

Ecology and Evolution of Swimming Performance in Fishes: Predicting Evolution with Biomechanics

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INTRODUCTION

Residing within the immense diversity of fishes on earth is an equally impressive array of locomotor abilities. Some fish continuously swim virtually their entire lives; some move primarily in brief bursts of rapid acceleration; some gracefully maneuver through spatially complex habitats; and some even walk on land. What are the evolutionary root causes of such diversity in swimming abilities? Has swimming performance largely been shaped by random factors, evolving at the whim of genetic drift? If not, then what ecological mechanisms might be responsible for the evolution of swimming performance? Here we investigate some of the major ecological factors that might have shaped the evolution of locomotor performance in fishes. Using an integrative approach, we

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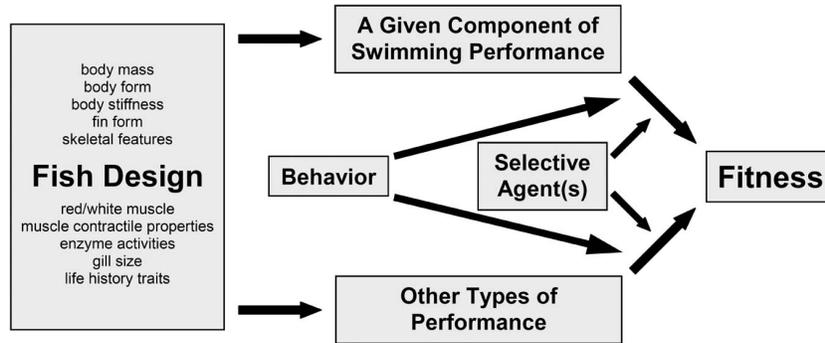


Fig. 7.1 Conceptual path diagram summarizing the ecology and evolution of swimming performance in fishes. The diagram is based on Arnold's (1983) morphology → performance → fitness paradigm, and largely represents an extension of Fig. 3 in Domenici (2003).

acknowledge the complexity of swimming performance, addressing how its evolution depends on numerous underlying organismal features, and is both influenced by and influences multiple fitness components.

At the outset, we should first describe what we mean by “swimming performance.” In this chapter, swimming performance simply refers to any quantifiable component of locomotor ability that selection might act upon (e.g., endurance, metabolic rate, maximum acceleration, turning radius). As such, the ecology and evolution of swimming performance is complex, reflecting the net effects of numerous potential targets and agents of selection. Figure 7.1 illustrates the complexity of the evolution of swimming performance in fishes, and several important points can be deduced from this figure. First, as a whole-organism performance measure, swimming performance is influenced by numerous underlying traits (i.e., “Fish Design” in Fig. 7.1). Second, the same traits affecting swimming performance also influence other types of performance. Thus, selection on one type of performance can indirectly affect other types of performance. Third, because performance mediates fitness, selection acts directly on performance and not fish design itself (*sensu* Arnold, 1983). Fourth, behavior can modify the relationships between performance and fitness, most notably by influencing the manifestation of performance values in the wild (e.g., exhibiting sub-maximal performance) and by modifying the nature of the relationship between performance and fitness (e.g., behaviorally increasing or decreasing the frequency with which certain types of performances are employed). As a corollary, selection on one type of performance can indirectly cause behavioral shifts that alter the form of selection on other types of performance. Finally, the form of selection on swimming performance depends on various selective agents (e.g., predators, foraging mode, abiotic factors), and thus will vary across time and space as

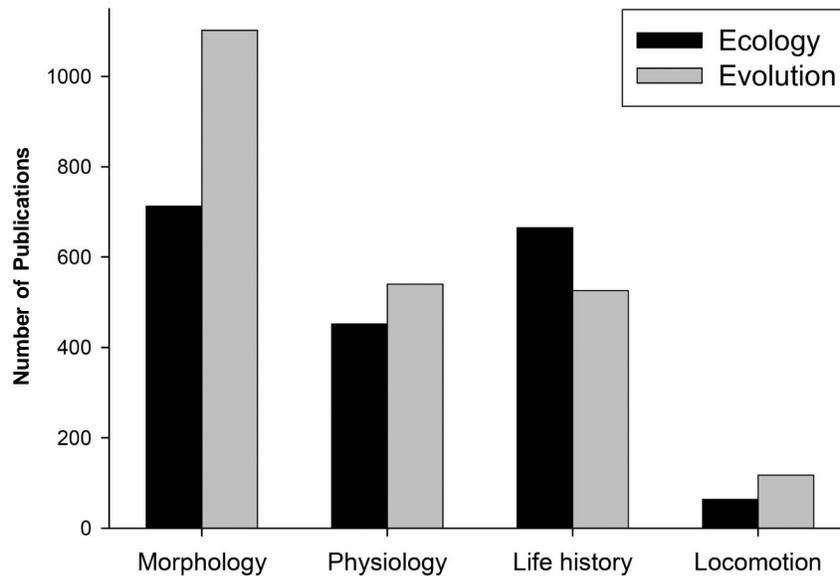


Fig. 7.2 The relative paucity of studies examining the ecology and evolution of fish locomotion compared to fish morphology, physiology, and life history. Data are from a search of the Institute for Scientific Information Science Citation Index, covering articles published between 1900 and 2007. Each search comprised the term “fish”, a term for either “ecolog*” or “evolution*”, and a term for a subdiscipline (either “morpholog*”, “physiolog*”, “life histor*”, or “locomot*”).

the relative importance of selective agents change. Because of all this complexity, acquiring a detailed understanding of the evolutionary ecology of swimming performance in fishes requires an appreciation of a multitude of interactions involving multiple traits and multiple environmental factors—while complex, we aim to demonstrate that such an understanding is possible.

To date, most research on the ecology and evolution of fish has centered on features of fish design, rather than aspects of locomotor performance (Fig. 7.2). This approach is interesting, as it is performance, and not design, that is directly linked to individual fitness. This has probably occurred, at least partially, because the underlying traits are typically much easier to measure than swimming performance for large sample sizes of multiple populations/species. However, the investigation of the evolutionary ecology of swimming performance is not so difficult that it is out of reach. Indeed, owing to a strong foundation that has grown in the realm of biomechanics of fish locomotion, the time is ripe for an explosion of ecological and evolutionary work on fish swimming performance.

Swimming performance lies in the middle of the general morphology → performance → fitness paradigm (Arnold, 1983). As part of this general interaction system, the generation of swimming abilities is understood by

inspection of lower-level features (i.e., fish design), while the importance of these abilities is appreciated by understanding their influence on higher levels (i.e., fitness). A great deal of research has examined the links between fish design and swimming performance (e.g., reviewed in Webb and Weihs, 1983; Videler, 1993; Sfakiotakis *et al.*, 1999; Triantafyllou *et al.*, 2000; Lauder and Drucker, 2002; Blake, 2004; Colgate and Lynch, 2004; Müller and van Leeuwen, 2006; Shadwick and Lauder, 2006). Much of this work has had a bio-engineering focus, attempting to understand how specific structures work, largely in the absence of an explicit ecological or evolutionary context (typically lacking a comparative approach, which is the hallmark of ecological and evolutionary approaches; see Lauder *et al.*, 2003). Although considerably less work has explicitly examined the relationships between swimming performance and fitness (but see Katzir and Camhi, 1993; Walker *et al.*, 2005), copious working hypotheses and common assumptions abound (e.g., high burst speeds increase escape ability). Thus, there is no shortage of hypotheses regarding the form of selection on various types of swimming performance via various selective agents. While not originally developed for this purpose, the purely biomechanical approach can be combined with ecological knowledge regarding the links between swimming performance and fitness to generate detailed hypotheses regarding the form of natural selection and the course of evolution. Thus, we suggest evolutionary ecologists tap the wealth of biomechanical theory and empirical work (a field that is still rapidly growing) to formulate hypotheses testable within a comparative framework. Here, we review some key areas where strong biomechanical and ecological knowledge exists, and make some accurate and sometimes remarkably general evolutionary predictions (as well as generate other hypotheses yet to be tested). In the years to come, we encourage researchers in this arena to employ more pluralistic approaches as hypotheses become more refined to further uncover the multitude of mechanisms responsible for the evolution of swimming performance in fishes.

Formulating Evolutionary Predictions

Locomotor performance in fishes is shaped by so many factors that uncovering the ecological mechanisms actually responsible for its evolution might seem unattainable. For example, we know body shape is important in determining swimming performance; however a number of other aspects of organismal function are also inextricably linked to morphology (e.g., diet, mode of reproduction), and hence might also interact with the evolution of locomotor abilities (see Fig. 7.1). Not only can a multitude of design features influence various components of swimming performance, but selection likely operates on numerous types of performance simultaneously, and varies across time

and space (e.g., Lowell, 1987; Dudley and Gans, 1991; Wainwright and Reilly, 1994; Lauder, 1996; Reznick and Travis, 1996; Vamosi, 2002; DeWitt and Langerhans, 2003; Ghalambor *et al.*, 2003). One approach to understanding the ecology and evolution of swimming performance is to begin with a few design features and a few selective agents where we can generate well-supported hypotheses for the course of phenotypic evolution. That is, we can build generalized mechanistic models describing how a system operates based on a specified set of assumptions—i.e., how design features determine performance, how performance determines fitness, and consequently what the evolutionary response(s) should be. A similar approach has been taken with fish foraging and labriform locomotion (e.g., Wainwright and Richard, 1995; Westneat, 1995; Wainwright, 1996; Huckins, 1997; Shoup and Hill, 1997; Clifton and Motta, 1998; Fulton *et al.*, 2001, 2005; Ferry-Graham *et al.*, 2002; Grubich and Westneat, 2006; Fulton Chapter 12 in this book), and is proving highly successful. Here, our assumptions are that we correctly understand specific relationships linking fish design, swimming performance, and fitness (see below), and also that adequate genetic variation exists to allow significant evolutionary responses to selection (including the evolution of phenotypic plasticity). We can then test our models' predictions using comparative analyses. The degree of correspondence between predictions and observations should provide insight into the accuracy of our understanding of the biomechanics and evolutionary ecology of fish locomotion (e.g., Endler, 1986; Wainwright, 1988, 1996; Losos, 1990; Williams, 1992; Lauder, 1996; Walker, 1997; Koehl, 1999; Domenici, 2003). Because we cannot hope to cover in detail all factors relevant to the ecology and evolution of swimming performance in one chapter, we will narrow our focus and make evolutionary predictions for a specific set of attributes in a specific set of circumstances.

First, we will center on what is probably the most obvious component of fish design, morphology. Body and fin form is strongly linked to locomotor performance in fishes, and a long history of research has delved into understanding these relationships (e.g., Webb, 1982, 1984, 1986a; Weihs and Webb, 1983; Sfakiotakis *et al.*, 1999; Triantafyllou *et al.*, 2000; Blake, 2004; Lauder, 2005; Lauder and Tytell, 2006; Domenici Chapter 5 in this book). Because any attribute that affects morphology can also affect locomotor performance, we will further consider some components of fish design that can indirectly influence swimming performance via their effects on morphology (e.g., number and size of eggs/embryos, gut length). Second, we will center on only a few common selective agents for fishes: environmental structural complexity, water flow, and predation. Thus, our predictions will focus on divergent evolution of body and fin morphology based on hypotheses regarding the form of natural selection on swimming performance across these three major ecological gradients.

