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The evolution of phenotypic plasticity in fish swimming

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Abstract

Fish have a remarkable amount of variation in their swimming performance, from within species differences to diversity among major taxonomic groups. Fish swimming is a complex, integrative phenotype and has the ability to plastically respond to a myriad of environmental changes. The plasticity of fish swimming has been observed on whole-organismal traits such as burst speed or critical swimming speed, as well as underlying phenotypes such as muscle fiber types, kinematics, cardiovascular system, and neuronal processes. Whether the plastic responses of fish swimming are beneficial seems to depend on the environmental variable that is changing. For example, because of the effects of temperature on biochemical processes, alterations of fish swimming in response to temperature do not seem to be beneficial. In contrast, changes in fish swimming in response to variation in flow may benefit the fish to maintain position in the water column. In this paper, we examine how this plasticity in fish swimming might evolve, focusing on environmental variables that have received the most attention: temperature, habitat, dissolved oxygen, and carbon dioxide variation. Using examples from previous research, we highlight many of the ways fish swimming can plastically respond to environmental variation and discuss potential avenues of future research aimed at understanding how plasticity of fish swimming might evolve. We consider the direct and indirect effects of environmental variation on swimming performance, including changes in swimming kinematics and suborganismal traits thought to predict swimming performance. We also discuss the role of the evolution of plasticity in shaping macroevolutionary patterns of diversity in fish swimming.

Key words: environmental variation, evolution, fish, phenotypic plasticity, swimming kinematics, swimming performance.

Introduction

The ability of an organism to phenotypically respond to variation in ecological pressures can be critical for survival as the phenotypic shift is often advantageous (Dudley and Schmitt 1996; Meyers and Bull 2002). Phenotypic plasticity has been well investigated for many years [see Nicoglou (2015) for a review of a debate stemming from the 1960s on the causes of plasticity evolution]. It has been shown to occur in many different phenotypes including behaviors, life-history traits, and morphology, to name a few, and in response to different types of abiotic and biotic factors (e.g., temperature, diet, and predation intensity). For example, Crucian carp *Carassius carassius* that are reared in an environment with predators such as northern pike *Esox lucius* have been shown to exhibit plasticity in

their body shape by developing deeper bodies to exploit the gape limitations of the pike (Brönmark and Pettersson 1994; Nilsson et al. 1995). However, the deeper bodies have also been shown to be beneficial in producing thrust, thus increasing the bursting abilities of individuals in environments with predators (Domenici et al. 2008). This example demonstrates a plastic response in both the morphology and the physiological performance of the carp to enhance their survival when living with the predator. Plastic responses of locomotion may therefore be adaptive and have been documented for traits of several species (Gibert et al. 2001; Angilletta et al. 2003; Clusella-Trullas et al. 2010), including the swimming performance of fish (e.g., Nelson et al. 2015). However, how these shifts in locomotor abilities evolve has not been well investigated (Garland and

Kelly 2006). Because of the complex, integrative nature of locomotion and its importance for Darwinian fitness (Oufiero and Garland 2007), it may be an excellent trait for future studies interested in understanding how plasticity evolves. Using previous definitions of phenotypic plasticity, simply the ability of one genotype to produce multiple phenotypes, we highlight studies of phenotypic plasticity in fish swimming performance in response to various ecological pressures including temperature, oxygen availability, CO_2, and habitat (e.g., flow patterns and predation), at multiple biological levels. We then discuss the potential for the plasticity of fish swimming to evolve and the effects of the plasticity of fish swimming on patterns of macroevolution (West-Eberhard 1989; Pigliucci 2005). We highlight the different components of the locomotor system that can be affected by various ecological pressures and discuss whether subsequent changes in swimming performance are beneficial (i.e., adaptive plasticity) or not.

Swimming performance, and physiological performance in general, has often been depicted as a path model to capture the integrative nature of locomotion (Arnold 1983; Garland and Losos 1994; Oufiero and Garland 2007; Langerhans and Reznick 2010). These path models encompass the many factors that can affect locomotion and allow for the inclusion of direct and indirect effects on the phenotypic trait. Here we build on previous models of fish swimming performance to unify the principles that may govern how a fish swims. Using the paradigm depicted in Figure 1 as a model we examine the effects of ecological variation on the plasticity of swimming performance and discuss how this plasticity may evolve.
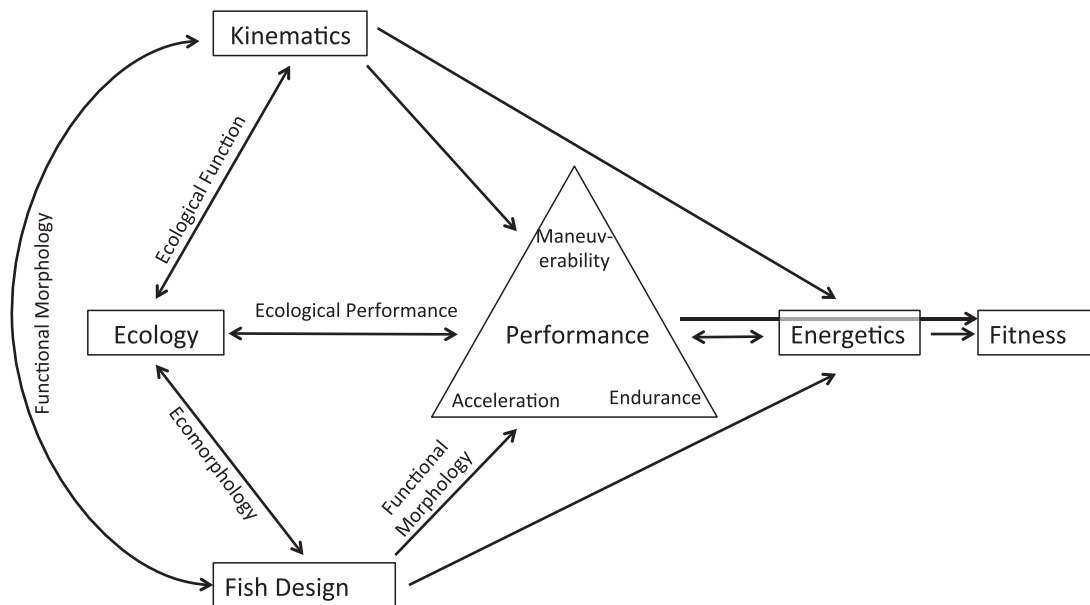
Unifying Principles of Fish Swimming

Swimming performance has often been broken up into different categories including steady and unsteady swimming (Blake 2004;

Langerhans 2009); sustained, prolonged, and burst swimming (Beamish 1978); and acceleration, endurance, and maneuverability (Webb 1984a), which are not mutually exclusive. For example, prolonged swimming can be a form of steady swimming or represent endurance. In general, we define performance according to Lauder (1991), as the ability to complete a task, such as the time it takes to swim a given distance, or how long a fish can swim against a current. We adopt the swimming performance classification of Webb (1984a), who classified swimming performance into fish specialized to be accelerators, cruisers, and maneuverers based on body shape (Figure 1). We use Webb's classification because of the focus of studies on phenotypic plasticity of body shape as a proxy for swimming performance differences (Georgakopoulou et al. 2007; Gerry et al. 2011; Binning and Roche 2015). We also use this performance paradigm because it identifies potential trade-offs in swimming performance that might be evaluated in studies of phenotypic plasticity (Langerhans 2009). For example, an environment that selects for deeper body shape to increase bursting abilities might come at the cost of endurance abilities.

We include body shape in an overall "Fish Design" box in our paradigm, adopting the approach of Langerhans and Reznick (2010). This allows for the inclusion of multiple components of the fish architecture that may affect performance, including body shape as well as sub-organismal traits such as muscle fiber type, enzyme activity, fin shape, etc. The fish design box can be expanded to examine the correlation of these design traits, potentially through a principal component analysis (Langerhans et al. 2003), with the assumption that they are predicted to potentially affect performance directly. For example, more red muscle in the caudal peduncle should be related to increased endurance abilities (Gibb and Dickson 2002).

