Predictability of phenotypic differentiation across flow regimes in fishes

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Synopsis Fish inhabit environments greatly varying in intensity of water velocity, and these flow regimes are generally believed to be of major evolutionary significance. To what extent does water flow drive repeatable and predictable phenotypic differentiation? Although many investigators have examined phenotypic variation across flow gradients in fishes, no clear consensus regarding the nature of water velocity's effects on phenotypic diversity has yet emerged. Here, I describe a generalized model that produces testable hypotheses of morphological and locomotor differentiation between flow regimes in fishes. The model combines biomechanical information (describing how fish morphology determines locomotor abilities) with ecological information (describing how locomotor performance influences fitness) to yield predictions of divergent natural selection and phenotypic differentiation between low-flow and high-flow environments. To test the model's predictions of phenotypic differentiation, I synthesized the existing literature and conducted a meta-analysis. Based on results gathered from 80 studies, providing 115 tests of predictions, the model produced some accurate results across both intraspecific and interspecific scales, as differences in body shape, caudal fin shape, and steady-swimming performance strongly matched predictions. These results suggest that water flow drives predictable phenotypic variation in disparate groups of fish based on a common, generalized model, and that microevolutionary processes might often scale up to generate broader, interspecific patterns. However, too few studies have examined differentiation in body stiffness, muscle architecture, or unsteady-swimming performance to draw clear conclusions for those traits. The analysis revealed that, at the intraspecific scale, both genetic divergence and phenotypic plasticity play important roles in phenotypic differentiation across flow regimes, but we do not yet know the relative importance of these two sources of phenotypic variation. Moreover, while major patterns within and between species were predictable, we have little direct evidence regarding the role of water flow in driving speciation or generating broad, macroevolutionary patterns, as too few studies have addressed these topics or conducted analyses within a phylogenetic framework. Thus, flow regime does indeed drive some predictable phenotypic outcomes, but many questions remain unanswered. This study establishes a general model for predicting phenotypic differentiation across flow regimes in fishes, and should help guide future studies in fruitful directions, thereby enhancing our understanding of the predictability of phenotypic variation in nature.

Predicting evolution

As scientists, we seek patterns, and the processes that explain those patterns. Once we understand the processes at work in a given system, we can then predict the system's behavior—at least, to the extent that its behavior is in fact predictable. Evolutionary biologists yearn to understand the general predictability of phenotypic change (Robinson and Wilson 1994; Travisano et al. 1995; Reznick et al. 1997; Losos et al. 1998; Huey et al. 2000; Schluter 2000; Gould 2002; Grant and Grant 2002; Langerhans and DeWitt 2004; Couñago et al. 2006; Langerhans et al. 2006). To what extent does natural selection drive repeatable and predictable evolution in nature? One approach to address this question is to derive *a priori* predictions based on our understanding of a particular system, and then test the predictions in the wild using comparative data. If we adequately understand the form of selection acting on a given set of organisms, then we should be able to accurately predict the course of evolution, assuming that other factors (e.g., genetic drift, genetic constraints, and gene flow) do not overwhelm the signal of focal evolutionary responses.

Understanding all the intricacies of selection acting on organismal traits in the wild is challenging at best. Rather than attempt to explain all aspects of selection

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and evolution, we can instead construct simple models designed to explain major patterns of phenotypic evolution. These generalized models center on a subset of traits and environments hypothesized to be of critical importance for the evolutionary ecology of particular taxa. Predictions derived from the models can be tested using comparative or experimental analyses. That is, we build a generalized mechanistic model describing how a system operates, based on a specified set of assumptions, and then test the model's accuracy of predicting phenotypic outcomes—e.g., how leg morphology mediates running performance, how running performance translates to fitness, and what the evolutionary response(s) should be in particular environments. A similar approach has been taken with respect to foraging by fish, and is proving highly successful in gaining a richer understanding of the evolutionary diversity of feeding structures in fish (e.g., Wainwright and Richard 1995; Westneat 1995; Wainwright 1996; Clifton and Motta 1998; Collar and Wainwright 2006; Wainwright et al. 2007). The ideal model is simple, makes clear, testable evolutionary predictions, and eventually garners enough applications in diverse organisms that one can test the general utility of the model in predicting phenotypic differentiation using meta-analysis. Here, I take this approach to evaluate the predictability of morphological and locomotor differentiation across water-flow regimes in fishes.