Our predictions derive from a hypothesized trade-off between the two primary swimming modes, steady and unsteady swimming. This trade-off is presumed to exist because of conflicts involving features of fish design, whereby traits that increase performance in one swimming mode necessarily decrease performance in the other (e.g., Blake, 1983, 2004; Webb, 1984; Videler, 1993; Reidy *et al.*, 2000; Domenici, 2003; Langerhans, 2006; Domenici chapter 5 in this book). With specific regard to fish morphology, this general trade-off between steady and unsteady swimming is not expected to apply to all fishes. Rather, the tradeoff should be stronger in fish employing more coupled locomotor systems—that is, cases in which the same morphological structures are used for propulsion during both steady and unsteady swimming. While this scenario applies to the great majority of fish because it is virtually impossible to completely decouple all propulsors, some species have evolved locomotor systems with varying degrees of independence among swimming modes. Specifically, some fish employ different body parts during different swimming activities—e.g., boxfish, *Ostracion meleagris*, use median-and-paired fin propulsion for low-speed cruising and body-and-caudal-fin propulsion for burst-and-coast swimming (Hove *et al.*, 2001). The generalized model we describe below is assumed to apply to fish using a variety of locomotor systems, as the predictions we focus on should apply equally to most fish—i.e., we center on body shape and caudal fin form, and fish have only one body and one tail. When formulating our predictions, we assume that existing theory (typically based on rigid bodies) and empirical work linking morphology and locomotor performance applies equally to fish using various sources of propulsion, excluding flatfish. Because the use of median and paired fins in locomotion varies considerably among fishes, we avoid making generalized predictions for these fins; although some clear predictions do exist for pectoral fin shape in labriform swimmers (e.g., see Wainwright *et al.*, 2002; Walker and Westneat, 2002; Fulton *et al.*, 2005). While other design features also influence swimming performance (e.g., muscle mass/type), and could complicate our morphological predictions, we will simply assume *ceteris paribus*, or at least that these potentially confounding factors do not overwhelm and conceal the predicted patterns. Because our predictions rely on a tradeoff between steady and unsteady locomotion, let us first assess exactly what is meant by these terms.

Steady swimming is constant-speed locomotion in a straight line. While this form of swimming specifically refers to laboratory measures of swimming performance, steady swimming is commonly employed in nature during routine cruising, as well as long-distance movements such as migrations. For instance, fish often utilize steady swimming when searching for food, chasing and obtaining mates, seeking favorable abiotic conditions, and holding station amidst water current (e.g., Plaut, 2001; Domenici, 2003; Blake, 2004; Rice and Hale Chapter 6 in this book). As steady swimming

activities are often of critical importance, natural selection is believed to often favor various means of reducing the energetic cost of movement (see Fish Chapter 4 in this book). Steady swimming performance is typically assessed in the laboratory using various estimates of endurance or energy expenditure (e.g., Reidy *et al.*, 2000; Plaut, 2001; Nelson *et al.*, 2002). A wealth of theoretical and empirical work has developed some clear links between morphology and steady swimming (e.g., Wu, 1971; Lighthill, 1975; Webb, 1975, 1984; Blake, 1983; Weihs, 1989; Hobson, 1991; Videler, 1993; Vogel, 1994; Fisher and Hogan, 2007). Steady swimming is generally enhanced with a streamlined body shape (deep anterior body depth, tapering to a narrow caudal peduncle; see further details in Testing Evolutionary Predictions) and a high aspect ratio lunate caudal fin (long span with a short chord; height²/surface area). These features act to maximize thrust while minimizing drag and recoil energy losses. While much of this work has been either theoretical/biomechanical in focus (e.g., using mathematics, physical models, manipulated organisms) or empirically compared distantly related and divergently shaped species, some recent research supports this work using only natural intraspecific variation. For instance, recent studies employing three-dimensional estimations of streamlining have revealed that more streamlined zebrafish (*Danio rerio*) exhibit lower drag coefficients (McHenry and Lauder, 2006), and more streamlined western mosquitofish (*Gambusia affinis*) exhibit higher endurance (R.B. Langerhans unpubl. data).

Unsteady swimming refers to more complicated locomotor patterns in which changes in velocity or direction occur, such as fast-starts, rapid turns, braking, and burst-and-coast swimming. In the wild, such activities are common during social interactions (e.g., courtship, antagonistic interactions), predator evasion, the capturing of evasive prey, and navigating structurally complex environments. For instance, the most commonly studied form of unsteady swimming is the Mauthner-cell initiated escape response present in most fish, called a “C-start” (e.g., Weihs, 1973; Eaton *et al.*, 1977; Domenici and Blake, 1997; Hale *et al.*, 2002; Blake, 2004; Domenici Chapter 5 in this book). During this fast-start, the fish body bends into a “C” shape and then produces a propulsive stroke of the caudal region in the opposite direction, resulting in a sudden, high-energy swimming burst. High unsteady performance is typically produced by a deep body (particularly in the caudal region; this might also be accomplished by median fins rather than the body) and a large caudal fin with a low aspect ratio (e.g., Blake, 1983, 2004; Webb, 1983, 1984, 1986b; Walker, 1997; Langerhans *et al.*, 2004; Domenici *et al.*, 2008). These features maximize thrust and stability during rapid bouts of swimming activity. Numerous theoretical and empirical studies have provided support for these relationships, and recent work at the intraspecific scale has also found supportive evidence. For instance, *G. affinis* individuals with larger caudal regions produce higher

burst speeds (Langerhans *et al.*, 2004), and *G. hubbsi* individuals with larger caudal regions produce greater acceleration and angular velocity during fast-starts (R.B. Langerhans unpubl. data).

Because opposite suites of morphological traits optimize steady and unsteady swimming, this creates a scenario where no body form exists which can simultaneously optimize both swimming modes. Thus, fish bodies must reflect some form of compromise between competing swimming demands. Based on this knowledge, we can make general predictions for the course of evolution for fish inhabiting particular environments hypothesized to favor alternative swimming modes (Fig. 7.3). Specifically, we hypothesize that

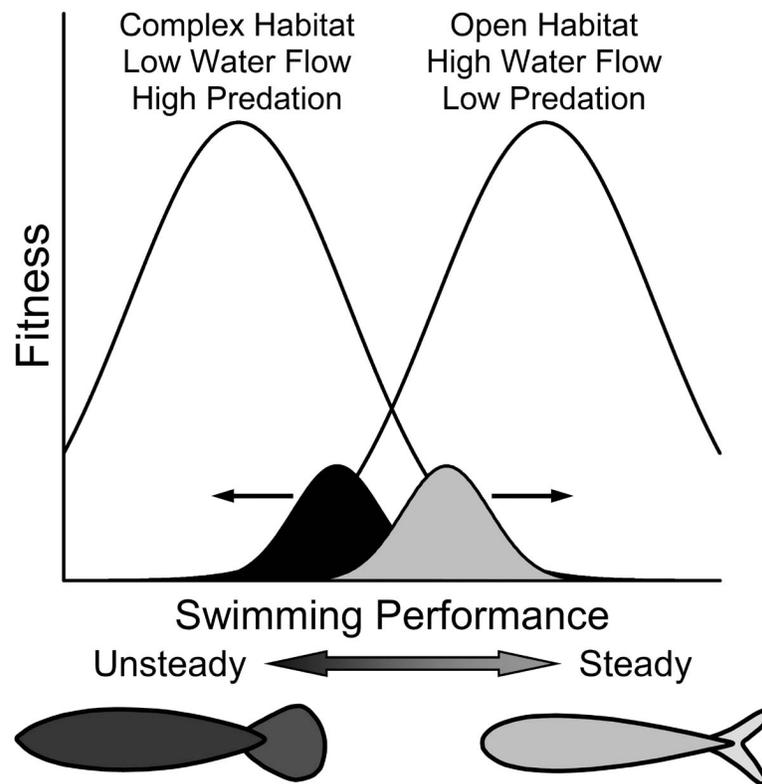


Fig. 7.3 Illustration of the hypothesized divergent natural selection between environments favoring either unsteady or steady swimming performance. Curves represent hypothesized fitness functions, with trait distributions for fishes inhabiting the alternative environments represented by the shaded areas. Arrows illustrate the direction that natural selection is predicted to pull trait means within each environment. The text above each curve describes the environmental gradients examined in this chapter where divergent natural selection is predicted to exist. Figures beneath the x-axis illustrate the general morphological predictions: more streamlined bodies and higher caudal fin aspect ratio in environments favoring steady swimming.

fish will evolve body forms which enhance steady swimming in environments where the importance of steady swimming outweighs unsteady swimming, such as open-water habitats, high-flow environments, and other circumstances where prolonged swimming behaviors are greatly important (e.g., areas with relatively high competition for patchily-distributed resources). In contrast, we predict fish will evolve body forms which enhance unsteady swimming performance in environments where the importance of unsteady swimming outweighs steady swimming, such as structurally complex habitats, low-flow environments, and areas with a high level of predation intensity. While it is certainly true that relationships between morphology and swimming ability can be quite complex—e.g., form-function relationships are often more complicated than predicted by theory, and multiple body designs can produce similar swimming performance (e.g., Wainwright and Reilly, 1994; Koehl, 1996; Lauder, 1996; Domenici and Blake, 1997; Schultz and Webb, 2002)—we focus here on relationships with particularly strong theoretical and empirical support in an effort to elucidate general and predictable trends.

Testing Evolutionary Predictions

The ideal scenario for testing evolutionary predictions would entail an experiment where similar organisms (preferably, genetic clones) are placed into alternative, *a priori* defined environments in a replicated fashion. Then, we would return to these environments many generations later to assess whether the predicted phenotypes evolved. Because this scenario is obviously infeasible for testing general trends across a group as ancient and diverse as fishes, we perform the next best approach for historical data, the comparative method. With the comparative method, we are essentially comparing the outcomes of nature's experiments—however, we must be careful to incorporate the evolutionary relationships among species into our analyses, as species are not independent of one another, but rather reflect a shared evolutionary history (e.g., Felsenstein, 1985; Harvey and Pagel, 1991; Rose and Lauder, 1996; Martins, 2000). The approach is most effective at establishing cause-and-effect (e.g., invasion of Environment A caused evolution of Trait 2) when comparisons are made between closely related organisms, as there are fewer potentially confounding variables to contend with (e.g., less time for development of phylogenetic structure, less divergence in non-focal traits). Historically, most work relevant to our predictions has lacked a strong comparative approach (e.g., commonly comparing few highly divergent taxa, ignoring phylogeny), and thus can only provide cautionary hints regarding relationships among morphology, swimming performance, and habitat. To provide broad and rigorous tests of our predictions, we will use the comparative method at various taxonomic scales (i.e., from distantly related species to inter-population variation within

species), incorporating phylogenetic information where appropriate. Our tests will draw from both previously published work and new analyses conducted here for the first time.

Let us begin by explicitly stating our two general predictions: (1) fish should evolve more streamlined bodies and higher aspect-ratio caudal fins in environments where selection favors enhanced steady swimming performance, and (2) fish should evolve less streamlined bodies with a greater posterior body allocation (i.e., deeper/larger caudal peduncles, shallower/smaller heads) and lower aspect-ratio caudal fins in environments where selection favors enhanced unsteady swimming performance (see Fig. 7.3). We will test these predictions by comparing morphology among organisms inhabiting environments hypothesized to favor either steady or unsteady swimming abilities. For all analyses, we use one-tailed tests because we have directional hypotheses.