We treat "Kinematics" separately in this paradigm and define it as the amount of time taken to carry out an activity, and the

Figure 1. Unifying principles of fish swimming. This visual depiction of fish swimming demonstrates the complex and integrative nature of fish swimming performance. Single headed arrows represent causal paths, providing hypotheses for the effect of fish design and kinematics on swimming performance and energetics. Double headed arrows represent correlational hypotheses among groups of traits. This depiction of fish swimming is based on previous representations of the relationship of morphology, performance, fitness, and ecology (Arnold 1983; Garland and Losos 1994; Irschick and Garland 2001; Oufiero and Garland 2007; Langerhans and Reznick 2010). Within each category there may be relations among traits, for example, trade-offs in performance, modularity in design, or correlation in ecology. Further details about the traits and their links are provided in the text.

magnitude of the motion (Biewener and Daniel 2010). Kinematics can include variables such as displacement, timings, and velocities of body parts (Wainwright et al. 2008). Fish are unique among vertebrates in having diversified in their means of propulsion, utilizing any number or combination of their five sets of fins and body regions (Webb 1982, 1984a, 1994). The kinematics of fish swimming can include traits such as fin beat amplitude and frequency as well as various gaits fish use, whether intraspecifically to produce more power (Korsmeyer et al. 2002; Cannas et al. 2006; Svendsen et al. 2010) or interspecifically in fish that utilize specific gaits (Webb 1982, 1984b, 1994). For example, fish may rely on median-paired fin gaits at lower velocities, but transition to body-caudal fin propulsion at higher velocities (Korsmeyer et al. 2002; Svendsen et al. 2010, 2013). Additionally, entire groups may rely on a specific gait, such as several reef fish including Labridae and Ballistidae (Webb 1982, 1984b, 1994). Kinematics are treated separately from performance because the underlying mechanical traits of swimming often determine performance (Wainwright 2007). For example, a fish that is subjected to increasing flow speeds may exhibit a reduction in the timing of each tail beat (Oufiero et al. 2014), therefore the timing of the motion of the tail predicts how fast the fish is swimming.

We also treat "Energetics" as a separate box in this paradigm because the amount of energy used during locomotion depends on many of the preceding factors. For example, a fish subjected to increasing flows will exhibit an increased tail beat frequency allowing for faster speeds, which will require more energy (Bainbridge 1958). The amount of energy used at a given swimming speed or tail beat frequency will also depend on the efficiency of the muscles used. Therefore, how much energy is used to move through the environment is dependent upon the variation in the structures used for locomotion, how those structures are used, and the resulting performance output of those structures. Energy is often measured by examining the oxygen consumption during rest or an activity; and is represented by the resting or standing metabolic rate, maximal metabolic rate, maximum oxygen consumption, aerobic scope, or cost of transport (Bushnell et al. 1984; Lee 2003; Domenici et al. 2007; Binning et al. 2014; Tirsgaard et al. 2015).

Finally, we use the term "Ecology" to encompass all of the varying environmental pressures that may cause a plastic response in fish swimming. This includes abiotic factors such as temperature, flow patterns, dissolved oxygen (DO) content; and can also include biotic factors such as predation and competition. As explained through Figure 1, the ecology of an organism can affect each of the components of fish swimming both directly and indirectly. Therefore, the resulting effect of ecological variation on fish swimming performance may or may not be beneficial. For example, if temperature affects enzymatic function causing a decrease in swimming performance, the indirect effect of temperature on swimming performance may not be beneficial. Studies examining the plasticity of fish swimming have focused on varying paths within this paradigm as discussed in detail below.

The links throughout the paradigm depicted in Figure 1 represent some of the major areas of fish swimming that have been focused on through the years. For example, the ecomorphology of physiological performance defines the link between ecological and morphological variation, and is concerned with the influence of environmental factors, such as habitat, on structural diversity among organisms. Ecomorphology is often used as proxy to infer function/performance with the assumption that patterns of ecomorphological variation will be functionally adaptive.

Ecomorphology has been the subject of many studies in fish biology (Wikramanayake 1990; Wainwright and Bellwood 2002; Recasens et al. 2006), including studies of phenotypic plasticity (Peres-Neto and Magnan 2004; Langerhans 2009). Functional morphology, the link between fish design and performance and/or kinematics, focuses on inferring differences in how an organism works based on its structure alone. Functional morphology is often studied in the context of ecomorphology, as the environment may be selecting for structural variations that perform better in a given environment, including both performance-based and/or kinematic-based differences. Ecological performance examines performance in the context of ecological variation as well as what an animal does in the laboratory versus what it does in nature (Irschick and Garland 2001). In the case of performance, kinematics, and morphology relating to ecology, we can assume these relationships might encompass behavioral differences in the organism (Garland and Losos 1994). For example, if a fish has a reduced swimming performance it may behaviorally chose areas with low flow (Binning et al. 2015). Lastly, the link between ecology and kinematics (ecological function) focuses both on ways variation in environmental features causes differences in organismal function as well as how an organism functions determining what environment it is best suited to inhabit (McGee and Wainwright 2013; McGee et al. 2013). In this paradigm, several paths assume a causative effect of one trait on another (single headed arrows), while others have a correlational relationship (double headed arrows) because of the potential uncertainty in the relationship. In essence, the model depicted in Figure 1 provides hypotheses for the relationships of fish swimming plasticity.

Phenotypic Plasticity of Fish Swimming

Phenotypic plasticity of fish swimming has been examined in response to varying environmental pressures [e.g., temperature, habitat, DO, and carbon dioxide (Claireaux et al. 2007; Munday et al. 2012; Fu et al. 2014)], exposure to the environmental variation at different life stages of the fish [embryo, juvenile, and adult (Georgakopoulou et al. 2007; Johansen and Jones 2011; Scott and Johnston 2012)], and the plastic responses of different levels of biological organization [behavior to biochemical (Dhillon and Schulte 2011; Ottmar and Hurst 2012)]. The methods, experimental design, study species, and results of phenotypic plasticity of fish swimming have all varied greatly. For example, exposure times can range from a few hours (Dutil et al. 2007), to weeks (Nowicki et al. 2012), or even across generations (Crispo and Chapman 2010). The number and intensity of treatment conditions varies greatly [compare Johansen and Jones (2011) with Claireaux et al. (2006)], while species investigated range from Antarctic (Wilson et al. 2001) to tropical (Binning and Roche 2015), and many groups in between (Stevens 1979; Georgakopoulou et al. 2007; Scott and Johnston 2012). Furthermore, few studies have examined the evolution of plasticity in fish swimming. Because of the variety of studies and results, we highlight some areas that have received greater attention and suggest areas of future research.

There are several ways environmental variation may affect the plasticity of fish swimming. First, there may be a direct effect of environmental variation on swimming performance. For example, if a fish experiences an increase in flow velocity it will need to swim faster in order to maintain its position in the water column (Plaut 2001). Therefore, the swimming performance of the fish would be

plastic, but would most likely be due to plasticity in underlying traits, such as changes in the kinematics (Figure 2C or D). This scenario would produce beneficial plasticity in both the kinematics and swimming performance of the fish in response to flow variation. Second, there may be plasticity in underlying traits, such as fish design or kinematics, in response to environmental variation without changes in swimming performance (Figure 2A,B) (Stevens 1979). This scenario might be one seen in response to temperature variation and may not be beneficial. There should not be a need for fish to alter their swimming performance in response to temperature; rather temperature will affect the biochemical and enzymatic processes responsible for swimming performance (Angilletta 2009). It is therefore important to keep these differences in mind when studies examine the evolution of plasticity of locomotor performance. Should swimming performance directly respond to environmental variation (and what are the underlying traits responsible for this variation) or is variation in swimming performance an indirect effect of the plasticity of underlying traits in response to environmental variation?