Recently, Langerhans and Reznick (in press) described a general model for fishes that predicts phenotypic diversification across three major ecological gradients (structural complexity, predation, and water flow). In this study, I more fully develop this model and test its predictions with respect to one particular environmental gradient, water flow. Fish inhabit environments varying extensively in magnitudes of water flow, ranging from the low-flow regimes of ponds, lakes, backwaters, and calm tidal pools to the high-flow regimes of swift streams, rapid rivers, and wave-swept, near-surface oceanic waters. Throughout this article, ''flow regime'' refers to the intensity of externally generated water flow experienced by fish. Although the term ''flow regime'' often refers to Reynolds numbers (*Re*) in studies of aquatic locomotion (e.g., viscous versus inertial; laminar versus turbulent), it does not here, as most fish presumably experience primarily inertial forces at the high *Re* achieved during locomotor activities relevant for this study (e.g., cruising during foraging, fast-start escape bursts; $Re > 1000$), and properties of the boundary layer are not directly pertinent to predictions examined here.

For most fish, locomotor behaviors are essential for carrying out innumerable tasks, and strong currents can impose serious challenges to performing ecologically important activities. As such, natural selection is predicted to favor different locomotor capabilities under alternative flow regimes, and consequently to drive major patterns of phenotypic variation in fishes (see below). The general hypothesis of differential selective pressures driving phenotypic differences across flow regimes has a long history (e.g., Hubbs 1940, 1941; Hynes 1970; Blake 1983; Videler 1993; Vogel 1994) and empirical investigations are numerous (see studies listed in the Appendices). However, despite the volume of literature, we still lack an understanding of the major patterns of water velocity's effects on fish phenotypes. Using a generalized framework making specific *a priori* predictions, this study synthesizes existing data to test the predictability of phenotypic differentiation across flow regimes in fishes.

Introduction of the model

The general model described here is founded upon prior theoretical and empirical investigation of the biomechanics of fish locomotion (linking morphology to swimming abilities) and the ecology of fish inhabiting divergent flow regimes (linking swimming abilities to fitness). The model posits that divergent natural selection on locomotor performance between flow regimes drives morphological and locomotor differentiation due to a combination of selection favoring either steady or unsteady locomotor performance in different flow environments and a trade off between these locomotor modes, whereby fish cannot simultaneously optimize both steady and unsteady locomotor capacities. So, what is meant by ''steady'' and ''unsteady'' locomotion, why might these performance traits trade off with one another, and why might natural selection favor different locomotor modes in different flow regimes?

Steady swimming (cruising) describes constant-speed locomotion in a straight line, and is commonly employed in nature during various activities such as holding station amidst water current, searching for food, patrolling for predators or competitors, chasing and obtaining mates, seeking favorable abiotic conditions, and migration (Blake 1983; Plaut 2001). Unsteady swimming refers to more complicated locomotor patterns in which changes in velocity or direction occur, such as fast-starts, rapid turns, maneuvering, braking, and burst-and-coast swimming (Blake 1983; Videler 1993). In the wild, such activities are common during social interactions, predator evasion, the capturing of evasive prey, and navigating structurally complex environments. At first glance, it might appear that fish could simply optimize both steady and unsteady capacities, thus solving many of their problems—however, this is not a perfect world, as fish face a dilemma in the form of a functional trade off. That is, propulsive mechanisms are coupled in most fish (i.e., the same structures are used for force generation, transmission, and delivery during different swimming modes) and many traits that enhance performance at one mode necessarily compromise performance in the other. This general trade off, analogous to the commonly discussed endurance-sprint trade off in many terrestrial organisms, has long been hypothesized to play an important role in the ecology and evolution of fish (Lighthill 1969, 1970; Webb 1982, 1984; Blake 1983; Videler 1993; Reidy et al. 2000; Domenici 2003; Blake 2004; Langerhans 2006; Langerhans et al. 2007b; Langerhans and Reznick, in press).