Before we test these predictions, we should first describe what is meant by the term streamlining. To be precise, a streamlined body is not simply elongate, but rather exhibits a fusiform shape that minimizes drag while maximizing volume (i.e., approximating an airfoil shape; Fig. 7.4a). Streamlining in fish has been measured in many ways, but the most common and straightforward method is the fineness ratio (FR) which is simply body length divided by maximum diameter (typically estimated as maximum body depth). While this is obviously a crude estimate—largely because maximum diameter might be located at various locations along the body—and primarily summarizes the general slenderness of a body, it has a long history in ichthyology, has proven quite useful for comparisons among taxa, and has a direct connection to streamlining theory (i.e., aerodynamics, hydrodynamics) as a symmetric airfoil which exhibits the minimum drag for the maximum volume has a FR around 4.5 (e.g., von Mises, 1945; Hoerner, 1965; Hertel, 1966; Alexander, 1968; Webb, 1975; Blake, 1983; Weihs and Webb, 1983). Thus, an optimum FR exists at the value of 4.5, providing an obvious target for evolutionary predictions of drag minimization. Moreover, the drag coefficient for a given volume can be estimated from FR (von Mises, 1945; Hoerner, 1965)—thus relating body shape directly to swimming performance (Fig. 7.4b). In an attempt to provide a more precise estimate of three-dimensional streamlining, McHenry and Lauder (2006) recently described a streamlining ratio comparing the volume distribution of a fish body to a body having the profile of a streamlined shape (i.e., an airfoil drawn from the U.S. National Advisory Committee for Aeronautics, NACA; see Fig. 7.4). Briefly, the procedure reconstructs the 3D shape of a fish body from dorsal/ventral and lateral views of the fish by approximating its shape as an ellipsoid, and then compares its volume distribution to that of a NACA-streamlined body of the same length, maximum depth, and maximum width, using second moments of area, $I_{\text{fish}}/$

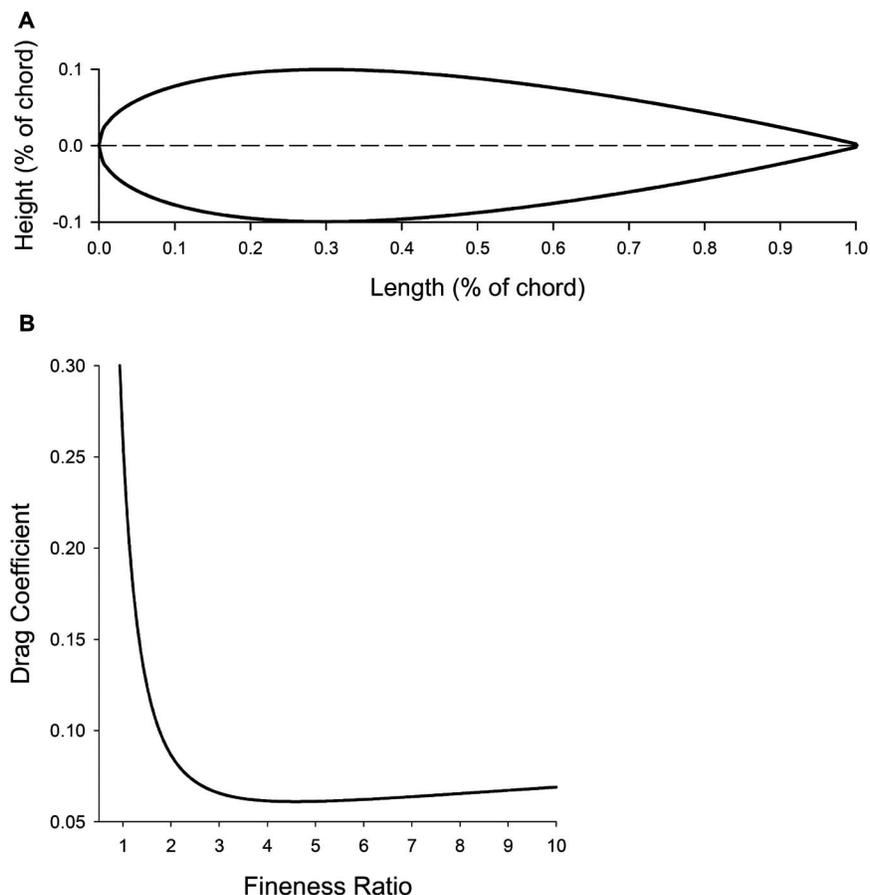


Fig. 7.4 Streamlining and its importance in drag reduction. **(A)** A streamlined shape illustrated using a foil without camber described by the 0000-series of foils from the U.S. National Advisory Committee for Aeronautics (NACA). Figure adapted from Jacobs *et al.* (1933). **(B)** Expected relationship between fineness ratio (length / maximum diameter) and the drag coefficient for a given volume, indicating that a streamlined body with least resistance has a fineness ratio around 4.5 (following Hoerner, 1965).

I_{NACA} (see McHenry and Lauder, 2006 for details). As with FR, an optimum streamlining ratio (SR) exists, where a value of 1.0 represents a perfect match in volume distribution between a given body and the airfoil. Thus, there are theoretical optima for both FR and SR (4.5 and 1.0, respectively), meaning that relationships between these ratios and steady swimming performance should be hump-shaped (see Fig. 7.5a for an empirical relationship with SR). This is because bodies can deviate from each optima in two different ways: either more elongate or rotund than a FR of 4.5, and either too much volume toward the leading or trailing edge compared to a

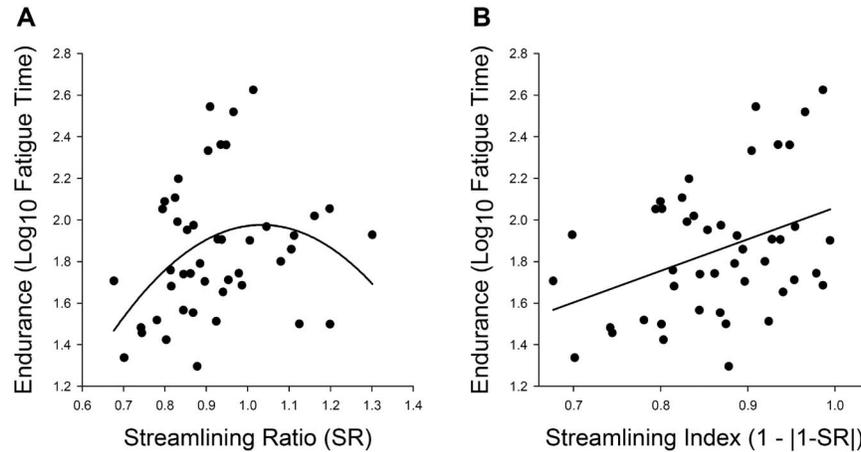


Fig. 7.5 Positive association between body streamlining and endurance in *Gambusia affinis* (R.B. Langerhans unpubl. data). Individuals were first and second generation lab-born descendants of wild-caught fish. **(A)** Matching *a priori* predictions, the raw streamlining ratio (SR) exhibits a hump-shaped relationship with endurance (quadratic regression; $F_{2,42} = 3.25$, one-tailed $P = 0.024$), where the maximum endurance is observed for fish with body forms most closely resembling an airfoil (predicted maximum = 1.0; modeled maximum = 1.03). SR values can be interpreted as follows: values less than 1 represent body shapes with more anterior volume relative to an airfoil, values greater than 1 have more posterior volume relative to an airfoil, and the value 1.0 represents a perfect match in volume distribution between a fish's estimated body form and an airfoil. **(B)** As predicted, the streamlining index (SI) exhibits a positively linear relationship with endurance (linear regression; $F_{1,43} = 7.13$, one-tailed $P = 0.005$). SI values can be interpreted as proportional similarity to the volume distribution of an airfoil (i.e., 0.9 reflects a 90% similarity to an airfoil, while 1.0 perfectly matches an airfoil).

SR of 1.0. Because we often prefer linear relationships in statistical analyses, we can perform simple transformations to these ratios to produce indices ranging from 0 to 1, ignoring the specific nature of how a body deviates from the optima and linearizing their predicted relationship with steady swimming performance (see Fig. 7.5b): Fineness Index (FI) = $1 - |1 - (FR/4.5)|$; Streamlining Index (SI) = $1 - |1 - SR|$. Values for most fish fall between 0 and 1 for both indices. Note that this linearization will not hold across all of parameter space, but rather is most useful when comparing relatively similar shapes. That is, the relationships between these indices and drag are nearly linear across small ranges of shapes, but nonlinear across a broad range of shapes—this is because the increased drag experienced by bodies relative to the optimum is not symmetric about the optimum (von Mises 1945, Hoerner 1965; see Fig. 4b). Because these ratios and indices have clear and direct connections to streamlining theory, we will use these metrics when possible for investigations of streamlining. However, if our questions extend beyond streamlining *per se*, and greater detail is desired for lateral body shape (e.g., larger lateral surface area in

the caudal region generates more thrust during fast starts), then we will employ other, more appropriate techniques, such as landmark-based geometric morphometrics.

Structural complexity

We will begin testing our predictions by comparing fish from environments of differing structural complexities. Fish inhabit environments greatly varying in structural complexity, ranging from pelagic environments, such as the open ocean, to the spatially complex networks of coral reefs and rocky outcrops. Our *a priori* hypothesis is that divergent natural selection between structure regimes arising via alternative locomotor demands has played an important role in driving divergent evolution in fishes. Domenici (2003) recently illustrated this particular hypothesis, where selection is predicted to favor steady swimming performance in structurally-open environments—where resources are widely distributed and continuous swimming is commonplace—but instead favor unsteady swimming performance in structurally-complex environments—where maneuvering, braking, and accelerating are of great importance for both foraging and escaping predation during brief encounters. We specifically predict greater streamlining and a higher caudal fin aspect ratio for fish inhabiting open habitats relative to those in more complex ones (e.g., Webb, 1983; Hobson, 1991; Videler, 1993).

Perhaps the most common—and most studied—axis of divergence in fishes falls under this rubric: phenotypic differentiation between benthic and limnetic environments. Benthic habitats refer to shallow, littoral areas where structural complexity often abounds from sources such as aquatic vegetation, woody debris, and rocks; limnetic habitats simply refer to the open-water environment, such as off-shore lake habitat. While studies of benthic-limnetic divergence have typically centered on foraging adaptations (e.g., number of gill rakers)—because benthic fish feed more commonly on benthic invertebrates, while limnetic fish feed heavily on plankton—body form divergence presumably is largely related to locomotor demands for diverse activities, including foraging, avoiding predation, and pursuing and attracting mates. This form of structure-driven divergence has been described under various names (e.g., benthic-limnetic; littoral-pelagic; stream-lake, where structurally complex, slow flowing inlet streams are compared to open-water areas of the lake), and has been implicated in numerous cases of intraspecific differentiation and recent or incipient speciation in fishes (e.g., Echelle and Kornfield, 1984; Ehlinger and Wilson, 1988; Robinson and Wilson, 1994; Schluter, 1996; Smith and Skúlason, 1996; Taylor, 1999; Robinson *et al.*, 2000; Jonsson and Jonsson, 2001; Hendry *et al.*, 2002; McKinnon and Rundle, 2002; Hendry and Taylor, 2004). Some of the classic examples include intra-lake differentiation in northern latitudes, such

as stickleback (*Gasterosteus aculeatus*), whitefish (*Coregonus* spp.), arctic char (*Salvelinus alpinus*), pumpkinseed sunfish (*Lepomis gibbosus*), and bluegill sunfish (*Lepomis macrochirus*); although tropical examples exist as well (e.g., Meyer, 1990; Schliwen *et al.*, 2001; Barluenga *et al.*, 2006). In some cases, the predicted swimming performance tradeoff has been investigated—sometimes being confirmed. For instance, Taylor and McPhail (1986) found that anadromous threespine stickleback (open habitat) exhibit higher endurance, but lower fast-start performance than stream stickleback (complex habitat). Further, limnetic threespine stickleback (open habitat) exhibit lower drag coefficients and higher endurance than benthic stickleback (complex habitat) which evolved in the same lake (Blake *et al.*, 2005); although both limnetic and benthic forms produce similar fast-start performance (Law and Blake, 1996). In both of these examples, and with the vast majority of documented cases, the limnetic (open habitat) forms exhibit more slender bodies than the benthic (complex habitat) ones, matching *a priori* predictions (caudal fin form is very rarely examined). Thus, there is strong empirical support for this general hypothesis, where numerous distantly related lineages have repeatedly undergone parallel cases of predictable evolution. Note that phenotypic plasticity's role in these instances of phenotypic differentiation should not be underestimated, as inducible changes seem to represent an important component of observed patterns in many cases, and may facilitate subsequent genetic divergence (e.g., Day *et al.*, 1994; Robinson and Wilson, 1996; Robinson and Parsons, 2002; West-Eberhard, 2003; 2005; Svanbäck and Schluter unpubl. data). As an extension to this existing evidence, here we use comparative data to test the generality of this hypothesis across highly diverse fish taxa. This analysis is meant as a broad-brush approach to the question, seeking evidence for general trends across a diverse subset of fishes, spanning 11 orders.