Temperature

Temperature is one of the most well studied factors in relation to phenotypic plasticity (Angilletta et al. 2002, 2003; Angilletta 2009) and can have effects on ectotherms ranging from acute to chronic, ontogenetic, and evolutionary, depending on the timescale of exposure (Kingsolver et al. 2004). The effects of temperature on an ectotherm's performance are represented by thermal performance curves (Figure 3), with an optimal temperature where performance is maximized during acute temperature fluctuations. On a longer time scale we would expect to see shifts in the performance curves (Figure 3), with variation in the response of the trait based on the properties of the system and the selection acting upon the organism. For example, if the plasticity of a trait is evolving in response to temperature we might expect to see shifts in the breadth of the thermal performance curves as depicted in Figure 3B, D, F, and H.

Like other ectotherms, the swimming performance of fish is affected by variations in temperature. Fish may experience temperature fluctuations on varying timescales, including daily or seasonal variations and could be forced to tolerate these fluctuations in order to survive, particularly in situations where oxygen content limits their ability to migrate in the water column. For example, fish that reside in eutrophic lakes can experience surface temperatures that vary seasonally from 4 °C to 30 °C, and the cool depths tend to turn anoxic quickly in the summer. These fish should evolve some level of plasticity in order to cope with these extreme conditions and maintain performance (Figures 2B,D and 3B,D,F,H). However, the response of fish swimming to temperature is generally the indirect effect of temperature acting on fish design and kinematics (Figure 1). A fish residing in a eutrophic lake with thermal variation might be expected to experience changes in swimming performance due to the thermal effects on biochemical pathways, protein structure, and enzymatic reactions related to swimming (Guderley and Blier 1988; Johnston and Temple 2002; Johnston 2006) . Therefore, *the potential goal of an adaptive plastic response to temperature in fish swimming is to preserve functional abilities, through the plasticity of fish design and kinematics* (Figure 2A,B). In fact, much of the research of temperature effects on swimming has focused on sub-organismal traits and muscle physiology (Cole and Johnston 2001; Watabe 2002; Johnston 2006). The results of these studies show mixed

patterns of thermal acclimation on muscle physiology and anatomy across species of fish.

Studies on the plasticity of swimming in relation to temperature have examined exposure at all stages of life history, from embryo exposure to adult, and at varying time scales, from acute responses within a few hours to chronic (Lee 2003; Claireaux et al. 2007; Carey and Franklin 2009; Johansen and Jones 2011). Chronic exposures to temperature differences have shown mixed results for their effects on swimming performance as well as fish design. For example, some studies have shown increasing temperatures increase swimming performance (Claireaux et al. 2006, 2007), while others document a decrease in swimming performance in relation to an increase in temperature (Wilson et al. 2001; Johansen and Jones 2011). This is likely due to differences in thermal performance curves (Figure 3) of the species being tested.

Despite the lack of generalities for the effects of temperature on swimming performance plasticity in fish [compare results of Wilson et al. 2001 with Claireaux et al. 2007, for example], several conclusions and future directions can be drawn to examine how this plasticity will evolve. First, because of the nature of thermal performance curves, any study interested in the evolution of plasticity in response to thermal variation should first determine the acute responses to temperature [(Kingsolver and Huey 1998; Schulte et al. 2011), and see (Stevens 1979; Claireaux et al. 2006), for examples]. For example Wilson et al. (2001) examined the thermal performance curves of burst swimming among three species of Antarctic fish and found that the performance breadth varied by less than 20%. Their results suggest that these stenotherms respond to temperature as well as some eurytherms (see below). While these temperature specialists do not seem to vary in the breadth of the performance curve (Figure 3E,C,G), how these curves will evolve in response to temperature variation remains to be tested. Recent work on Atlantic cod *Gadus morhua* investigated the thermal performance curves of varying sized fish for metabolic scope and found that all size groups exhibited a maximum metabolic scope around 10 °C, with the smallest fish exhibiting the widest breadth (Figure 3B), however comparisons among species or to chronic temperature acclimation were not performed (Tirsgaard et al. 2015). Finally, Scott and Johnston (2012) investigated thermal performance of critical swimming speed (U_{crit}), muscle fiber types, and transcription activities of zebrafish *Danio rerio* reared at different temperatures using a fully crossed design. They found that fish initially performed better at the temperature they were collected from, but these differences were weaker after longer acclimation times to new temperatures. They also found that cold acclimated fish had increases in their cross-sectional area of swimming muscles, which may explain differences in performance (e.g., Figure 2D). However, the authors note that not all of the changes seen in these fish were beneficial; that is, the response of fish swimming performance to temperature might be the indirect effect of temperature on fish design (Figures 1 and 2A,B). These studies highlight the effect of acute temperature responses of swimming performance in establishing thermal performance curves. Once the thermal performance curves are estimated they can provide a baseline for how the plasticity of swimming performance might evolve in response to thermal variation (Figure 3).

A second conclusion and future direction for the evolution of plasticity of swimming performance in fish is related to the indirect effect of temperature on performance through its effect on fish design and kinematics. Studies should therefore focus on the effects of temperature on swimming performance as well as on aspects of fish design or kinematics in order to understand the underlying causes of
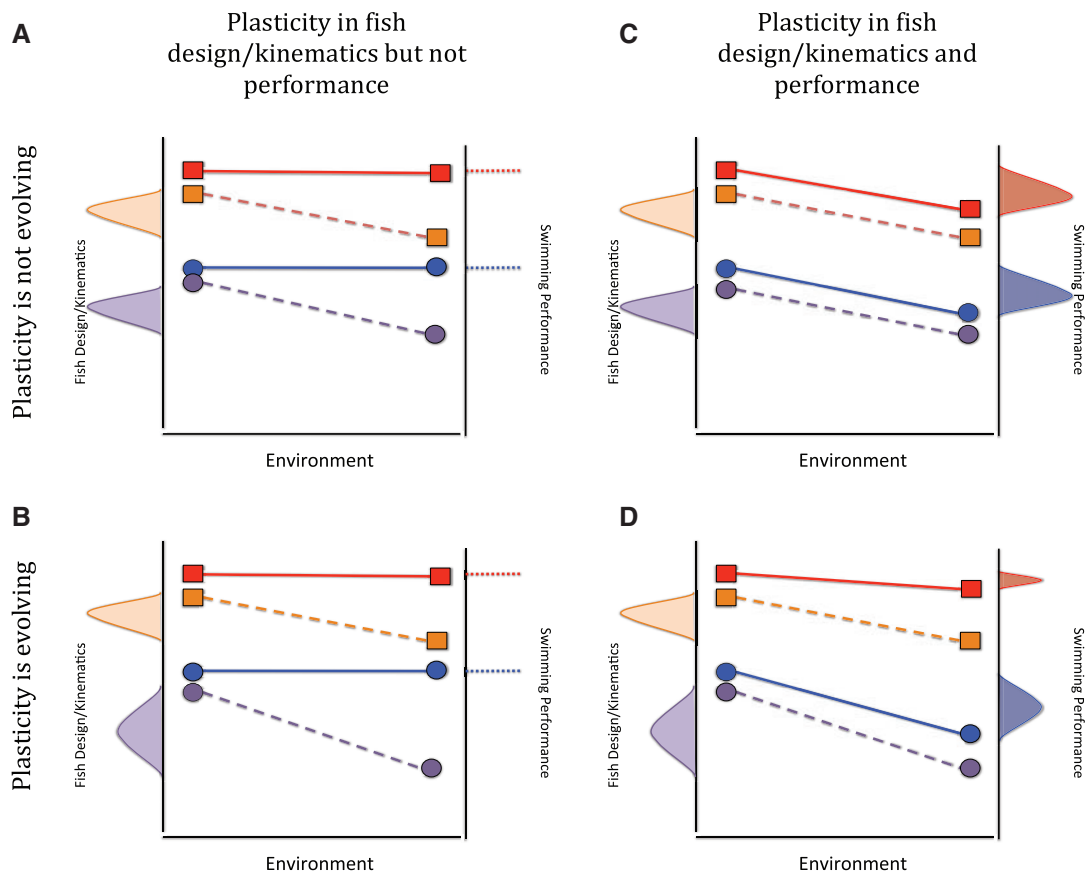
Figure 2. The response and evolution of fish design/kinematics and swimming performance to environmental variation. Figure based on Futuyma (2013). Squares and warm colors represent swimming performance (red and solid lines) and fish design/kinematics (orange and dashed lines) in one population or species, circles and cool colors represent swimming performance (blue and solid lines), and fish design/kinematics (purple and dashed lines) in another population or species. On the *x*-axis is a hypothetical environmental variable that the swimming performance (right *y*-axis) and fish design/kinematics (left *y*-axis) may respond to. The curves located outside the L/R *y*-axes represent the distribution/plasticity of the respective response (design/performance) to the environment. If a population does not exhibit plasticity in relation to the environmental variable, its distribution for that character (fish design/kinematics or swimming performance) is represented by a dotted line. In (**A**) the two populations/species show differences in swimming performance, but no plasticity. Conversely each has a similar amount of plasticity in some underlying character. For example, no change in swimming performance in relation to hypoxia variation, but changes in the delivery of oxygen. This situation might arise if plasticity is not evolving, and fish design/kinematics are varying to maintain a constant swimming performance across environments. In (**B**) the two populations/species again differ in their performance ability and lack plasticity in relation to the environment. However, now there is a change in the amount of plasticity in underlying fish design/kinematics suggesting the two groups are evolving different plasticities. This might occur if one species has a bigger change in ventilation rate in response to hypoxia. In (**C**) there is again a difference in overall swimming performance fish design/kinematics between the groups, but now there is similar plasticity for all traits between the populations, suggesting that plasticity is not evolving. For example, two species living in seasonally hypoxic waters exhibiting a similar change in ventilation rate and swimming performance. Lastly (**D**) demonstrates the evolution of the plasticity in both fish design/kinematics and swimming performance between the two populations/species, while rarely tested in swimming performance of fish, this scenario could arise given different selective pressures for the populations or species of fish. These hypotheses can be used to examine how the plasticity of swimming performance and its underlying traits might evolve.

