}$ yr^{-1} (Ward et al. 1991; Excoffier and Schneider 1999), Wilson et al. (2004) concluded that current hap-

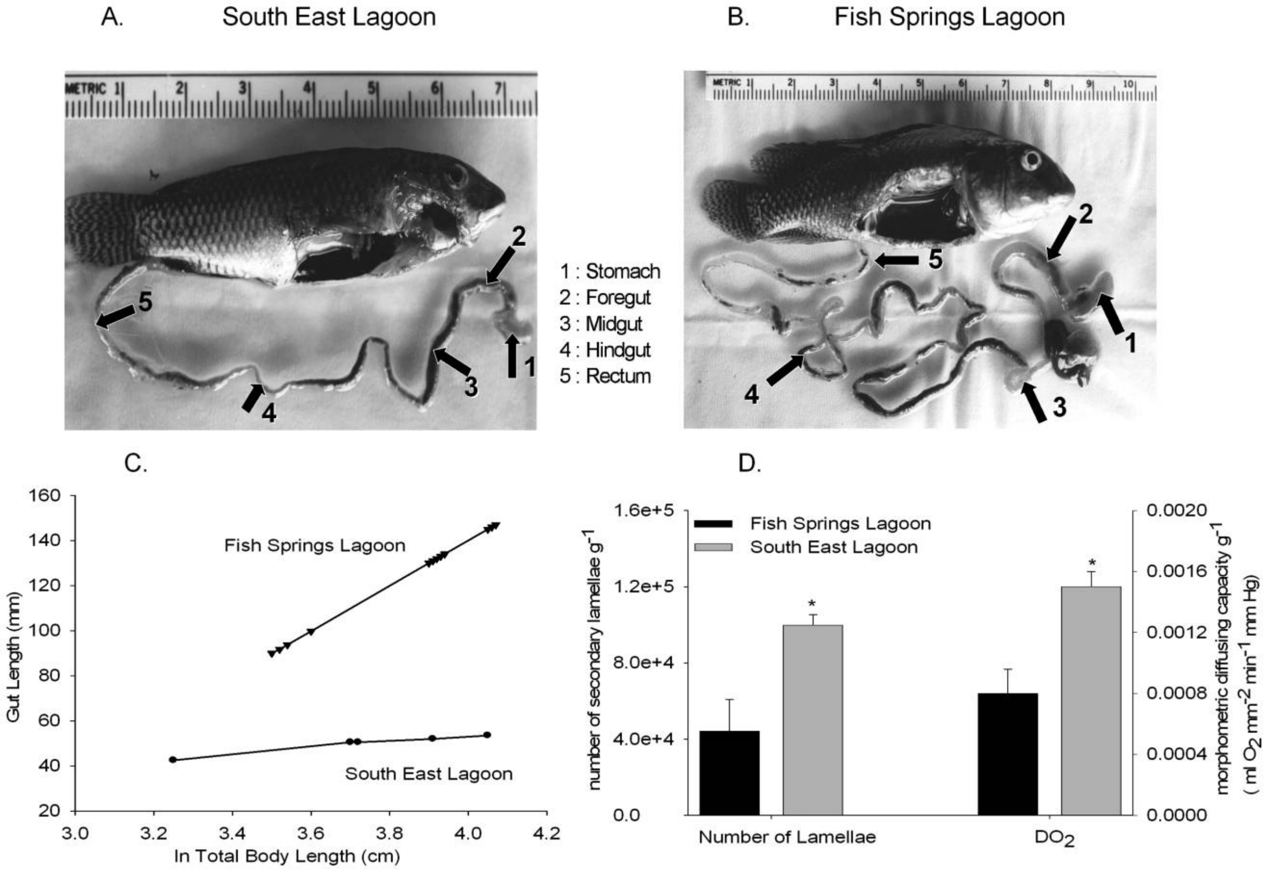


Figure 5. Morphological differences between two different populations of Lake Magadi tilapia living in different lagoons. *A*, Dissection illustrating the short gut length in a fish from South East Lagoon (SEL). *B*, Dissection illustrating the much longer gut length in a fish from Fish Springs Lagoon (FSL). Unusually large fish were selected for the sake of illustration, but relative gut lengths are typical. Photographs courtesy of P. Laurent and A. N. Bergman. *C*, Comparison plots of the relationships between gut length and the natural logarithm of total body length in SEL versus FSL fish (A. N. Bergman, P. Laurent, G. Otiang'a-Owiti, H. L. Bergman, P. J. Walsh, P. Wilson, and C. M. Wood, unpublished data). *D*, Allometrically normalized number of secondary lamellae and morphometric diffusing capacity, illustrating the larger gills of SEL versus FSL fish. Means ± 1 SEM. Asterisks indicate significant differences ($P < 0.05$). Data from Maina et al. (1996). Note that SEL was mislabeled as South West Lagoon in the original publication. A color version of Figure 5 appears in the online edition.