A new test across diverse fishes

Domenici (2003) assembled a dataset of 32 fish species for which swimming performance data was available, assigned each species to a habitat category (complex, intermediate, open), and tested for the predicted performance tradeoff (see methodological details in Domenici, 2003). Results matched predictions for both steady and unsteady swimming performance, where fish inhabiting more open environments exhibit higher steady swimming abilities (endurance) but lower unsteady swimming abilities (turning radius and acceleration) than fish in more complex environments. If our predictions are accurate, then these performance differences derived, at least partially, from morphological differences. Here we use this dataset to test for the predicted morphological differences between habitats (see Fig. A1 in *Appendix* for species included in the dataset). We obtained

morphological data (finesness ratio [FR] and caudal fin aspect ratio) from FishBase (Froese and Pauly, 2007). These variables were extracted from the “Morphometrics” section of the web pages for each species, and comprise measurements conducted on digital photographs of specimens. For three species (*Xenomystus nigri*, *Odontesthes regia*, and *Chromis punctipinnis*), no morphological data were available on FishBase. For these species, we used the same methods employed by FishBase to complete the dataset. We averaged cases where data from multiple specimens for a given species were available (eight species). Because FR ranged from less than to greater than the optimum of 4.5, we calculated finesness index (FI; see description above). We also estimated the drag coefficient based on volume (C_D) for each fish from its FR (following Hoerner, 1965; equation 36, pg. 6–19; assuming a common Re of 10^5). To ensure the methods for obtaining morphological variables were adequate for the examination of interspecific differences in morphology, we performed a repeatability analysis using the intraclass correlation coefficient from a model II ANOVA (Lessells and Boag, 1987; Sokal and Rohlf, 1995). We found significant repeatability for FI (intraclass correlation coefficient, $r=0.94$, $P < 0.0001$), C_D ($r=0.82$, $P=0.002$), and caudal fin aspect ratio ($r=0.56$, $P=0.036$), suggesting the variables likely represent a fair approximation of morphological variation among these distantly related species.

We conducted both standard and phylogenetic ANOVAs, testing for differences in FI, C_D , and caudal fin aspect ratio between species inhabiting environments of varying structural complexity. We used the PDSIMUL and PDANOVA programs (Garland *et al.*, 1993) to perform phylogenetic ANOVAs. Using these programs, we simulated trait evolution as Brownian motion with the means and variances of the simulations set to the means and variances of the original data. We performed 1000 simulations, producing a null distribution of F -statistics against which the F -value from the actual data could be compared to assess statistical significance (i.e., determine how different the observed patterns were from that expected via genetic drift alone). We constructed a best-estimate phylogenetic hypothesis for this group of species based on previous morphological and molecular studies (Fig. A1 in *Appendix*; Johnson and Patterson, 1993; Nelson, 1994; Bernardi and Bucciarelli, 1999; Inoue *et al.*, 2001; O’Toole, 2002; Miya *et al.*, 2003; Crespi and Fulton, 2004; Smith and Wheeler, 2004; Shinohara and Imamura, 2007; Smith and Craig, 2007). All branch lengths were set equal to one. Some species were excluded from statistical analysis based on their highly divergent phenotypic values. For FI, *Anguilla anguilla* (European eel) was excluded, as it was an extreme outlier (4.3 standard deviations from the nearest species). For C_D , *Pterophyllum scalare* (freshwater angelfish) was an extreme outlier (5.3 standard deviations from the nearest species), and excluded from analysis. For caudal fin aspect ratio, *A. anguilla* and *X. nigri* (African knifefish) were excluded as these species essentially lack a

caudal fin. In all cases, these procedures were conservative, as results would have more strongly supported predictions had these species been included.

Results matched *a priori* predictions for all three traits: fish in more open habitats tended to exhibit a higher FI ($F_{2,28} = 5.88$, one-tailed $P_{\text{raw}} = 0.0037$, one-tailed $P_{\text{phy}} = 0.025$), a lower C_D ($F_{2,28} = 3.12$, one-tailed $P_{\text{raw}} = 0.030$, one-tailed $P_{\text{phy}} = 0.078$), and a higher caudal fin aspect ratio ($F_{2,27} = 10.30$, one-tailed $P_{\text{raw}} = 0.0002$, one-tailed, $P_{\text{phy}} = 0.008$) (Fig. 7.6). These results suggest that fish do indeed generally evolve predictable morphologies and swimming abilities in these alternative habitat types. Thus, despite the complicated nature of morphology \rightarrow performance relationships, we can apparently still predict broad trends across a diverse group of fishes. Taken alone, these results provide cautionary evidence supporting our hypotheses of divergent natural selection between structure regimes and subsequent divergent evolution. However, when combined with the abundant supporting evidence from closely related groups of fishes (see above), we have strong confidence that structural complexity plays an important role in the evolution of body form and swimming performance—the nature of which is quite predictable.

Water flow

Fish inhabit environments greatly varying in the intensity of water movement, such as ponds, lakes, backwaters, calm tidal pools, stream riffles, rapid rivers, and wave-swept near-surface ocean waters. While fish virtually always contend with competing demands for steady and unsteady swimming performance, we hypothesize that this balance will swing toward favoring steady swimming in high-flow environments—where fish must constantly swim to maintain position and perform routine tasks under arduous conditions—but unsteady swimming in low-flow environments—where fish are largely freed from the severe demands on endurance and can instead exploit strategies requiring high acceleration or maneuverability. Thus, we predict greater streamlining and a higher caudal fin aspect ratio in fish found in high-flow habitats compared to fish inhabiting less-flowing waters. This general prediction has been outlined numerous times in the past (e.g., Blake, 1983, 2004; Webb, 1984; Videler, 1993; Vogel, 1994; Boily and Magnan, 2002), and empirical support for water-flow's role in fish evolution is non-trivial (e.g., Hubbs, 1941; Swain and Holtby, 1989; Claytor *et al.*, 1991; McLaughlin and Grant, 1994; Hendry *et al.*, 2000, 2006; Pakkasmaa and Piironen, 2000; Brinsmead and Fox, 2002; Imre *et al.*, 2002; Langerhans *et al.*, 2003, 2007a; McGuigan *et al.*, 2003; Neat *et al.*, 2003; Collyer *et al.*, 2005; Sidlauskas *et al.*, 2006; Zúñiga-Vega *et al.*, 2007). Let us briefly review the existing evidence to assess the degree to which evolution across flow regimes is predictable.

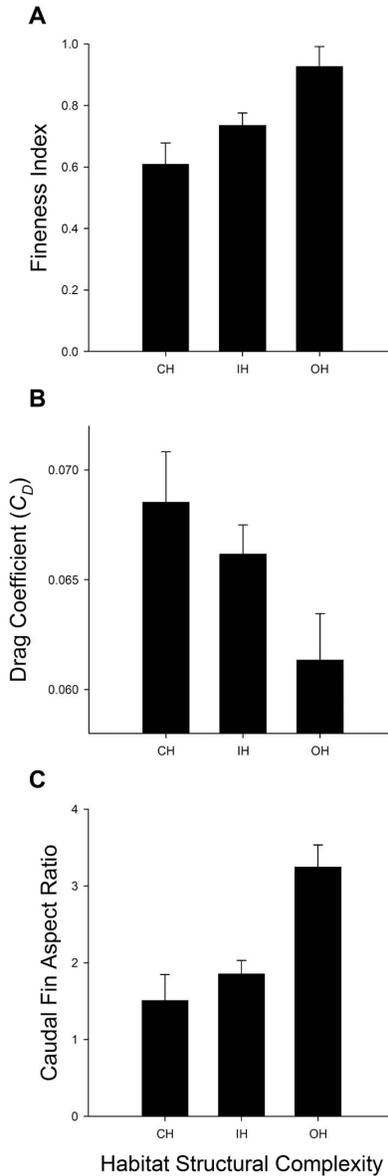


Fig. 7.6 Association between morphology and habitat structural complexity for 32 fish species spanning 11 orders. **(A)** Species inhabiting more open environments exhibit fineness index values closer to 1 (i.e., fineness ratios closer to the optimum of 4.5). **(B)** Drag coefficient per volume (estimated from fineness ratios, following Hoerner, 1965) tends to be lower for species inhabiting more open habitats. **(C)** Species in more open environments exhibit higher caudal fin aspect ratios. Least-squares means \pm 1 S.E. are presented. CH = complex habitat, IH = intermediate habitat, OH = open habitat.

Examples of flow-driven phenotypic differentiation come from diverse groups of fishes—including characids, cichlids, cyprinids, salmonids, and poeciliids—and from numerous biogeographic regions—including all continents but Antarctica. For instance, in South American tropical systems, recent work has revealed intraspecific morphological variation within several species (Family Characidae: *Bryconops caudomaculatus*, *Bryconops* sp. cf. *melanurus*; Family Cichlidae: *Biotodoma wavrini*, *Cichla temensis*); in each case, a more streamlined body is evident in populations experiencing greater water flow (Langerhans *et al.*, 2003; Sidlauskas *et al.*, 2006; R.B. Langerhans unpubl. data). In rainforest streams of East Africa, *Barbus neumayeri* (Family Cyprinidae) populations experiencing higher water velocity exhibit both more fusiform bodies and higher aspect-ratio caudal fins (Langerhans *et al.*, 2007a). In central North America, recent work has revealed that *Cyprinella lutrensis* (red shiner, Family Cyprinidae) populations inhabiting fast-flowing inlet rivers exhibit more streamlined bodies than their dammed, non-flowing reservoir counterparts (R.A. Blaine and K.B. Gido, unpubl. data). In Canadian watersheds, two sunfish species (Family Centrarchidae), *L. gibbosus* (pumpkinseed) and *Ambloplites rupestris* (rock bass), exhibit more slender bodies in streams compared to conspecific populations inhabiting adjacent lakes (Brinsmead and Fox, 2002).

As these examples illustrate, a general pattern of increased streamlining for fish experiencing higher flow regimes is evident from the literature, however there are a number of cases that do not directly correspond to predictions. While some of these cases can be explained by species' natural histories (e.g., fish may not actually spend much time in the current, or other behaviors may diminish the predicted selective effects of water flow), others simply point to our lack of a complete understanding in this regard (e.g., McGuigan *et al.*, 2003; Neat *et al.*, 2003; Hendry *et al.*, 2006). Further, much fewer studies have used comparative data to test for greater caudal fin aspect ratio in higher-flow environments, although a number of studies have demonstrated taller caudal fins in such habitats (likely reflecting higher aspect ratios; e.g., Beacham *et al.*, 1989; Imre *et al.*, 2002; Peres-Neto and Magnan, 2004). Overall, velocity's effects on morphology appear to often, but not always, match our predictions based on divergent natural selection on swimming abilities.

Much of this empirical work has centered on intraspecific differentiation, at least some of which likely represents phenotypic plasticity. For instance, McLaughlin and Grant (1994) demonstrated a pattern in the field where brook charr (*Salvelinus fontinalis*; Family Salmonidae) exhibit more streamlined bodies and higher caudal fin heights (presumably resulting in higher caudal fin aspect ratio) in populations experiencing higher water velocity. Later, Imre *et al.* (2002) demonstrated that the observed differences in caudal fin height, but not body depth, could be due to phenotypic plasticity. Granted

that the evolution of inducible adaptive phenotypes in alternative flow environments is impressive in its own right, we would also like to know whether evolutionary divergence between flow regimes is common and predictable. Thus, we will provide a new test of this hypothesis using comparative data across multiple congeneric species for which morphological differences have been shown to have a genetic basis (e.g., Hubbs and Springer, 1957; Greenfield *et al.*, 1982; Greenfield, 1983; Greenfield and Wildrick, 1984; Greenfield, 1985; Langerhans *et al.*, 2004, 2005; R.B. Langerhans unpubl. data).