performance variation (Scott and Johnston 2012). Johnston (2006) reviewed the effects of temperature on many components of fish design. For instance, muscle fiber type, mitochondrial density, muscle mass, and body shape have all been shown to exhibit plasticity in response to temperature. Linking these changes to performance is crucial to understanding the effects on whole-organismal physiology and performance and to determining if suborganismal changes in response to temperature are adaptive. For example, Allen et al. (2006) found that the U_{crit} of juvenile green sturgeon *Acipenser medirostris* increased with acclimation to higher temperatures, and found that six of seven heat shock proteins tested also increased (in muscle and/or pelvic fin) at higher temperatures, potentially allowing for the higher U_{crit} performance. Additionally, Georgakopoulou et al. (2007) investigated morphological changes associated with rearing

European sea bass *Dicentrarchus labrax* at different temperatures. Koumoundouros et al. (2009) expanded this study to investigate swimming performance and muscle histology and found that fish acclimated to 15 °C had increased swimming performance and red muscle fiber types. Fewer studies have examined the effect of temperature variation on the kinematics of swimming; however, Stevens (1979) found that kinematic changes due to temperature vary by species: trout had lower tail beat frequencies at increased temperatures while bass showed an increase in tail beat frequency with increased temperature. Both tail beat frequency and/or amplitude should increase power output and swimming speed (Oufiero et al. 2014), but how kinematic changes in relation to temperature affect swimming performance and interact with fish design has yet to be explicitly tested in detail. Therefore, when examining the evolution
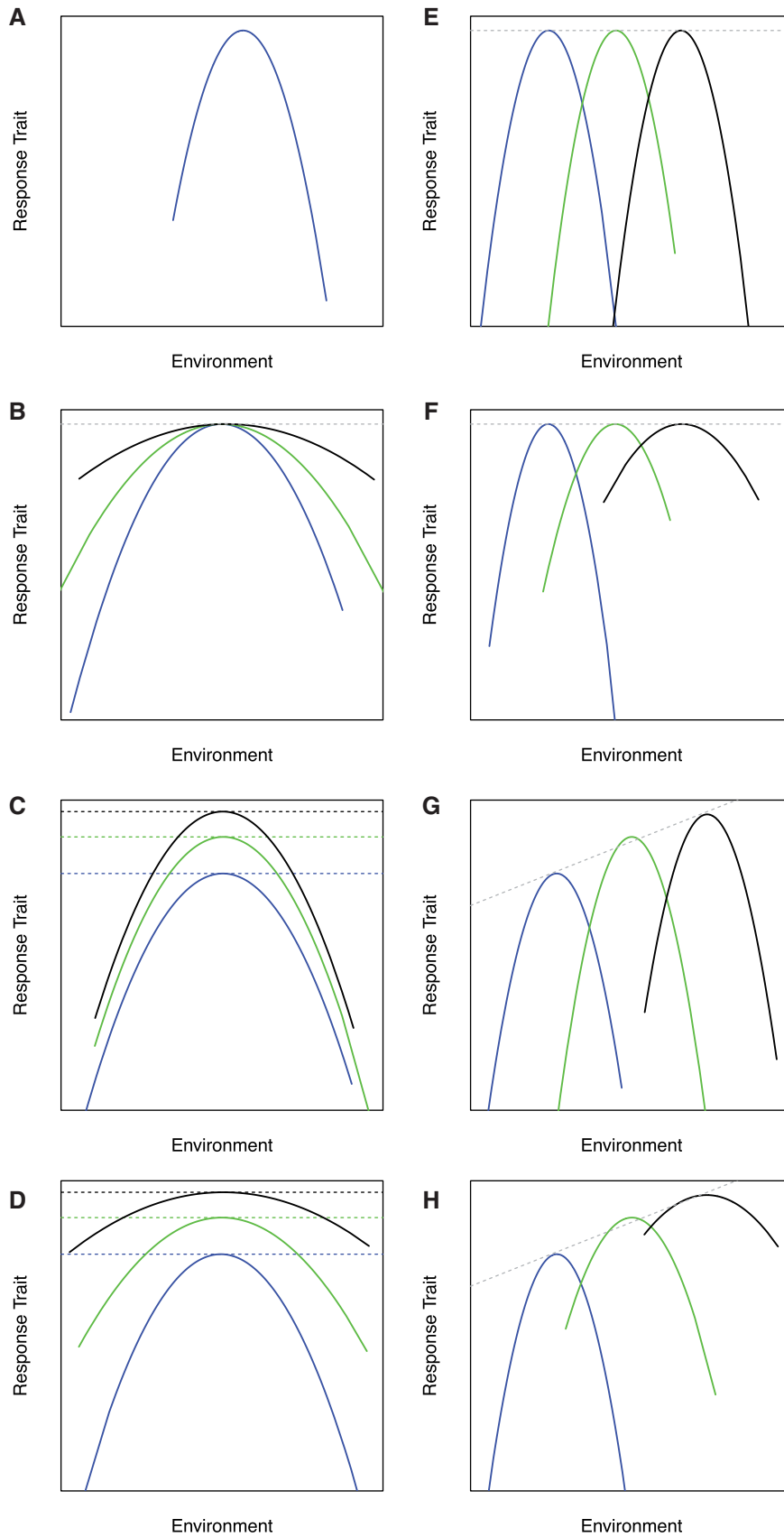
Figure 3. Models for the evolution of thermal performance curves of fish swimming. This figure represents potential hypotheses for the evolution of plasticity in response to the environment. They resemble thermal performance curves, but can be applied to other factors (e.g., DO). The *x*-axes represent the environmental variation, such as temperature, the *y*-axes represents the response trait, such as swimming performance. The dashed lines represent the maximal response. The

of plasticity of swimming performance it is important to consider aspects of fish design and kinematics that might be responsible for any similarities or differences in performance observed. It is also important to keep in mind that not all changes are beneficial.