While fish virtually always contend with competing demands for steady-swimming and unsteady-swimming performance, this balance is expected to swing toward favoring steady swimming in high-flow environments—where fish must often swim to maintain position and perform routine tasks under arduous conditions—but unsteady swimming in low-velocity environments—where fish are largely freed from the severe demands on endurance and can instead exploit strategies requiring high acceleration or maneuverability. For instance, in the face of high water velocities, large magnitudes of hydrodynamic forces are exerted on fish bodies, and fish must overcome these drag forces to maintain position and conduct routine activities. Most fish utilize steady locomotion to overcome these forces, and thus fish that optimize steady swimming by minimizing the energetic costs of swimming should exhibit high fitness in high-flow environments (e.g., locate and obtain food more readily, acquire mates more effectively, retain greater energy supplies for reproduction) (Vogel 1994; Plaut 2001; Roff 2002; Domenici 2003; Blake 2004). Note that some fish use means other than steady locomotion to hold position in flow, such as resting against the substrate, using clasping devices to attach to the substrate, or seeking refuge in rock crevices. This model does not necessarily apply to such fish. On the other hand, fish inhabiting low-flow environments no longer require strong cost-reducing mechanisms for steady swimming and can instead respond to selective pressures favoring enhanced unsteady locomotion, which might be elevated in low-flow habitats due to the increased frequency of unsteady locomotion and the prevalence of structurally complex habitats (e.g., littoral vegetation and woody debris that is common in ponds, lakes, and backwaters). Thus, a clear hypothesis exists for divergent natural selection—selection pulling trait means of two or more populations toward different adaptive peaks—on locomotor abilities between flow regimes in fishes.

Details of the model

Putting this together, we have a generalized, conceptual model based on four assumptions (Table 1), which predicts phenotypic differentiation between flow regimes. If the first two assumptions are met, then selection will be divergent between flow regimes. If the last two assumptions are met, then fish should exhibit divergent phenotypes in different flow regimes via either genetic differentiation, phenotypic plasticity, or both. This conceptual model can be formally expressed using a combination of the Lande equation (Lande 1979; Lande and Arnold 1983) and the functional-constraints equation (Ghalambor et al. 2003; Walker 2007). Placing the model in a quantitative framework highlights the specific assumptions of the model (Table 1) and the range of parameter space that would satisfy the assumptions.

The Lande equation describes the single-generation change in phenotypes ($\Delta\bar{\mathbf{z}}$, vector of the change in population means for each trait) as a function of the additive genetic variances and covariances of traits (**G** matrix), and directional selection acting on those traits ($\bar{\boldsymbol{\beta}}$, vector of partial regression coefficients of fitness on phenotypes): $\Delta\bar{\mathbf{z}} = \mathbf{G}\bar{\boldsymbol{\beta}}$. Selection on morphological traits ($\bar{\boldsymbol{\beta}}$) can be decomposed into the

Table 1 Assumptions of the general model used to predict phenotypic differentiation across flow regimes in fishes

Conceptual assumptions	Model assumptions
(1) Functional trade off between steady and unsteady swimming	Captured in **F** matrix
(2) Shift in the balance of selection on steady and unsteady locomotion between flow regimes, overall favoring steady in high flow and unsteady in low flow	Captured in $\bar{\mathbf{w}}$ vectors
(3) Genetic constraints do not preclude evolutionary responses to selection in the predicted directions	Captured in **G** matrix
(4) Forces other than natural selection on locomotion (e.g., natural selection from other agents, selection on correlated traits, sexual selection, and gene flow) do not obscure responses to selection	Closed system with all relevant traits and fitness components included