A new test in *Gambusia* fishes

Of the approximately 50 species in the livebearing fish genus *Gambusia* (mosquitofishes; Family Poeciliidae), 15 can be readily classified as either inhabiting primarily low- or high-flow environments. We measured FR, C_D (calculated from FR; as described above), and lateral body shape for five adult males from each of 12 of these *Gambusia* species, ranging from Texas, Central America, the Caribbean, and southern Florida (see *Appendix 1* for species included and source of specimens). Species were classified to flow regime according to published accounts and museum records for all species (e.g., Hubbs, 1929; Hubbs and Springer, 1957; Rosen and Bailey, 1963; Hubbs and Peden, 1969; Miller and Minckley, 1970; Fink, 1971; Peden, 1973; Miller, 1975; Brune, 1981; Greenfield *et al.*, 1982; Rauchenberger, 1989; de León *et al.*, 2005; Tobler *et al.*, 2006), personal communications for three species (pers. comm. O. Dominguez, C. Hubbs), and personal observations (R.B.L.) for five species. The low-flow species inhabit lakes, ponds, tidal shores and pools, and slow-flowing springheads. The high-flow species inhabit rivers, streams, and fast-flowing spring runs. Although *Gambusia* species tend to seek slower-flowing microhabitats even within generally fast-flowing environments (with a few exceptions), the species included in the “high-flow” category must still regularly negotiate considerably stronger water velocities than the species included in the “low-flow” category which only rarely experience measurable flow.

To quantify lateral body shape, we digitized 10 landmarks (see Fig. 7.7b) on digital images of each specimen using tpsDig (Rohlf, 2006), and used geometric morphometric methods to examine morphological variation (Rohlf and Marcus, 1993; Marcus *et al.*, 1996; Zelditch *et al.*, 2004). For further description of landmarks and methods, see text and figures in Langerhans *et al.* (2004), Langerhans and DeWitt (2004), and Langerhans *et al.* (2007b). We used tpsRelw software (Rohlf, 2005) to obtain shape variables (relative warps) for analysis. Relative warps are principal components of geometric shape information. We visualized variation in landmark positions using the thin-plate spline approach, which maps deformations in shape from one object to another (Bookstein, 1991).

We calculated species averages for fineness ratio, drag coefficient, and relative warps using least-squares means from an ANCOVA with log standard length as the covariate (larger individuals tended to have deeper bodies) and species as the main effect (slopes were homogeneous)—i.e., we used size-adjusted trait values. We then conducted both standard and phylogenetic ANOVAs following methods described above, testing for differences in traits between species in low- and high-flow environments. Phylogenetic information was based on molecular and morphological data (Rivas, 1963; Rosen and Bailey, 1963; Rauchenberger, 1989; Lydeard *et al.*, 1995a; b; R.B. Langerhans, M.E. Gifford, O. Dominguez, I. Doadrio unpubl. data), and represents the best current phylogenetic hypothesis for these taxa (Fig. A2 in *Appendix*). All branch lengths were set equal to one.

We found that *Gambusia* species inhabiting higher velocity environments tended to exhibit FR values closer to the optimum of 4.5 ($F_{1,10} = 2.82$, one-tailed $P_{\text{raw}} = 0.062$, one-tailed $P_{\text{phy}} = 0.039$; Fig. 7.7a), and thus lower drag coefficients ($F_{1,10} = 5.48$, one-tailed $P_{\text{raw}} = 0.021$, one-tailed $P_{\text{phy}} = 0.010$)—matching *a priori* predictions. When examining overall body shape, we found significant differences between flow regimes for the first relative warp (RW 1; $F_{1,10} = 3.48$, one-tailed $P_{\text{raw}} = 0.046$, one-tailed $P_{\text{phy}} = 0.028$), but not for other relative warps. RW 1 (explaining 49.95% of shape variation) was highly correlated with FR among species ($r = 0.78$, $P = 0.003$), however it also provided some additional morphological information (Fig. 7.7b). RW 1 results revealed that not only do high-flow species tend to be more slender, but they also differ in their location of maximum depth, which is more anteriorly positioned in higher-velocity environments. Further, much of the shape differences involve the caudal peduncle, where species in high-flow environments have longer and shallower caudal peduncles than those in low-flow habitats. All of these differences suggest that *Gambusia* species inhabiting high-flow environments exhibit increased streamlining compared to low-flow species. Combined with previous work discussed above, it seems that water velocity generally plays an important role in the phenotypic evolution of fishes.

Predation

For our final prediction, we will evaluate the role of predation in driving morphological and locomotor evolution in fishes. The strong role of predation in shaping phenotypic evolution in many, diverse taxa is undisputed (reviewed in Edmunds, 1974; Greene, 1988; Caro, 2005; Vamosi, 2005; Langerhans, 2006). Like most organisms, fishes inhabit environments that vary in predation intensity across time and space. Multiple types of selection might differ between predator regimes, but here we focus on one specific prediction: natural selection should favor steady swimming performance in environments with a low level of predation, but instead

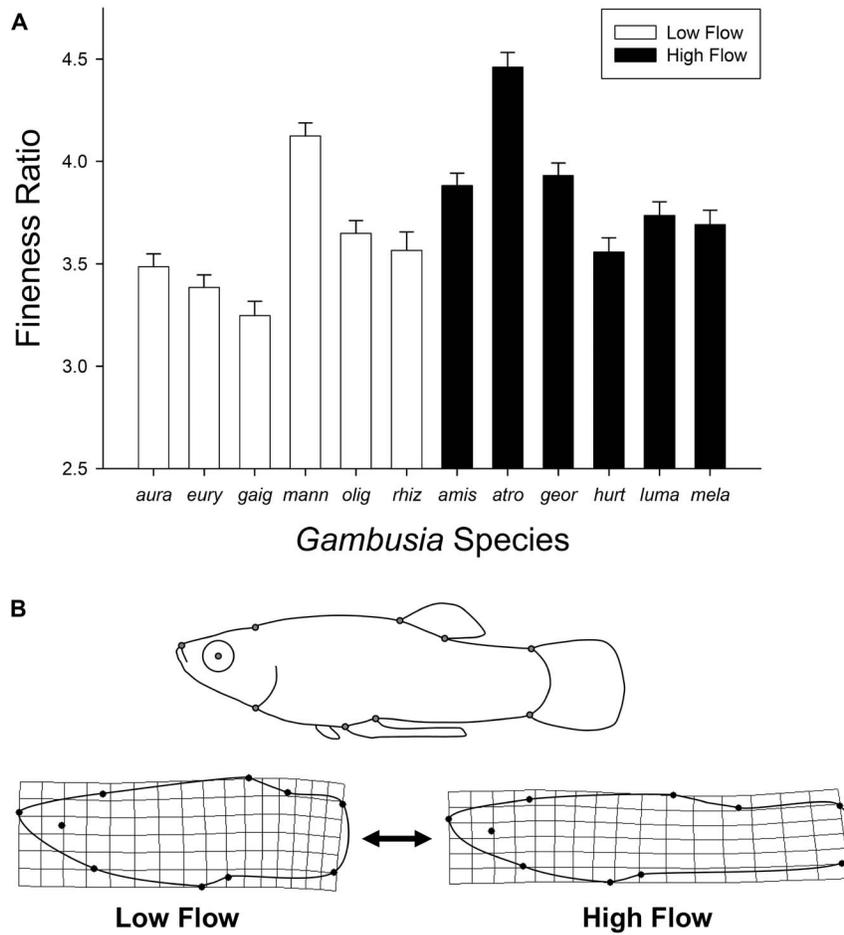


Fig. 7.7 *Gambusia* species inhabiting environments with a greater magnitude of water flow tend to exhibit more streamlined bodies. **(A)** Species in high-flow environments have fineness ratios closer to the optimum of 4.5. Values represent least-squares means \pm 1 S.E. from an analysis of covariance with log standard length as the covariate and species as the main effect (slopes were homogeneous). Species labels are from left to right: *G. aurata*, *G. eurystoma*, *G. gaigei*, *G. manni*, *G. oligosticta*, *G. rhizophorae*, *G. amistadensis*, *G. atrora*, *G. georgei*, *G. hurtadoi*, *G. luma*, and *G. melapleura*. **(B)** Landmarks used in the examination of lateral body shape (upper panel) and thin-plate spline transformation grids illustrating the nature of morphological differences between flow regimes as described by the first relative warp (lower panel; magnified 2 \times). Solid lines connecting outer landmarks are drawn to aid interpretation.

favor unsteady swimming abilities in high-predation environments. This prediction stems from ecological knowledge of prey populations inhabiting divergent predator regimes.

First, fitness should largely depend on competitive interactions in low-predation environments (e.g., low extrinsic mortality, high population density). Because steady swimming is used during most competitive activities (see *Formulating Evolutionary Predictions*), selection should favor enhanced steady swimming performance in low-predation environments (i.e., obtain and consume food more quickly, acquire mates more effectively, contain greater energy supplies for reproduction) (e.g., Vogel, 1994; Plaut, 2001; Roff, 2002; Domenici, 2003; Blake, 2004). Second, escape ability should be of paramount importance in high-predation environments. Because unsteady swimming activities, such as fast-starts and rapid turns, are highly important in escaping predation, fish with greater unsteady swimming performance should possess higher fitness in high-predation environments (e.g., Howland, 1974; Webb, 1986b; Domenici and Blake, 1997; Walker, 1997; Langerhans *et al.*, 2004; Walker *et al.*, 2005; Domenici Chapter 5 in this book). Third, predator regime can influence prey habitat use by altering the structural complexity of the environment experienced by prey—a factor already shown to affect fish evolution (see *Structural complexity*). This fact can reinforce divergent selection on steady and unsteady swimming performance between predator regimes. This is because many fishes utilize more open-water habitats in low-predation environments compared to high-predation environments, where fish are often restricted to complex habitats, such as the littoral zone, as a behavioral mechanism reducing predatory encounters (e.g., Horwood and Cushing, 1977; Stein, 1979; Mittelbach, 1981; Werner *et al.*, 1983; Tonn *et al.*, 1992; Winkelman and Aho, 1993; Eklov and Persson, 1996). Thus, as a combination of differences in competition, necessity of escape ability, and structural complexity, selection is predicted to favor alternative swimming modes in low- and high-predation environments.

Based on our understanding of how morphology influences swimming performance, we can make general predictions for morphological evolution in divergent predator regimes. We expect fish to evolve (or evolve the ability to developmentally induce) a less streamlined body with greater posterior allocation (i.e., shallower/smaller heads, deeper/larger caudal region, including median fins) and a larger, lower aspect-ratio caudal fin in high-predation environments compared to those inhabiting low-predation environments. These predictions derive from biomechanical predictions described above for enhancement of steady swimming performance in low-predation environments and enhancement of fast-start performance in high-predation environments via accentuation of thrust-producing regions and minimization of drag-producing regions. Here we review the existing

evidence for this hypothesis. Because this prediction was only recently explicitly proposed (Walker, 1997; Langerhans *et al.*, 2004, 2007b), there are still relatively few studies which specifically test this hypothesis. However, as we reveal, there is a fair quantity of relevant work amassing. We will primarily focus our review on studies using comparisons among low- and high-predation environments defined by densities of piscivorous fish (often, presence vs. absence), as predictions are most clear for these interactions—and because most studies to date have involved predatory fish. However, note that other types of predators (e.g., invertebrates, snakes, birds) may be important in some systems, and may or may not generate similar selective pressures.

During the past decade, a number of examples of predator-associated morphological divergence have accumulated. All cases involve intraspecific differentiation between populations, and thus provide a set of comparisons that should be capable of establishing mechanistic relationships (e.g., presence of predators caused phenotypic changes in prey). Threespine stickleback (*G. aculeatus*) in the Cook Inlet region of Alaska, USA inhabit postglacial lakes differing in the presence of predatory fish. In the presence of predators, stickleback populations exhibit a relatively smaller head and larger median fin lengths compared with conspecific populations in lakes without predatory fish (Fig. 8A; Walker, 1997; Walker and Bell, 2000). In East African lakes, introduction of Nile perch (*Lates niloticus*)—a highly piscivorous fish—has led to subsequent morphological changes in multiple native fishes. For both a cichlid (*Pseudocrenilabrus multicolor*) and a cyprinid (*Rastrineobola argentea*), a posterior shift in body depth is apparent in the presence of the predator (R.B. Langerhans, L.J. Chapman, and T.J. DeWitt unpubl. data). These results were obtained using either temporal comparisons within lakes (before and after introductions) or contemporary comparisons among lakes with and without Nile perch. Perhaps the best case studies to date come from four species of poeciliid fishes (*Brachyrhaphis rhabdophora*, *G. affinis*, *G. hubbsi*, *Poecilia reticulata*), as these systems have the most thorough set of evidence relevant to the hypothesis at hand (Table 7.1). Here we will briefly review this evidence.