lotype distributions could be explained if the Lake Magadi population originated 10,000 yr BP and the Lake Little Magadi and Lake Natron populations about 5,500 yr BP. These estimates are in excellent accord with the geological record. Interestingly, the base substitution rate employed has been commonly used for other taxa, including humans, but is threefold faster than earlier assumed for cichlids (Nagl et al. 2000). Both surveys assume that the severity of the environment (alkalinity, salinity, free radicals, ultraviolet light, etc.) has created a very high mutation pressure, promoting the rapid evolution of new haplotypes.

Alcolapia grahami can also help us attack another important question: how quickly can a species adapt to a new niche and, in so doing, start the evolution of a new species? We cannot yet answer the question, but it seems likely that the answer is a very short period for founder populations invading extreme environments with high mutation pressures, small population sizes, and frequent bottleneck events. Within Lake Magadi itself, there is strong evidence of variation in anatomy and some evidence of variation in physiology among populations, but it is not yet clear how much of this variation is of genotypic versus phenotypic origin.

In 1997, an interdisciplinary team of scientists identified six different populations of Lake Magadi tilapia and also made collections from Lake Little Magadi and Lake Natron (Wilson et al. 2004). Particularly remarkable were differences in gross anatomy (e.g., coloration, mouth, gill, and gut morphology) and behavior between the different populations. Figure 5 provides an illustrative example. At South East Lagoons (SEL), the tilapia had a much shorter total gut length than at Fish Spring Lagoons (FSL) yet a much larger gill area and, consequently, a much larger morphometric diffusing capacity for O_2 (DO_2). Most aspects of water chemistry were similar between the two sites, but there was one key difference: very high [ammonia] at SEL versus zero [ammonia] at FSL, reflecting the presence of massive flamingo populations and their associated guano at the SEL site. It is likely that bacterial action converts uric acid-N deposits in the sediments here into ammonia-N. The SEL fish appeared to be supplementing their diet with large amounts of N-rich guano, which is presumably easier to digest than cyanobacteria, thereby explaining the much shorter gut length. At the same time, respirometry tests demonstrated that these fish were actually extracting ammonia-N from the water and detoxifying it to excreted urea-N, a novel but metabolically costly use of the OUC, resulting in higher metabolic rates (Wilson et al. 2004). The latter may explain the much larger gills and greater DO_2 in SEL fish than in FSL fish previously documented by Maina et al. (1996).

Among some of the other sites, water chemistry varied greatly. In contrast to the midrange composition of FSL (the source of fish for most previous physiological research), alkalinity ranged from 120 to 835 mmol L^{-1}, $[Cl^-]$ from 46 to 693 mmol L^{-1}, $[Na^+]$ from 183 to 978 mmol L^{-1}, osmolality from 278 to 1,689 mOsm kg^{-1}, and pH from 9.13 to 10.05 in the various lagoons. While there were some marked differences in physiology among the fish from different sites (e.g., in whole-body Na^+, Cl^-, and urea concentrations and in survival times when challenged with high alkalinity), there were also some important similarities: all expressed a full complement of OUC enzymes in their livers, and all were 100% ureotelic, characteristics that are likely critical to survival in these highly alkaline, highly buffered waters (Wilson et al. 2004). On a recent return visit 11 yr later, the smallest population living in one of the most extreme water chemistries (Sports Club Lagoon) had disappeared (C. M. Wood, unpublished data), testament to the intensity of catastrophic selection.