Lastly, if studies are interested in examining the evolution of thermal plasticity in swimming performance, the appropriate species/population should be examined. The plasticity of fish swimming performance should evolve in populations or species that are more likely to experience consistent shifts in thermal habitats. Fish have often been classified as stenotherms versus eurytherms based on whether they can function over a narrow range of body temperatures (stenotherms) or a wide range of body temperatures (eurytherm) (Somero and Dahlhoff 2008). Previously mentioned studies have compared distantly related stenotherms to eurytherms and found little variation in thermal performance curves (Wilson et al. 2001). A potential future avenue of research could focus on model systems in which there are closely related warm and cold "optimized" fish, both of which experience some natural temperature variations, such as the Atlantic killifish (e.g., Dhillon and Schulte 2011; Healy and Schulte 2012). Standardizing the exposure of fish, both in terms of length and developmental time, is also important so that results from multiple studies can be compared in a meaningful way (Kingsolver and Huey 1998; Peres-Neto and Magnan 2004; Pigliucci 2005; Dhillon and Schulte 2011). In order to truly understand the mechanisms behind the evolution of plasticity in fish swimming, studies would ideally investigate multiple parameters laid out in Figure 1 to understand, for example, how changes in suborganismal traits due to temperature are linked to changes in performance [see Seebacher et al. (2012) as an example, Figure 2]. Furthermore, because of the relationship between temperature and swimming performance (Figure 3) studies should focus on the evolution of thermal performance curves of both the swimming performance of interest and the underlying traits (fish design or kinematics).

Habitat

The habitat fish encounter varies from fast moving streams to still lakes (Langerhans 2008; Crispo and Chapman 2010; Fu et al. 2014), benthic to limnetic (Law and Blake 1996; Blake et al. 2005; McGee and Wainwright 2013), high predation to low predation (Langerhans 2009; Oufiero et al. 2011), areas of high wave energy on reefs to areas of low wave energy on reefs (Fulton et al. 2005; Binning et al. 2014), rural to urbanized (Nelson et al. 2008, 2015), and open water to complex environments (Beukers and Jones 1997; Price et al. 2011, 2013). In general, there should be a direct effect of habitat variation on the swimming performance of a fish, as the various habitats likely favor enhancement of different aspects of fish swimming performance. Therefore, plastic responses of fish swimming in relation to habitat should be beneficial, unlike those discussed above for temperature. For example, high predation environments should favor an increase in acceleration performance (i.e., burst swimming); and conversely, high flow environments should favor an increase in endurance swimming. While swimming performance may vary adaptively in response to environmental differences, the change in performance is likely due to changes in the kinematics or in aspects of fish design (Langerhans 2008).

The plasticity of swimming performance in relation to habitat can be seen in response to either acute or chronic exposure [compare Dickson et al. (2012) to Nelson et al. (2008)]. Acute responses to alterations in habitat, such as flow, are generally accompanied by alteration in swimming kinematics (Lauder 2015). Most fish will respond to the acute changes in habitat through an increase in fin beat amplitude, frequency, or both to enhance power output in response to changes in flow (Webb 2002; Dowis 2003; Dickson et al. 2012; Nudds et al. 2014; Oufiero et al. 2014). Furthermore, because of the flexibility in structures used for propulsion in fish, at faster velocities that require more power from a fish there is often a gait transition (Drucker 1996). This acute plastic response in a laboratory setting may be what fish use in natural settings if faced with sudden changes in flow, such as flooding after rain, in order to maintain position in a stream. Similarly, the presence of predators should increase the bursting abilities, such as an increased tail amplitude, to ensure successful escape (Domenici 2010). How these changes in kinematics evolve has not been well investigated, but could presumably be an area of interest as changes in kinematics of functional systems within a species may be a step toward transitions in lifestyle and eventually speciation (Standen et al. 2014).

Chronic exposure to variation in habitat has shown similar patterns to acute responses, but has also shown alterations in fish design to meet the performance demands of the altered habitat (Peres-Neto and Magnan 2004; Langerhans 2008; Binning et al. 2015). In fact, one of the most well-studied phenotypes that exhibits plasticity in relation to habitat is the morphology of fish (Langerhans 2009; Ellerby and Gerry 2011; Binning and Roche 2015). Studies have demonstrated that exposure to higher flows during development causes a shift to a more streamlined body (Peres-Neto and Magnan 2004), which has been proposed to be beneficial to endurance type swimming (Webb 1984a, 1984b). As mentioned at the beginning of the paper, studies have shown plastic responses in morphology in response to predation, with deeper bodies developing in the presence of a predator (Brönmark and Pettersson 1994; Nilsson et al. 1995; Domenici et al. 2008). Recent studies have highlighted the plasticity of morphology in response to living on the leeward versus windward

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different color lines represent changes in curves among populations or species. (**A**) Represents a single thermal performance curve, if all species or populations exhibit the same response to temperature. (**B**) Represents a shift in performance breadth (i.e., evolution of plasticity) in response to temperature, but no horizontal or vertical shift. In this case, the species are evolving to be more plastic, while maintaining the same optimal environment for performance. In (**C**) there is no difference in the breadth (i.e., plasticity is not evolving), but a vertical shift represents species performing better at the optimal condition. This might be seen in studies acclimating fish to low DO that outperform normoxic fish. In (**D**) there is a vertical shift of the performance at optimal environmental conditions and an evolution of the plasticity, with differences in performance breadth. In (**E**) there are no differences in performance breadth, but a horizontal shift where species/populations are shifting their performance optima to match local environmental conditions. In (**F**) there is a horizontal shift as well as the evolution of plasticity as the performance breadths change, but no change in maximum performance. In (**G**) there is no evolution of plasticity as the performance breadths are the same, but a horizontal shift in optima and a vertical shift in maximum performance, with an increase in maximal performance as the environment of populations or species changes. Lastly, in (**H**) there is a horizontal shift, evolution of plasticity, and change in maximum performance in response to environmental conditions. These performance curves have been highlighted elsewhere (Kingsolver et al. 2004; Angilletta 2009) and represent hypotheses for how swimming performance, fish design, and kinematics may respond to temperature variation. They could also represent responses to other environmental factors such as DO or carbon dioxide, but these have not been examined in detail in an evolutionary context.

side of reefs, with those on the windward side that experience higher flows exhibiting higher aspect ratios of the pectoral fins and increased endurance swimming (Binning et al. 2014; Binning and Roche 2015). This group went on to perform a common garden experiment and found that being raised under high flow conditions caused these fish to have higher maximum metabolic rates, aerobic scope, blood hematocrit, and cortisol levels regardless of initial population location (Binning et al. 2015).

While studies of morphological plasticity in response to habitat are common, there are fewer examples of studies examining aspects of swimming performance plasticity in relation to habitat. Recent studies on blacknose dace *Rhinichthys atratulus* have demonstrated that swimming performance also responds plastically to flow. For example, Nelson et al. (2008) collected fish from 8 watersheds representing a rural–urban gradient. All fish were then kept in the laboratory under no-flow conditions and tested for U_{crit} 3 and 6 months later. This chronic exposure to no-flow resulted in a decrease in U_{crit} for populations with a higher starting U_{crit} such that fish from all populations converged in their performance after "detraining". Nelson et al. (2015) furthered the study of plasticity of swimming performance in blacknose dace by rearing 4 populations under constant flow conditions and found that after 40–50 days fish increased in U_{crit} and sprint speed, regardless of initial population. They also raised some lab-born fish under no-flow conditions and found that they had very low U_{crit} and sprint performances, providing further evidence for plasticity of swimming performance in these fish. While the studies on blacknose dace assessed the effect of flow environment on swimming performance plasticity, they did not investigate whether changes in performance were due to underlying kinematics and/or fish design. Therefore, in relation to the hypotheses in Figure 2, the blacknose dace may not be evolving in their plasticity of swimming performance, as there is no difference in performance among populations after training; however, whether plasticity of fish design or kinematics is evolving remains to be tested.