For all four of these species, conspecific populations inhabit environments differing in the presence of predatory fish. Table 7.1 summarizes the relevant results for these four species. In sum, there is strong evidence for predator-driven evolution in these fishes. In all cases, high-predation fish exhibit larger caudal regions than low-predation fish (see Fig. 7.8b for results in *G. affinis*). Moreover, differences in swimming performance match predictions in all tests to date, fitness advantages have been documented in two species, a genetic basis to phenotypic differences have been confirmed for three species, and molecular evidence suggests multiple events of predictable phenotypic evolution within three species

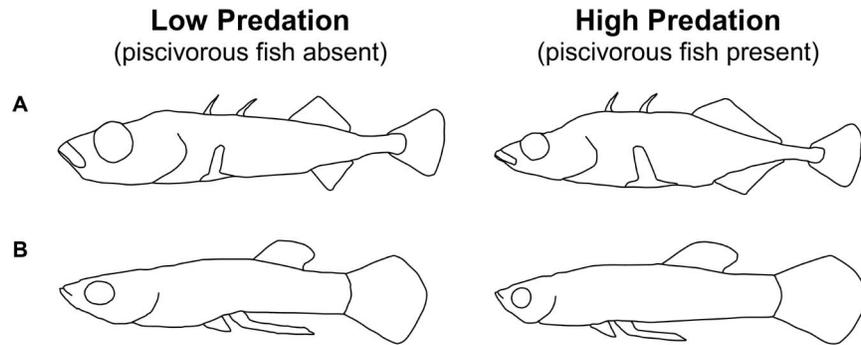


Fig. 7.8 Illustration of morphological differences between populations inhabiting low- and high-predation environments within two distantly related fish species. Note the smaller anterior/head region and larger caudal region in populations coexisting with predatory fish. Figures represent results of thin-plate spline deformations from the grand mean in each species, and are magnified 2x to aid visualization. **(A)** Threespine stickleback, *Gasterosteus aculeatus*, from 40 lakes in Alaska, USA (data from Walker and Bell, 2000). **(B)** Western mosquitofish, *Gambusia affinis*, from six ponds in Texas, USA (data from Langerhans *et al.*, 2004).

(Table 7.1). Further, in both *G. affinis* and *G. hubbsi*, fish with larger caudal regions—irrespective of population of origin—are faster (Langerhans *et al.*, 2004; R.B. Langerhans unpubl. data), and in both *G. hubbsi* and *P. reticulata*, faster fish—irrespective of population of origin—exhibit higher survival with predators (Walker *et al.*, 2005; R.B. Langerhans unpubl. data). Additionally, more streamlined fish (like those found in low-predation populations) exhibit higher steady swimming abilities in *G. affinis* (R.B. Langerhans unpubl. data; see Fig. 5). Thus, our assumptions concerning the links between morphology, performance, and fitness have at least been partially confirmed for these livebearing fishes. While confounding variables do exist in some cases here (e.g., ponds and streams with predators tend to be larger and have higher productivity), at least for one species (*G. hubbsi*) these variables have been kept to a minimum. This is because *G. hubbsi* inhabit isolated blue holes (vertical solution caves) which are highly similar in most abiotic parameters other than predator regime (Langerhans *et al.*, 2007b), yielding a very strong test of the hypothesis.

While in some cases these differences are known to have a genetic basis (see Table 7.1), phenotypic plasticity has also been demonstrated in several cases (e.g., Brönmark and Miner, 1992; Andersson *et al.*, 2006; Eklov and Jonsson, 2007; Januszkiewicz and Robinson, 2007). So, divergent selection across predator regimes has apparently resulted in both the evolution of adaptive plasticity and local adaptation. For most cases, it is perhaps most likely that morphological differences reflect both plastic changes as well as genetic differentiation. Whether or not such intraspecific divergence translates into macroevolutionary patterns has not yet been revealed.

Table 7.1 Summary of predator-driven adaptive divergence within four livebearing fish species (Family Poeciliidae). Temporal persistence of differences are evident when results are consistent across multiple years of examination. Swimming performance refers to confirmation of predicted differences in either steady (S) or unsteady (U) swimming. Fitness advantages refer to elevated fitness of native fish over fish transplanted from the alternative predator regime, and can be tested within either low-predation (LP) or high-predation (HP) environments. Genetic basis refers to persistent differences in morphology, performance, fitness or some combination thereof in lab-born fish raised in a common environment for one (F1) or two generations (F2). Multiple origins refers to molecular evidence suggesting replicated trait evolution.

Species	Geographic Region	Populations Examined	Larger Caudal Region	Temporal Persistence	Swimming Performance	Fitness Advantage	Genetic Basis	Multiple Origins	References
<i>Brachyraphis rhabdophora</i>	Costa Rica	6	Y	NA	NA	NA	NA	Y	1,2
<i>Gambusia affinis</i>	Texas, USA	6	Y	Y	S, U	NA	F1, F2	NA	1,3,4
<i>Gambusia hubbsi</i>	Bahamas	12	Y	Y	U	HP	F1	Y	5,6
<i>Poecilia reticulata</i>	Trinidad	23	Y	Y	U	HP	F2	Y	1,7-12

Note: All *P. reticulata* populations from the Paria drainage were treated as a single unit of replication here because there are no high-predation localities within the entire drainage. Y = yes, N = no, NA = no data available. References: 1: Langerhans and DeWitt (2004), 2: Johnson (2001), 3: Langerhans *et al.* (2004), 4: R.B. Langerhans unpubl. data; 5: Langerhans *et al.* (2007b), 6: R.B. Langerhans unpubl. data; 7: Hendry *et al.* (2006), 8: Ghalambor *et al.* (2004), 9: Walker *et al.* (2005), 10: Carvalho *et al.* (1991), 11: Fajen and Breden (1992), 12: O'Steen *et al.* (2002).

However, evidence for ecological speciation as a by-product of divergent natural selection between predator regimes has recently been described for *Gambusia* fishes (Langerhans *et al.*, 2007b). Further, ongoing work is revealing that interspecific morphological divergence mirrors intraspecific divergence in the genus *Gambusia* (R.B. Langerhans unpubl. data), suggesting that predator-driven divergence can produce broader macroevolutionary patterns.

Unfortunately, no studies to date have examined predation's influence on caudal fin aspect ratio. However, our *a priori* predictions for body shape have been upheld in numerous empirical tests. Considering the predictions have been observed in distantly related species inhabiting different habitat types (e.g., ponds, lakes, streams) in widely distant geographic regions (e.g., Alaska, Bahamas, East Africa), we have fairly strong evidence that predation can drive predictable evolution (see Fig. 7.8). Yet for some species, researchers have made different predictions, such as increased defensive plates or spines and maximum body depth in environments with higher predation intensity (rather than a posterior shift in body depth as we predict here). This is because some species might be expected to enhance post-capture survival via increased handling time or even complete gape limitation. This prediction has been confirmed in multiple systems (e.g., Brönmark and Miner, 1992; Reimchen, 1994, 1995, 2000; Walker, 1997; Reimchen and Nosil, 2004; Eklov and Jonsson, 2007; Januszkiewicz and Robinson, 2007). Whether these morphological differences also entail a posterior shift in depth or increased fast-start performance is unknown in most cases. Moreover, when we might expect enhanced capture deterrence (i.e., fast-start escapes) versus consumption deterrence (i.e., post-capture survival) is often not clear in nature, and how these two selective forces might interact is also less than obvious. For instance, deeper bodies—which can gape limit some predators—might sometimes enhance maneuverability or fast-start performance. Thus, it may be possible for fish to evolve morphologies that simultaneously increase both handling time and unsteady swimming performance. Recent work in crucian carp (*Carassius carassius*) supports this proposition. Crucian carp are known to induce deeper bodies in the presence of pike (*Esox lucius*) predators; a phenotypic shift which reduces predation risk by increasing handling time of gape-limited piscivores (Brönmark and Miner, 1992; Brönmark and Pettersson, 1994; Nilsson *et al.*, 1995). Domenici *et al.* (2008) demonstrated that these deeper-bodied carp also produce higher velocity, acceleration, and turning rates during fast-start escapes than shallow-bodied individuals, suggesting that predator-induced crucian carp exhibit reduced vulnerability to predation for multiple reasons. Yet sometimes, defensive traits might incur costs associated with escape locomotor performance. For instance, a negative effect of defensive armor on fast-start performance has been observed in some fishes (Taylor and McPhail, 1986;

Andraso and Barron, 1995; Andraso, 1997; Bergstrom, 2002), suggesting a possible conflict between the evolution of armor and swimming performance in high-predation environments. More work is needed to better understand the integrated roles of these various defensive strategies.

Reproduction and diet

Reznick and Travis (1996) argued that adaptation is not simply optimizing some feature of an organism with regard to some feature of the environment. Natural selection acts on whole-organism performance. As a consequence, individual adaptations often represent a compromise among multiple types of selection and multiple competing internal features of an organism (see Fig. 7.1). Thus, the way any organism adapts to its environment should represent an integration of all of these external and internal factors. Up until now, we have focused on the role of body shape in determining swimming performance, and then on a few major environmental gradients where we might be capable of predicting evolution of performance and hence shape: structural complexity, water flow, and predation. Because of the strong relationship between shape and performance, we argue that any other feature of a fish's biology that influences shape will potentially be integrated with selection on swimming performance. While a number of factors might influence body shape in addition to direct selection on locomotor performance (e.g., sexual selection, selection for gape limitation, minimizing detection by prey via reduction of body profile), we focus here on two internal factors that might often alter shape and hence affect performance: reproduction and diet. There is not, at the present time, any experimental system that considers how the evolution of swimming performance represents a balance among all of these potentially competing functions. There is, however, sufficient characterization of enough pieces of this puzzle for us to argue that such an integrated study of the evolution of performance is justified.

The organ systems supporting both reproduction and digestion occupy the body cavity, and the size of each system can influence the shape and flexibility of a fish. Because swimming performance is influenced by shape and flexibility, the joint volume of the gut and gonads can influence performance. So an adaptation that causes an increase in the volume of either organ system can influence the evolution of the other organ system and/or the evolution of locomotor ability. Consequently, we can make the general prediction that increased volume in these organ systems will impair locomotion (see below). Thus, selection favoring larger gut or reproductive systems might constrain the evolution of swimming performance. We will begin assessing this prediction by examining the links between reproduction, body shape, and swimming performance. Then we will discuss similar

relationships for diet—however, because few studies to date have directly assessed associations between diet, body shape, and locomotor ability, we can only briefly review and speculate about diet's potential significance in the evolution of swimming performance.

One obvious scenario where the reproductive system might have large effects on body shape in fishes is in the case of livebearers. This is because female livebearers not only carry eggs, but actually carry developing embryos which can sometimes be of considerable size or number. During pregnancy, a female's body shape can be significantly altered. In most livebearers in the family Poeciliidae, females carrying late term embryos are visibly robust and easily distinguished from non-pregnant females or females with young in early stages of development (Fig. 7.9a). Here we quantify this effect in pregnant females by presenting new data from our ongoing work in the livebearing fish genus *Gambusia*, establishing a relationship between reproduction and body shape.

We measured average embryo weight and fineness ratio (FR) of pregnant females for four *Gambusia* species (see *Appendix 2* for species included and source of specimens). To test whether each species exhibited a similar relationship between FR and embryo weight, we conducted an analysis of covariance with FR as the dependent variable, species as the main effect, and natural-log transformed mean embryo weight as the covariate. We found a significantly negative relationship between FR and mean embryo weight ($F_{3,66} = 16.46$, $P = 0.0001$; Fig. 7.9b)—a trend which did not significantly differ among species (interaction term: $F_{3,66} = 1.22$, $P = 0.309$). Thus, female *Gambusia* carrying larger embryos tend to exhibit deeper (less streamlined) bodies. Because we have already shown that body shape is well correlated with performance and have now shown that intraspecific variation in life histories can influence body shape, it is logical to propose that the evolution of life histories can have a collateral impact on the evolution of swimming performance.