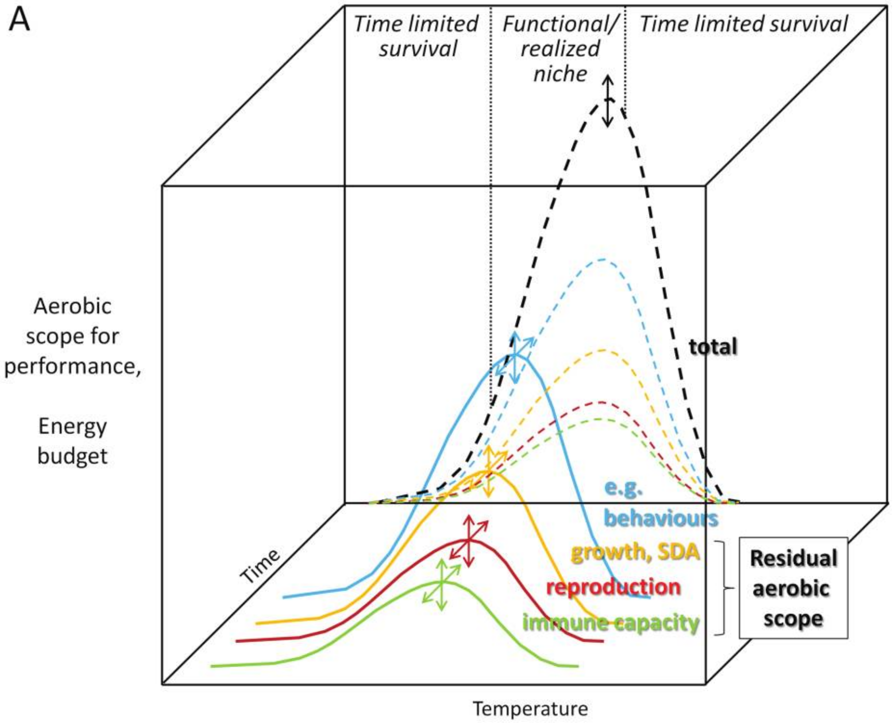
At first glance, the six different lagoon sites within Lake Magadi are physically separated from one another by at least several kilometers of trona, while Lake Little Magadi and Lake Natron are separated by land barriers. Within Lake Magadi, it is not known how long the various lagoon populations have been separated by trona or even if they truly are. Potential genetic mixing could occur by human activity, avian transport, or rainstorm events that are known to periodically flood the surface of the trona. However, the latter may constitute an effective toxicity barrier. Survival tests with water duplicating rainwater overlying the trona (Wilson et al. 2004) and field observations of massive fish kills following rainstorm events (Coe 1966) suggest that transtrona genetic exchange is minimal.

Analyses of mitochondrial DNA sequence haplotypes have provided important insights on this issue (Wilson et al. 2000, 2004). As noted earlier, these yielded clear evidence of substantial differences between Lake Little Magadi, Lake Natron, and Lake Magadi populations, the difference between the latter two backed up by microsatellite analysis. Within Lake Magadi, several populations showed differentiation in haplotype frequencies indicative of significant structuring (i.e., isolation, with little genetic exchange), while others showed very little. The apparent maintenance of haplotype diversity was remarkable, and the observed similarities and differences were discordant with geographical distribution of the lagoons. In isolation, traditional theory would predict that different haplotypes should have gone to fixation many times in the last 5,500–10,000 yr in these relatively small populations with short generation times. However, recent research on human races has suggested that mitochondrial DNA is not a neutral marker and that haplotypes are subject to natural selection (Mishmar et al. 2003). Wilson et al. (2004) therefore proposed a model whereby haplotype diversity was maintained by intense but balancing selection pressures despite effective isolation of some of the Lake Magadi lagoon populations. In Lake Malawi, which is arguably a much less extreme environment than Lake Magadi, Owen et al. (1990) estimated that cichlid speciation could occur in as little as 200 yr. Careful study of Lake Magadi tilapia populations over the foreseeable future should help us understand the process of speciation in action. Niche boundaries set by environmental abiotic factors undoubtedly play a key role in driving such evolutionary processes.