When examining the evolution of swimming performance plasticity in relation to habitat, as with other environmental effects, there is an important question to keep in mind: when would we expect to see plasticity of swimming performance evolve in relation to habitat? It is generally thought that plasticity for a trait will evolve in fluctuating, non-stable environments (Thompson 1991; De Jong 1995; Pigliucci 2005; Lande 2009). For instance, a population of fish living in non-flowing environment (such as a lake) that has evolved to live or feed in a particular niche might be a poor choice for plasticity of swimming performance to evolve. For example, cichlids have been model organisms for speciation (Kocher 2004; Seehausen 2006) and cranial morphological variation (Albertson et al. 2003; Hulsey and García de León 2005), but within species differences in plasticity for swimming performance might not be favored as they are often adapted to stable niches and inhabit lakes that likely don't experience alterations in flow. Therefore, while there may be genetic divergence in swimming performance, fish design, and kinematics, they may not experience alterations in microenvironments within the lake to select for variation in their plasticity (Figure 2C). Conversely, species of fish that encounter an array of differing flow regimes throughout development or their lifetime may benefit from plasticity in swimming performance. For example, as mentioned above, recent work has highlighted the differences in morphology (fish design) and swimming performance (mostly critical swimming speed, U_{crit}) among reef fish encountering areas of the reef that experience high alterations of flow (windward) and low

flow changes (leeward) (Fulton et al. 2005; Fulton 2007; Binning et al. 2014, 2015; Binning and Roche 2015). In particular, species or populations, such as Pomacentridae, that are likely to encounter both windward and leeward sides might evolve plasticity for swimming performance (Figure 2D) as the result of plasticity in fish design or kinematics. These fish may represent an area of future investigation into the evolution of plasticity in swimming performance in relation to habitat. Conversely, species or populations not likely to encounter both habitats may not have evolved plasticity in those traits. Similarly, species or populations in streams, such as the blacknose dace, that may encounter variation in flow are more likely to evolve plasticity in their swimming ability, kinematics, and fish design. To fully understand how flow patterns, and habitat in general, affect the plasticity of swimming performance, further comparisons, including measures of swimming performance and broader taxonomic sampling in common garden experiments are warranted.

In addition to the abiotic factors fish might experience in relation to habitat, there are several biotic factors that may influence the evolution of plasticity in swimming performance. These biotic factors could include predation (as discussed briefly above), intra- and inter-specific competition, and resource allocation. Most of these biotic factors' effects on swimming performance have not been well investigated, but prior research provides some insight into their potential role.

As noted above, predation may induce plasticity in the morphology of fish, which has been shown to be beneficial to their swimming abilities (Brönmark and Pettersson 1994; Nilsson et al. 1995; Domenici et al. 2008). However, the way plasticity evolves in relation to predation has not been well investigated. In order for plasticity to evolve in relation to predation, a species or population would have to experience variation in predator encounters. For example, fish living in the streams of Trinidad have been models for the evolution of life history and swimming performance in relation to predation (Reznick and Bryga 1996; Walsh and Reznick 2009, 2010; Oufiero et al. 2011). Two smaller fish, *Poecilia reticulata* and *Rivulus hartii*, occur throughout different regions of the streams which have been characterized as *Rivulus* only sites, where only *R. hartii* occur, *Rivulus*/guppy sites with both *R. hartii* and *P. reticulata* and high predation sites with *R. hartii*, *P. reticulata*, and several large piscivorous predators such as the pike cichlid, *Crenicichla alta* (Walsh and Reznick 2008, 2009, 2010; Oufiero et al. 2011). Part of the reason for this distribution in species is that smaller fish are able to traverse the shallower parts of the streams to get to other sites. If the fry of either of the two smaller fish make it to the high predation site, plasticity in swimming performance and its underlying components would be beneficial (Ghalambor et al. 2004; Walker et al. 2005; Oufiero et al. 2011). A system like the streams in Trinidad has the potential for plasticity of swimming performance to evolve in relation to predation, as there is a chance the fish may encounter predators by moving between sites. Contrast this against a population of guppies living in an isolated pond or lake where the community composition of the fish does not change. If there is no encounter with predators in the stable community, selection might not ever favor the ability for this population to be plastic in response to predation.

Similar to predation, competition and resource acquisition may have similar effects on the plasticity of swimming performance. Prior research has shown changes in components of swimming, such as morphology, in relation to differences in community composition and resource acquisition (Osenberg et al. 1992; Bouton et al. 2002; Svanbäck et al. 2008). There is also some work on the effects of

growth, which is often affected by competition and resources, on swimming performance in fish (Billerbeck et al. 2001; Oufiero et al. 2011). For example, Bouton et al. (2002) found plasticity in cranial morphology in relation to diet in cichlid fish, with differences between algae only and algae + zooplankton-eating fish. Differences in food can affect growth, and both of these factors (diet and growth) may affect fish design or swimming performance directly, though few studies have quantified this effect. Competition among or within species may have a similar effect as it often influences the niche occupied and therefore the diet available to an organism. For example, too many intra- or inter-specific competitors may cause a reduction in preferred food source availability (Osenberg et al. 1992). If fish are phenotypically plastic they may be able to respond by shifting diets, which again could affect growth and swimming performance. Similar to predation, the plasticity of swimming performance may only evolve in response to these biotic factors if there is consistent, somewhat predictable variation in exposure to the new environment. Few studies have examined the effect of these biotic factors on swimming performance and its underlying components to determine whether it may be adaptive or not, but this may provide for interesting areas of future investigation.

Dissolved oxygen

The amount of oxygen in the environment is important to locomotion as it can affect the delivery of oxygen to the tissues and thus aerobic capacity. The plasticity of swimming performance in fish has been examined in relation to the amount of dissolved oxygen (DO) in water [e.g., Fu et al. (2011)], with most studies focusing on the plastic response of endurance swimming because of the effect of low DO on the respiratory and oxygen delivery systems (Figure 1). Fish might encounter varying levels of oxygen spatially or temporally (Kramer 1987; Kress and Herut 2001), similar to temperature or habitat variations; and the levels of DO may be related to both habitat and temperature. For example, a faster moving body of water is likely to have higher DO levels compared with stagnant bodies of water (Fu et al. 2014). Similarly, because of the relationship of DO and temperature, as the temperature of the water increases there may be a decrease in the DO of the water because there is a reduction in the capacity of water to hold oxygen at higher temperatures (Carpenter 1966). Therefore, studies examining the evolution of plasticity in response to DO may consider other environmental variables that are linked to DO levels (e.g., Roze et al. 2013; Fu et al. 2014).

The amount of DO in the environment has the potential to affect swimming performance through its effects on fish design and kinematics (Figures 1 and 2). The subsequent change in swimming performance in response to DO may be beneficial and provide a performance advantage for the fish, similar to terrestrial animals training at high altitudes (Epthorp 2014). An acute depletion of O_2 tension in the water should inhibit O_2 delivery to the tissues causing a reduction in aerobic locomotion, such as endurance or metabolic scope. However, plasticity in fish design and/or kinematics might compensate for these low levels of oxygen. Because of the potential differences in the cardiovascular system's acute and chronic response to low O_2 tension, the resulting acute, chronic, and potentially evolutionary responses of fish swimming performance, design, and/or kinematics to varying DO levels may differ, which we consider below.