To date, the most thorough examination of the relationship between life history and performance has been conducted using natural populations of guppies (Ghalambor *et al.*, 2004). Guppies (*P. reticulata*) reproduce continuously after attaining maturity, so mature females are almost always found with a brood of developing young. The quantity of tissue devoted to developing young can be quite large relative to their body sizes, with the dry mass of developing young sometimes exceeding 20% of the total dry mass of the female. The wet mass and volume of the young increases between 3.5 and 4 fold between the fertilization of the egg and birth because of a substantial increase in the water content of the embryos (Ghalambor *et al.*, 2004). This means that the reproductive burden increases throughout development (e.g., see Fig. 7.9b for effects on body depth). Such dramatic changes associated with pregnancy might impact swimming performance

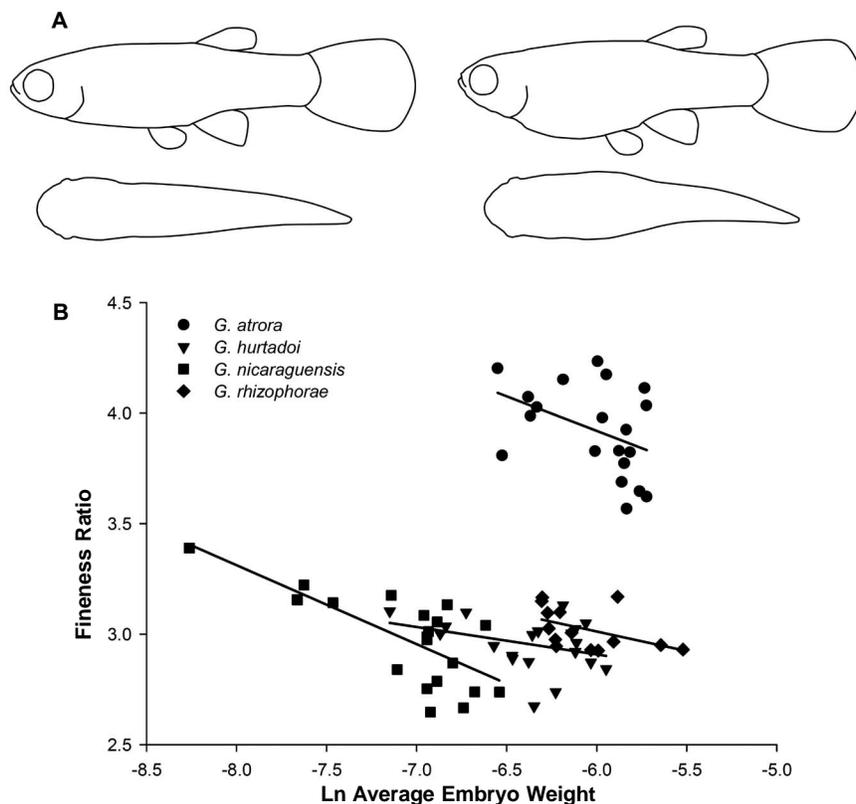


Fig. 7.9 Effects of pregnancy on body shape in poeciliid fish. **(A)** Lateral (top) and dorsal (bottom) illustrations of morphological differences between non-pregnant (left) and pregnant (right) female guppies (*P. reticulata*). Outlines are based on photographs of the same individual from the Oropuche drainage in Trinidad taken 1-day before parturition (right) and 1-day after parturition (left) (i.e., photographs were taken two days apart; photographs taken by C. Ghalambor). **(B)** *Gambusia* females carrying larger embryos exhibit lower fineness ratios (i.e., deeper bodies relative to their length). Slopes do not significantly differ among species ($P = 0.31$).

for a number of reasons (e.g., Plaut, 2002, see below). In guppies, selection on both reproductive allocation and swimming performance is predicted to differ between predator regimes. Evolving adaptations in response to either selective pressure might conflict with one another. We will assess the integrated role of reproductive traits in the evolution of swimming performance within this context.

As discussed above (see *Predation*), guppies on the island of Trinidad are found in communities that differ in the risk of predation. High-predation communities are found in the lower portions of streams, where guppies co-occur with predatory fishes. Low-predation communities are found in the

same drainages but above barrier waterfalls that exclude most piscivorous fish (Endler, 1978). Mark-recapture studies have shown that guppies in high-predation environments experience consistently higher mortality rates (Reznick *et al.*, 1996a; Reznick and Bryant, 2007). A guppy from a low-predation environment has a 20 to 30 fold higher probability of surviving for seven months than its counterpart from a high-predation environment (Reznick and Bryant, 2007). Life history theory predicts that the higher mortality rates that guppies experience in high predation environments will favor the evolution of earlier ages at maturity and an increase in the rate at which resources are allocated to reproduction (Charlesworth, 1994). Both of these changes will increase the rate of production of offspring early in life. These predictions are upheld in nature; high-predation guppies are significantly younger and smaller at sexual maturity, produce more offspring per litter, and have larger reproductive allocations (percent of total dry mass that consists of developing offspring) than low-predation guppies. These differences have been observed using comparisons of guppies from natural high- and low-predation environments (Reznick, 1982; Reznick and Endler, 1982; Reznick and Bryga, 1996; Reznick *et al.*, 1996b), as well as using experiments in which guppies were transplanted from high- to low-predation environments (Reznick and Bryga, 1987; Reznick *et al.*, 1990, 1997). This study system thus represents one of the rare occasions where it has been possible to experimentally test predictions derived from evolutionary theory in a natural setting.

Because selection is predicted to favor increased fast-start swimming performance in high-predation environments (see *Predation*), there could be a conflict between the way guppy life histories evolve and the way their swimming performance evolves in response to predation. For instance, the higher reproductive allocations seen in high-predation guppies means that at any stage of development, a guppy from a high-predation environment is carrying a reproductive burden that is 40% larger on average than a guppy from a low-predation environment (Ghalambor *et al.*, 2004). While predators favor the evolution of higher reproductive allocation, increasing the volume of reproductive tissues should have a concomitant impact on swimming performance for four reasons: (1) any increase in non-muscle mass associated with a larger ovary is expected to cause increased resistance to acceleration, (2) increased volume associated with a larger ovary can increase flexural stiffness and hence limit axial bending during acceleration (Beamish, 1978; James and Johnston, 1998), (3) any increase in surface and cross-sectional area caused by an enlarged ovary could increase drag (Beamish, 1978; Plaut, 2002), and (4) energy allocated to eggs and developing embryos could reduce the contractile properties of muscles and reduce power output (James and Johnston, 1998). For all of these reasons, selection by predators for increased allocation to reproduction could

indirectly alter locomotor abilities, perhaps reducing performance at critical tasks, such as fast-start escapes. Or on the flip side, selection by predators for increased fast-start performance might constrain the evolution of increased reproductive allocation. The question is then whether or not we see evidence for an interaction between the evolution of life histories and the evolution of swimming performance.

Three alternative hypotheses exist (Fig. 7.10). First, high-predation guppies may be faster than low-predation guppies, with no effect of reproduction on performance (Fig. 7.10a). Second, reproduction might impair locomotion, but the impairment is the same for guppies from high- and low-predation communities. Because the mass of developing young increases throughout pregnancy, this impairment is expected to increase throughout pregnancy, and thus performance should progressively decline. The consequence is that high-predation guppies retain their superior fast-start performance regardless of where they are in the reproductive cycle (Fig. 7.10b). Third, guppies from high-predation environments might sustain a higher cost of reproduction than those from low-predation environments. In this case, high-predation guppies should experience a more rapid decline in fast-start performance as their litter progresses through development (Fig. 7.10c). These hypotheses were tested by evaluating performance in female guppies that were the second generation lab-born descendents of wild-caught females from four localities (two paired sets of high- and low-predation populations) (Ghalambor *et al.*, 2004). Rearing fish in a controlled environment for two generations means that any differences that are seen between populations can be interpreted as genetic differences, rather than a product of the environment in which they were reared.

Guppies from high-predation environments exhibit higher fast-start performance than those from low-predation environments: higher maximum acceleration, higher maximum velocity, and travel a greater distance during the 22 ms assessment period (Fig. 7.11). There is also a cost of reproduction, manifested in the maximum velocity and distance traveled. Females that were more advanced in their reproductive cycle attained a lower maximum velocity and shorter distance traveled; however, there was no effect of reproductive status on maximum acceleration (Fig. 7.11). There was a significant interaction between predation and the rate of decline in performance for maximum velocity and distance traveled; high-predation guppies declined in performance with advancing pregnancy more rapidly than low-predation guppies. Performance differences of this magnitude are known to have a significant affect on the ability of a guppy to survive a real encounter with a predator (Walker *et al.*, 2005).

We conclude that there is indeed evidence for a conflict between life history evolution and the evolution of performance. Guppies from high-predation environments are significantly faster than those from low-

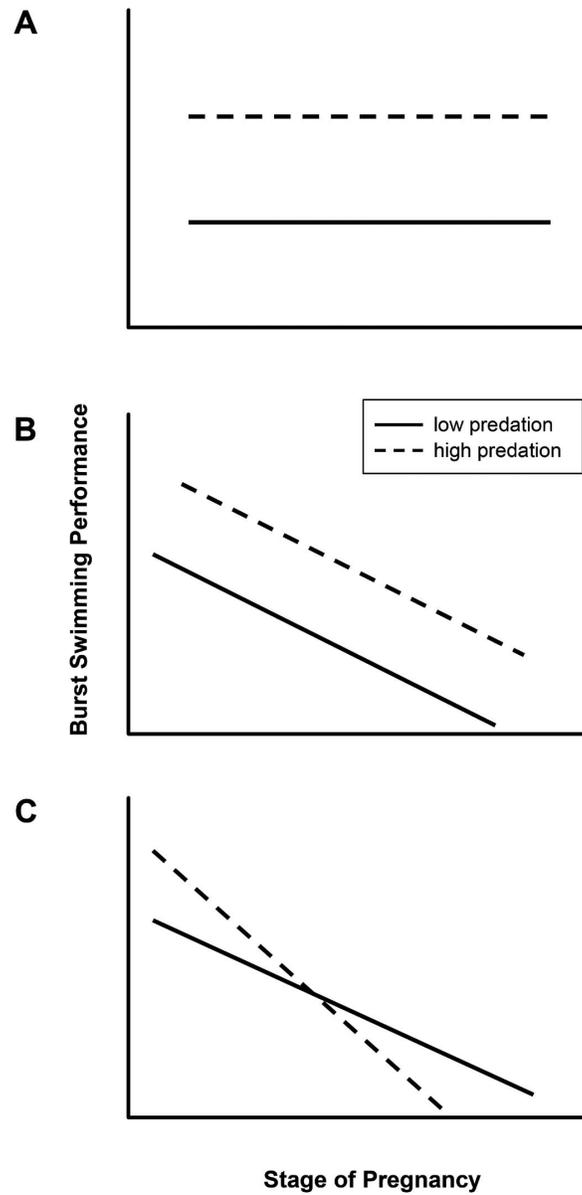


Fig. 7.10 Three alternative outcomes for the effects of predation risk and pregnancy on swimming performance of guppies (*Poecilia reticulata*). **(A)** Fish in high-predation localities exhibit higher burst-swimming performance, with no cost of pregnancy. **(B)** High-predation guppies possess greater burst-swimming performance, and similar costs of pregnancy are experienced by all populations. **(C)** Although predators select for increased performance, a higher cost of pregnancy in high-predation populations (which have larger reproductive allocations) constrains its evolution. Adapted from Ghalambor *et al.* (2004).

predation environments, but they also suffer a higher cost of reproduction. Adaptation to the higher mortality rate that they experience in high-predation environments causes the evolution of a higher rate of offspring production and a larger reproductive allocation, but is accompanied by a more rapid decline in maximum velocity and distance traveled relative to guppies derived from low-predation environments. The high-predation guppies are faster when early in their reproductive cycle, but they lose this advantage and may even be slower when they are in an advanced stage of pregnancy. This statistical interaction thus shows that the evolution of reproductive performance and the evolution of escape performance have constrained one another. Guppies from high-predation environments are not as fast as they could be if selection did not also favor the evolution of higher reproductive allocation and/or they do not allocate as much as energy to reproduction as they might if selection did not also place a premium on being able to escape predators. The end product that we see reflects a compromise between these two components of fitness.