Synthesis and Perspectives

Anthropogenic impacts at local scales—for example, during river engineering—as well as by global climate change have opened our eyes to the need for an understanding of the mechanistic background of ecosystem change and underlying niche dimensions. Our analysis suggests that a reinterpretation of available knowledge is required to identify the dimensions of the niche space of a species or its specific life stages. Such dimensions result from the consideration of both biotic and abiotic characters and from the dimensions of the functional niche (i.e., of functional capacity) as elaborated herein. In the context of thermal physiology, oxygen supply limitations at both sides of the thermal window set the scope for performance in animals, with an optimum at the upper pejus temperature. Because temperature has pervasive effects on all levels of biological organization, synergistic effects by other stressors may alter the thermal matrix of performance. Abiotic factors (such as CO_2, hypoxia, toxicants, and extreme water chemistry) and biotic factors (such as limited food availability, predation pressure, or competition) may narrow the performance window and lower the performance maximum. In the case of abiotic factors, this may occur through exacerbated hypoxemia, as seen in case of CO_2 (Metzger et al. 2007; Pörtner and Farrell 2008). The thermal niche displays a temperature-dependent threshold of minimum performance required to ensure competitiveness at the ecosystem level. This concept might be a suitable way to approach the dimensions of the niche (Fig. 6) and large-scale, temperature-dependent biogeography.

Furthermore, among environmental factors, species interactions might act as stressors demanding (aerobic) energy. Energy demand for such interactions (e.g., high foraging costs due to limited food availability; Fig. 4) may reduce residual aerobic scope for crucial life functions (growth, development, reproduction) and, thereby, cause fitness decrements. This may elicit behavioral changes and shifts to an alternative habitat, if available (Fig. 6). Competition might also consume a significant fraction of the energy budget. This will again occur at the expense of other crucial components—such as growth performance, developmental rate, and reproductive output—and their combinations, all of which are fuelled by residual aerobic



Shrinking niche widths in response to biotic factors, possibly causing niche shifts

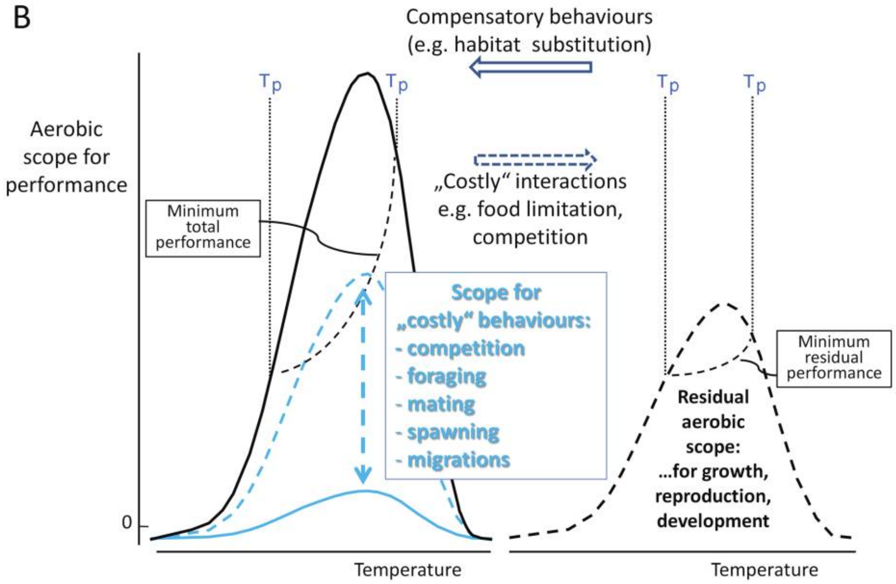


Figure 6. *A*, Conceptual illustration of an energy budget for processes beyond maintenance within the temperature-dependent window of aerobic scope for performance (Fig. 1). Acclimated pejus limits (T_p) are hypothesized to indicate the thermal borders of the functional/realized thermal niche (*dotted lines*; provided that exploitation of the passive range does not occur; Fig. 1). Arrows illustrate how the contribution of various processes to energy budget can change over time (order and timing arbitrary). Note that the thermal niche, once acclimatization limits are reached, can shift in position, width, and magnitude only during evolutionary adaptation. *B*, On the thermal matrix of performance, a restriction in aerobic scope (e.g., caused by CO_2 or hypoxia exposures, by low energy [food] availability, or by an energy-demanding biotic stressor) can cause unfavorable developments in energy budget partitioning. Assuming a temperature-dependent threshold of minimum residual performance (*dashed exponential line*) is required for sustainable fitness, this would lead to a shrinking thermal niche.

scope (Fig. 6). The maximization of one budget component at the expense of others crucial for survival and fitness will cause a narrowing of the niche. The fact that growth, development, and reproduction need to operate above a minimum rate may add to the narrowing of the niche. As a corollary, the dimensions of this functional niche will match those of the realized niche when sufficient allocation of residual aerobic scope sustains growth, development, and reproduction. The shape of the performance curve then demonstrates how the niche may narrow to the one realized under the prevailing abiotic and biotic conditions.