Acute responses to hypoxic conditions (low DO) compensate by increasing the uptake or delivery of oxygen, but often result in a reduced performance. For example, Atlantic cod *G. morhua* exposed to acute hypoxic conditions had reduced U_{crit}, reduced O_2 consumption at U_{crit}, and switched to burst-coast swimming earlier (Dutil et al. 2007). Therefore, while performance was reduced at lower DO levels, the kinematics changed to help compensate. Yang et al. (2013) found that normoxia-acclimated fish exposed to acute hypoxic conditions had reduced maximum metabolic rate, metabolic scope, and U_{crit}. Other plastic responses of fish to acute exposure to hypoxia include changes in hematocrit (Holeton and Randall 1967; Silkin and Silkina 2005), increasing ventilation (Kerstens et al. 1979), increased cardiac output (Brill and Bushnell 2001), and other components of cardiovascular physiology (Gamperl and Farrell 2004). While these acute exposures to hypoxic conditions are not beneficial to swimming performance and are compensatory mechanisms to ensure adequate supply and delivery of O_2 to tissues, chronic exposure to hypoxia has been shown to produce beneficial plastic responses in swimming performance in some species.

Plastic responses of fish design and kinematics to chronically hypoxic conditions often result in improved swimming performance because the compensatory mechanisms that change to maintain swimming ability at low O_2 levels (e.g., Figure 2A) give these fish a performance advantage when they are returned to normoxic conditions (e.g., Figure 2C or D). For example, although Yang et al. (2013) found that southern catfish *Silurus meridionalis* reared in normoxic conditions had a decrease in swimming performance when exposed to acute hypoxic conditions, fish reared in diel-cycled hypoxic conditions for 15 days performed better than normoxic fish when tested in hypoxia. Therefore, the acclimation of fish to hypoxic conditions can improve performance, potentially by increasing their plasticity in response to lower DO levels (Figure 2D). However, Petersen and Gamperl (2010) acclimated Atlantic cod (*G. morhua*) to hypoxic and normoxic conditions for 6–12 weeks and examined their U_{crit}, metabolic rate, cardiac output, stroke volume, and heart rate under both hypoxic and normoxic conditions. They found that hypoxic animals had reduced U_{crit}, cardiac output, and stroke volume, but an increase in heart rate and oxygen consumption. Therefore, the hypoxic conditions resulted in alterations of cardiovascular physiology to try and maintain cardiac output and O_2 delivery to tissues. Subsequent changes on U_{crit} were therefore not adaptive, but the result of hypoxia's indirect effects on swimming performance through fish design. Although these results are different than other chronic exposure studies, it highlights the importance of additional research to understand the potential beneficial plastic response of fish swimming to varying DO levels.

Several studies have begun to examine the evolution of plasticity in response to DO levels by comparing populations and species from different DO environments, with mixed results. These have focused on differences in DO tolerance among habitats, with higher flow streams expected to have higher DO levels compared with slower or stagnant bodies of water. For instance, Crispo, Chapman, and colleagues have been examining populations of African cichlid *Pseudocrenilabrus multicolor victoria* from swamp and river locales. The swamps experience more hypoxic conditions than the river locales (Gotanda 2012) and thus they proposed that fish from the swamp might be evolving in their plasticity. Using F1 offspring from both populations reared in common high and low DO levels they found that hypoxic reared fish had increased gill filaments (Crispo and Chapman 2010), larger heads, relatively deeper bodies (Crispo and Chapman 2011), and a decreased latency during escape response compared with fish raised in normoxic conditions (Gotanda 2012); but they saw no effect of rearing treatment on U_{crit} (Gotanda 2012). Therefore, while aspects of fish design are plastic in response

to hypoxic conditions in these fish, there does not seem to be a plastic response in their swimming performance or population differences in their plasticity of swimming performance (Figure 2A). They subsequently found similar morphological (i.e., fish design) changes in response to hypoxia in an isolated, normoxic lake population, which may suggest that this plasticity was an ancestral trait in these cichlids and isn't currently evolving (Wiens et al. 2014). Fu et al. (2014) compared the hypoxia tolerance of 12 species of cyprinids that originated from habitats that vary in their flow (rapid flow, intermediate flow, and slow flow). Here, rapid flow environments are likely to exhibit more stable O_2 levels compared with slow flow environments. Indeed, they found that species from slow flow environments tended to have higher hypoxia tolerances, lower swimming speeds, and a greater tolerance to O_2 tension changes. Therefore in this example, there is a difference in the mean swimming performance and performance breadth of fish from different environments, similar to the hypothesis depicted in Figure 3H. Furthermore, after hypoxia acclimation, the slow flow fish demonstrated improvement in swimming performance, suggesting the changes were adaptive, whereas rapid flow species showed no improvement. This demonstrates that the plasticity of swimming performance may be evolving in relation to O_2 tension levels experienced in nature in this group (Figure 2D).

Future studies interested in the evolution of the plasticity of swimming performance in relation to oxygen levels should take into account the timeframe of response, species, or populations being examined, and other environmental variables. Levels of DO are often related to other components of the environment such as water flow and temperature, therefore a 2-factor mixed design will help tease apart these effects. Furthermore, studies should focus on populations (Crispo and Chapman 2010; Gotanda 2012) or closely related species in a phylogenetic context (Fu et al. 2014) that experience natural variations in DO levels. Lastly, similar to studies investigating habitat and temperature differences alone, the kinematics and fish design components should be examined, particularly associated with the cardiovascular system, as this system has been identified as responding plastically to hypoxia over varying timescales (Holeton and Randall 1967; Kerstens et al. 1979; Brill and Bushnell 2001; Gamperl and Farrell 2004; Silkin and Silkina 2005).

Carbon dioxide

The plasticity of fish swimming performance in relation to CO_2 levels is one of the more recent areas of investigation. Rising CO_2 levels are becoming a concern for aquatic biologists as they can cause acidification of the water (Hoegh-Guldberg et al. 2007), which is an important issue in today's changing climate. Because CO_2 level variation is a new area of investigation, there are far fewer studies of swimming performance plasticity in relation to this environmental variable. However, much like the other environmental effects discussed, varying CO_2 levels have the potential to affect swimming performance on acute, chronic, and evolutionary timescales. Furthermore, varying CO_2 levels have the potential to affect swimming performance due to their potential effect on underlying neuronal processes and behavior (Nilsson et al. 2012). To date, the results for varying CO_2 levels on the plasticity of swimming performance are mixed and somewhat complicated.

An increase in CO_2 levels in the water results in a lower pH, and to compensate for the reduction in pH aquatic organisms, such as fish, increase levels of bicarbonate (HCO_3^-) intracellularly and decrease levels of chloride (Cl^-) extracellularly (Nilsson et al. 2012). The relative changes of both of these ion concentrations affect the

GABA-A inhibitory neurotransmitter receptor. These receptors typically cause hyperpolarization, by the diffusion of Cl^- and bicarbonate into the cell; but in the presence of altered HCO_3^- and Cl^- ratios due to increased CO_2 levels, these ions leave the cell through GABA-A receptors, causing depolarization (Nilsson et al. 2012). Therefore, rising CO_2 levels have the potential to affect neuronal processes and subsequent behavior and performance of the fish.

Chronic exposure to elevated CO_2 levels over varying timescales has been linked with a change in fish behavior or increased activity levels (Munday et al. 2012, 2013; Allan et al. 2013). For example, Domenici et al. (2011) found that 4 day exposure to elevated levels of CO_2 reduced lateralization during a detour swimming test in a damselfish *Neopomacentrus azysron*. Lateralization, or turning of a fish during swimming such as escape responses, may be important to avoid predators. Fish tend to have a preferred side to turn toward, but exposure to increased CO_2 levels removed any turning preference (Domenici et al. 2011). Allan et al. (2014) examined the effects of both acute and chronic exposure to elevated CO_2 on the escape response of cinnamon anemonefish *Amphiprion melanopus*. They found decreases in distance traveled, mean response speed, and duration of the escape response when exposed to high levels of CO_2 (Allan et al. 2014). Lastly, Munday et al. (2009) looked at the interactive effects of chronic exposure to both temperature and acidity on the metabolic rate of two species of cardinalfish (*Ostorhinchus doederleini* and *O. cyanosoma*). They found that in both species resting metabolic rate increased when fish were exposed to high temperatures, lower pH, or both high temperature and low pH; however, their results for maximal metabolic rate were mixed and inconsistent between the species (Munday et al. 2009). They also found decrease in aerobic scope with increasing temperatures alone and lower pH alone, but there was no interaction between these effects.