Although effects of reproductive traits on morphology and locomotion might generally be greater for females than males, there is evidence suggesting significant effects exist in males as well. For instance, in some livebearing fish, males possess modified fins utilized for the transfer of sperm (gonopodia). External, non-retractable copulatory organs represent obvious alterations of morphology, and can affect swimming performance. In poeciliids, the gonopodium is an elongate modification of the anal fin, and attains a large size in some taxa (e.g., as long as 70% of the body length; Rosen and Gordon, 1953; Rivas, 1963; Chambers, 1987). In *G. affinis*, males with larger gonopodia experience reduced burst-swimming speeds, presumably caused by drag incurred by the large organ (Langerhans *et al.*, 2005). Consequently, two *Gambusia* species are known to evolve smaller gonopodia in high-predation environments where selection favors increased escape speeds (Langerhans *et al.*, 2005). Thus, reproductive impacts on locomotion should not be neglected in males—it may indeed be commonplace at least for poeciliid fishes.

Diet has a similar potential to influence shape and performance, but there does not seem to have been the same formal analysis of the potential interaction between diet, morphology, and performance as there has been for reproduction. We present here some of what is known about the effects of diet on gut development to build an argument for the potential of such an interaction. First, selection arising from diet and foraging activities often targets jaw features which enhance consumption of particular prey items, but can also influence head size and shape (e.g., Smits *et al.*, 1996; Bouton *et al.*, 2002). Such morphological effects of diet can indirectly affect swimming performance, and thus foraging adaptations might often be intimately tied to locomotor adaptations. Second, efficient digestion of

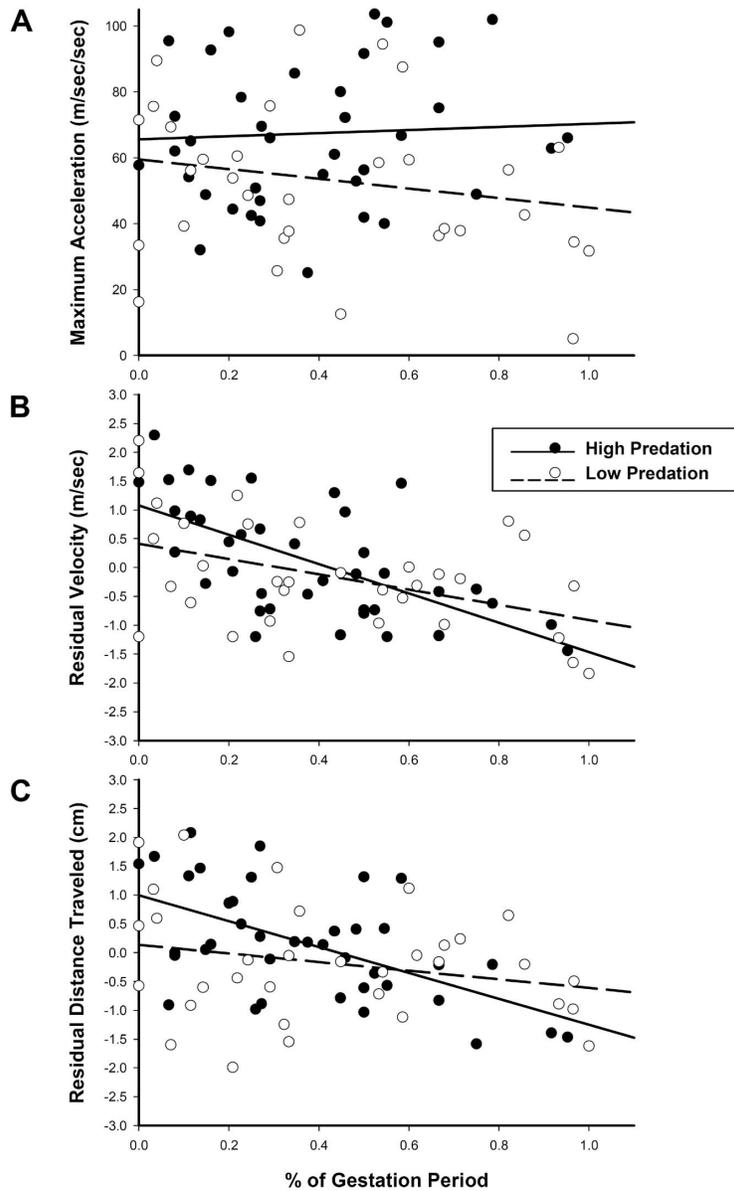


Fig. 7.11 Relationship between pregnancy (expressed as a percentage of the gestation period) and three components of fast-start swimming performance. **(A)** No cost of pregnancy for maximum acceleration. **(B)** Cost of pregnancy for residual maximum velocity (statistically controlling for effects of body mass and number of embryos). **(C)** Cost of pregnancy for residual distance traveled during the fast-start response (controlling for body mass). Adapted from Ghalambor *et al.* (2004).

various prey types often requires differences in gut length, which might influence swimming performance in a manner analogous to reproductive allocation. Kramer and Bryant (1995a; 1995b) quantified the relationship between gut length and diet, including correcting for the effects of body size. They found that there are non-overlapping values for the relative length of guts from carnivores, omnivores and herbivores. Carnivores have the shortest guts, omnivores are intermediate, and herbivores have the longest guts. Differences among diet type can exceed an order of magnitude. We could not find similar figures for the mass or volume of the gut relative to the body, but will assume for the sake of argument that the rank-ordering would be the same. If such differences in diet can have large impacts on gut volume, then it is reasonable to propose that they could impact shape and performance, just as differences in life history apparently do.

The herbivores and carnivores examined in Kramer and Bryant (1995a, b) were often distantly related organisms that differed in so many ways that it would be impossible to perform an unconfounded assessment of the interaction among diet, reproduction, shape and performance. However, similar diversity can be found among closely related species. For example, Kramer and Bryant (1995b) report on data for two poeciliid species: *Poecilia sphenops*, which is an herbivore, and *Brachyrhaphis cascajalensis*, which is an omnivore. These fish have similar body shapes and can be found in similar habitats. *Poecilia sphenops* has a standardized gut length that is more than ten times greater than *B. cascajalensis*. This difference is in part attributable to the larger average body size of *P. sphenops* but it exceeds that expected based on body size by a large margin. Other species in their study that had individuals in both size categories differed in relative gut length by only two to four fold. Such variation among closely related species, or within a species if it occurs, would exceed the volume differences associated with the ovaries of guppies from high- and low-predation localities and hence would be of a magnitude that could clearly cause an interaction among diet, reproduction, and swimming performance as adaptations to the local environment.

In conclusion, existing evidence for the interaction between the evolution of life histories, diet, body shape and swimming performance suggest that the evolution of locomotor ability does not happen independently of other adaptations. All of the factors that have been shown to influence the evolution of shape and performance, including environmental structure, water flow, predation, life histories, and diet, can interact with one another in shaping the response to selection. Using the approach illustrated above with the study on reproduction and performance in guppies, we can begin layering hypotheses on one another to better understand how multiple factors might interact with each another.

CONCLUSIONS

There are undoubtedly a multitude of factors involved in the ecology and evolution of swimming performance in fishes. While uncovering the various mechanisms responsible for the evolution of swimming performance seems quite complicated (and it truly is), it is not a futile endeavor. Here we constructed *a priori* predictions based on our current understanding of the relationships between morphology and swimming performance (built by biomechanical theory and experimental work) and between swimming performance and fitness in alternative environments (based on ecological theory and experimental work). It seems our predictions are fairly robust, as we found strong support in numerous, disparate systems and at several scales of analysis (within species, between closely related species, between distantly related species). Our results emphasize the utility of pinpointing predicted tradeoffs with strong theoretical and empirical support (e.g., between steady and unsteady locomotion), and using those tradeoffs as a starting point to formulate predictions testable with comparative data. We highlighted some selective agents that appear to be of widespread importance in the ecology and evolution of swimming performance in fishes, and pointed to some internal factors (e.g., reproductive allocation, gut length) which deserve greater attention in this regard. A major question remaining is how all these factors might interact with one another to influence locomotor abilities. We argue that increased employment of biomechanics-oriented research could provide key insights into ecological and evolutionary investigations of swimming performance in fishes. Building from the approach taken here, future studies might integrate predictions across multiple selective agents and multiple design features, strengthening our understanding of fish locomotion in its natural, albeit complex, context.

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APPENDIX

1. Sampling for morphology of *Gambusia* males across velocity regimes

Abbreviations—RBL: R. Brian Langerhans personal collection; TNHC: Texas Natural History Collection, University of Texas, Austin; UMMZ: University of Michigan Museum of Zoology.

Specimens—*G. amistadensis*: TNHC 7247; *G. atrora*: TNHC 4570; *G. aurata*: RBL; *G. eurystoma*: UMMZ 184717; *G. gaigei*: TNHC 4213; *G. georgei*: TNHC 7203; *G. hurtadoi*: UMMZ 211112; *G. luma*: UMMZ 190612, UMMZ 197235; *G. manni*: RBL; *G. melapleura*: RBL; *G. oligosticta*: RBL; *G. rhizophorae*: UMMZ 213650.

2. Sampling for morphology and life history of *Gambusia* females

Abbreviations follow Appendix 1.

Specimens—*G. atrora*: UMMZ 169499 (12 pregnant females), 210724 (8 pregnant females); *G. hurtadoi*: UMMZ 211112 (20 pregnant females); *G. nicaraguensis*: UMMZ 199657 (10 pregnant females), UMMZ 199689 (10 pregnant females); *G. rhizophorae*: UMMZ 213650 (10 pregnant females), RBL (4 pregnant females).



Fig. A1 Phylogenetic hypothesis for 32 fish species inhabiting environments of varying structural complexities and belonging to 11 orders (Anguilliformes, Atheriniformes, Clupeiformes, Cypriniformes, Esociformes, Gadiformes, Gasterosteiformes, Osteoglossiformes, Perciformes, Salmoniformes, Scorpaeniformes). Species included in this dataset are identical to the dataset examined in Domenici (2003)—although because of an error in Table 1 of that paper, *Cymatogaster aggregata* was not listed. Open squares = open habitat, dotted squares = intermediate habitat, filled squares = complex habitat.

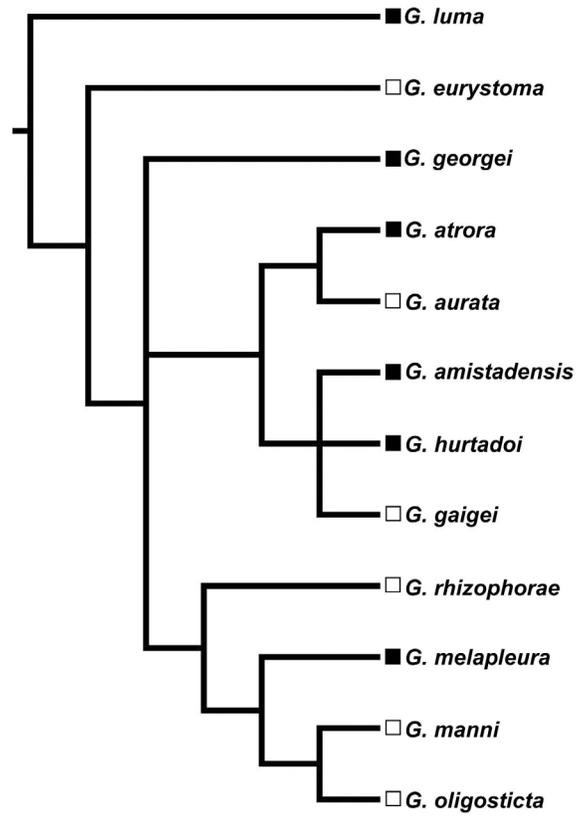


Fig. A2 Phylogenetic hypothesis for 12 *Gambusia* species inhabiting divergent velocity regimes. Open squares = low flow, filled squares = high flow.

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