The net result of synergistic abiotic and biotic stressors would thus be a narrowing of the thermal niche through a fall in residual aerobic scope caused either by enhanced hypoxemia (Fig. 1) or by unfavorable shifts in energy budget. This implies maintenance of total performance and minimum sustained performance thresholds (Fig. 6*B*). Conflicting demands on aerobic scope and associated unfavorable losses in growth, reproduction, or development would then explain from a physiological point of view why the realized niche is narrower than the fundamental niche defined by just one abiotic or biotic factor. Overall, the functional niche describes in energetic terms how an organism can maintain its scope and radius of operation or, if needed, its passive tolerance. This is the basis of the complex behaviors of a species in biotic interactions and of the positioning of the realized niche in time and space.

At the level of performance capacity, for fish to thrive in rivers or extreme environments such as alkaline lakes, they require specific functional adaptations (e.g., muscular performance in the former, ionoregulatory mechanisms and ureotely in the latter) but must still rely on aerobic scope to fuel these functions. Shifts in energy budget may occur, but at the expense of performance in other crucial tasks and therefore fitness. Acclimatization and evolutionary adaptation would have to balance or compensate for unfavorable shifts in energy budget.

In aquatic environments, the emerging knowledge of these principles supports explanations of regime shifts, shifts in biogeography, and changes in species interaction and in food web structure (Pörtner and Farrell 2008). Performance limitations in the warmth may be responsible for observed changes in the abundance and health of a species (Pörtner and Knust 2007; Farrell et al. 2008). On the cold side, the principles of oxygen- and capacity-limited thermal tolerance explain why in polar areas some fishes, such as the eelpout *Pachycara brachycephalum*, live and perform below their acclimated optimum but still above the lower pejus limits. On warming, these fishes show a limited capacity to warm acclimate and increase growth performance above the rate displayed at the habitat temperature (Brodte et al. 2006). Therefore, a species does not need to live at its optimum temperature in order to compete but can live permanently close to the lower pejus limits if no detrimental performance losses result. However, this finding also suggests that the thermal niche may not always be exploited under current habitat conditions but may still mirror a warmer evolutionary past (Pörtner et al. 2009).

Again, the understanding of the niche relies on a multifactorial approach, with respect to interacting abiotic and biotic factors. In many cases, the thermal niche clearly describes sensitivity to climate warming and reaches the same upper limits as the realized niche. This emphasizes that temperature is an overarching factor shaping ecosystem change. However, the specific abiotic and biotic influences shaping the niche are often highly variable and remain to be elaborated in each specific example. This situation is further complicated by the fact that the niche shifts during ontogeny according to life stage and allometry and that niches differ between populations according to local climate conditions. Differences between niches of species coexisting in the same ecosystem and their differential responses to change will, in turn, shape species interactions (Pörtner and Farrell 2008) and may thereby also impact the dimensions of a species' niche.

Situations in which ambient conditions are drifting outside of a species' niche are now occurring in the context of climate change and in regulated rivers, where the niche of several fish species in their early life-history phase is clearly out of tune with respect to temperature regime and food availability after regulation (Schiemer et al. 2003). Hydrological hazards have increased. Water currents became steeper and less predictable. As these challenges exceed the performance capacity of the fish, this has threatened formerly common and characteristic species for which nase is an excellent example. River restoration and remediation toward reference conditions is a main challenge at the moment, and a full understanding of niche dimensions will be critical in this regard. In general, the understanding of indicator species and their niches is a relevant element in the assessment, conservation, and restoration of habitats across biomes (e.g., as developed in the water framework directive of the European Union) and should form an important element in the emerging fields of conservation ecology and physiology.

To achieve this goal, we need to deepen our mechanistic understanding of how the different levels of physiological organization, molecular and cellular, tissue to whole animal are intertwined and how that integration is perturbed at the edges of the niche. What are the trade-offs and constraints between the different physiological traits fueled by the energy budget? What are the responses to acute changes, and how do they elicit acclimatization? How are limits in acclimatization defined at genomic levels? Such limits can then be overcome only through evolutionary adaptation. Here the tilapia example in alkaline lakes is very suitable to illustrate the possibilities, timescales, and mechanisms of evolutionary adaptation. Such questions will become more and more relevant to understanding present ecological patterns and the resilience of species and ecosystems under the current and future challenges of global and local anthropogenic change.

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