The effects of varying CO_2 and pH levels are a relatively new area of investigation. Based on a fish's response of its acid-base balance in the body, variation in CO_2 and pH has the potential to alter neuronal processes. The research that has been done on swimming performance demonstrates altered behavior and kinematics of swimming along with elevated resting metabolic rates (i.e., energetics, see Figure 1). To our knowledge no studies have examined how plasticity of swimming performance will evolve in response to varying levels of CO_2 and pH, but given the importance of these environmental traits it is an exciting area of future investigation. For instance, examining the effects on closely related species or populations of species in areas that experience fluctuations in CO_2 and pH levels would provide insight into the evolution of plasticity in swimming performance. Furthermore, few studies have examined how varying levels of CO_2 and pH affect other components of fish design and kinematics (Figure 1). There are many avenues of research that remain to be tested to understand how alterations of CO_2 and pH in the environment affect the plasticity of fish swimming.

Linking Phenotypic Plasticity to Macroevolutionary Patterns

Several researchers have noted the potential for phenotypic plasticity in traits to lead to macroevolutionary patterns of diversity (West-Eberhard 1989; Pigliucci 2005; Langerhans 2008; Pfennig et al. 2010; Levis and Pfennig 2016), however this has rarely been investigated, particularly in relation to fish swimming. Here we briefly discuss how plasticity in fish swimming may result in macroevolutionary patterns of diversity, focusing on swimming kinematics.

The idea that plasticity in a trait can lead to macroevolutionary patterns of diversity stems from the "plasticity first" hypothesis (Pfennig et al. 2010; Levis and Pfennig 2016). As noted recently by Levis and Pfennig (2016), "…environmentally induced phenotypic change sets in motion an evolutionary sequence in which selection promotes adaptation by acting on *existing* genetic variation." Therefore, changes in swimming performance, kinematics, or fish design due to plasticity may undergo genetic accommodation or assimilation to promote speciation and adaptive evolution. If plasticity is the starting point for speciation, it could eventually lead to large-scale macroevolutionary patterns of phenotypic diversity.

Pigliucci (2005) offered two hypotheses for the evolution of phenotypic plasticity facilitating macroevolution. First, he suggests that if one population or species is evolving greater plasticity, that population or species would be able to persist under a greater range of environmental conditions (Figure 2D). If the traits that initially responded plastically are favored in the new environment, then they may be assimilated genetically. Second, he suggests that there may be "genetically induced changes of the phenotype [that] are accommodated by the natural plasticity of the developmental system." For example, a mutation may cause a change in the fin structure of the fish that would make that structure less efficient in locomotion. The fish may therefore use another set of fins to generate thrust, a plastic ability. If this novel phenotype is favored by natural selection, the plasticity in use of the fins may lead to macroevolutionary change. Fish offer a unique opportunity to examine the relationship between phenotypic plasticity and macroevolution. Unlike other, terrestrial vertebrates fish are not bound by gravity and have therefore diversified in their means of thrust production. That is, fish use any number and/or combination of fins and body to propel themselves through water (Webb 1994). Many different gaits have been described in fish, from body-caudal fin swimmers, to median-paired fin swimmers, to more specific types of locomotion such as labriform, carangiform, ballistiform, gymnotiform, to name a few (Webb 1994). Interestingly, many of these gaits can be observed within a species during different types of swimming as well as among major taxonomic groups.

As noted above, the kinematics of swimming, a fish's gait, can respond plastically to environmental variation (Dutil et al. 2007). If a population of fish is more plastic in its fin use, for example switching between median-paired fin swimming and body-caudal fin swimming, and a new environment favors one over the other, that type of swimming may become fixed, resulting in an evolutionary transition of swimming mode. That is, plasticity in fin use may result in genetic accommodation or assimilation to use a specific set of fins, leading to microevolutionary change, which may drive macroevolutionary patterns (Langerhans 2008). For example, many reef fish rely on median-paired fin swimming, switching to body-caudal fin swimming when more power is needed (at higher flow velocities) (Korsmeyer et al. 2002; Fulton et al. 2013). If a population that is more plastic in its ability to utilize the body-caudal fin gait is subjected to increasing water velocities, selection may eventually favor strict body-caudal fin swimming in the new, fast moving environment. In fact, there is evidence that flow patterns on reefs select for different assemblages of fish (Fulton et al. 2005). Recent work has also provided evidence for the ability of fish to respond plastically to different environments, and has suggested it may be an indication of major locomotor transition. Standen et al. (2014) reared *Polypterus* fish, which can exhibit terrestrial locomotor behaviors, in two environments, an aquatic environment where they would rely on swimming and a more terrestrial environment. They found that the ones reared in the terrestrial environment developed a morphology and biomechanical gait that favors terrestrial locomotion, hinting at the initial transition from water to land (Standen et al. 2014). Thus, through developmental plasticity a major transition could be obtained, similar to results found among some terrestrial vertebrates diversifying in habitat use (Losos et al. 2000). The plasticity of fin use may therefore be a primer for the diversity of gaits exhibited among fish. Furthermore, given the diversity of ways fish respond to environmental variation in temperature, flow patterns, DO levels, and carbon dioxide levels, they may make excellent models to determine how these plastic changes might result in macroevolutionary patterns, although few have examined the plasticity of fish swimming from this perspective.

Concluding Remarks

Fish offer some unique opportunities to study the evolution of plasticity. Although few studies have examined how the plasticity of fish swimming has evolved, there are many avenues of future research to understand how this complex, integrative phenotype responds plastically to environmental variation. Garland and Kelly (2006) proposed several mechanisms to study the evolution of plasticity, some of which are now being employed in studies of fish swimming. For example, they suggest comparative studies, such as examining the performance curves and reaction norms (Figure 3) of two or more species from different environments (e.g., Wilson et al. 2001; Johansen and Jones 2011; Fu et al. 2014), which could elucidate the evolution of plasticity. On a broader scale this could be done across closely related species, incorporating phylogenetic comparative methods. A key to comparative studies would be subjecting populations or species to the same set of conditions; to date studies have used many methods, acclimation times, and performance measures. Therefore, consistency in these methods would help elucidate the evolution of plasticity. Garland and Kelly also stress the importance of experimental evolution, which to our knowledge has not been used to study the evolution of plasticity in swimming performance, although it has been used to study plasticity in terrestrial locomotion [see Garland and Kelly (2006) for review].

Fish have an incredible amount of diversity in their swimming abilities. Despite genetic divergence among populations or species, they have been shown to respond plastically to environmental variation in temperature, habitat, DO, and carbon dioxide. When examining the evolution of plasticity in swimming it is important to keep in mind what traits are likely to respond. That is, studies of thermal plasticity highlight the importance of biochemical pathways; whereas studies of flow focus on body shape and kinematics changes; responses to DO emphasize cardiovascular physiology; and CO_2 and pH levels concentrate on neuronal responses. Another important aspect to keep in mind is whether the change in swimming performance is adaptive. For example, there does not seem to be a direct benefit of swimming faster at warmer temperatures as the changes in performance are a result of the indirect effect of temperature acting on biochemical pathways. Conversely, variation in swimming performance in response to flow should provide an advantage to maintain body position in the moving water. Lastly, because of the integrative nature of swimming performance it is important to include a performance trait (e.g., sprint speed, burst speed, U_{crit}, or endurance) and a potential underlying trait that may be responding plastically (e.g., fish design or kinematics, Figure 2). Fish swimming has a long history of study, yet more can be learned from this trait to understand how phenotypic plasticity can evolve.

Acknowledgments

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