functional relationships between morphology and performance (**F**, matrix of partial regression coefficients of each performance trait on each morphological trait), and directional selection on performance traits ($\bar{\mathbf{w}}$, vector of partial regression coefficients of fitness on performance variables): $\bar{\boldsymbol{\beta}} = \mathbf{F}\bar{\mathbf{w}}$. This functional-constraints equation represents the matrix form of the morphology → performance → fitness pathway (Arnold 1983). Regarding the four assumptions of the model described here (Table 1), assumption 4 is unlikely to be fully satisfied empirically, but serves as a common simplifying assumption of *Ceteris paribus*. The other three assumptions might be met with a broad range of realistic parameter values, suggesting that the model could provide useful generalized predictions of phenotypic differentiation in fishes (see below).

To demonstrate how this general model predicts morphological and locomotor differentiation between flow regimes, let us consider a simplistic scenario involving one morphological trait that determines steady-swimming and unsteady-swimming performance. Moreover, let us assume that selection favors both steady and unsteady locomotion in all environments (i.e., it is never directly beneficial to exhibit poor locomotor performance), such that only the strength (not direction) of selection might vary among locomotor traits and environments.

First, using existing biomechanical information of fish locomotion (see above), I assume a functional trade off between steady and unsteady swimming, described here as oppositely signed slopes from regression of performance on morphology (Fig. 1A; **F** matrix). As long as the slopes are opposite in sign, a range of values might satisfy this assumption (see examples of relationships in Fig. 1A; note that net trade offs across multiple traits are measured by vector cross-products among columns of **F**). Second, ecological information suggests a shift in the balance of selection between low-flow and high-flow environments (see above) and I assume here that selection for unsteady swimming is stronger (i.e., higher slope) than for steady swimming in low-flow environments, but the reverse is true in high-flow environments (Fig. 1B; $\bar{\mathbf{w}}$ vectors). Again, a range of parameters might satisfy this assumption, so long as the difference in magnitudes of selection on locomotor performance across environments is maintained. Combined with the last two assumptions of the model (Table 1), this yields predictions of phenotypic trajectories in low-flow and high-flow environments (Fig. 1C). Thus, the predicted nature of divergent selection and phenotypic differentiation does not require highly restrictive scenarios regarding the functional trade off and selection on locomotor performance, but rather can result from a range of combinations of **F** and $\bar{\mathbf{w}}$.

Predictions of the model

The general model makes several predictions of phenotypic differentiation between flow regimes in fishes (Table 2). As described above, fish should exhibit locomotor differences between flow regimes, with fish in high-flow habitats exhibiting higher steady-swimming performance, and fish in low-flow habitats exhibiting higher unsteady-swimming performance. Because these traits represent performances by the whole organism, they are determined by underlying morphological traits (‘‘morphological’’ in the broad sense, including physiological and biochemical traits). Based on prior biomechanical work, the model makes some specific predictions regarding differentiation in these subordinate traits. That is, fish should exhibit divergent traits across flow regimes, in each case reflecting attributes that enhance the appropriate locomotor mode.

Fortunately, a wealth of research has investigated the links between fish morphology and locomotor performance (reviewed by Webb and Weihs 1983; Videler 1993; Sfakiotakis et al. 1999; Triantafyllou et al. 2000; Lauder and Drucker 2002; Blake 2004; Colgate and Lynch 2004; Lauder 2005; Müller and van Leeuwen 2006; Shadwick and Lauder 2006), and several traits can be identified which appear generally to meet our model's assumption of a functional trade-off (i.e., enhances one locomotor mode at the cost of the other). It is 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 performances (e.g., Wainwright and Reilly 1994; Koehl 1996; Lauder 1996; Domenici and Blake 1997; Schultz and Webb 2002)—however, I focus here on relationships with particularly strong theoretical and empirical support in an effort to elucidate general and predictable trends. To extrapolate this information to untested fish species (as the meta-analysis effectively does), I simply assume that relationships hold across most fish. I exclude flatfish in analyses, as these predictions are not straightforward for such fish; however I include fish using various primary propulsor systems (e.g., body/caudal fin, median-and-paired fin), assuming that rigid-body and elongated-body theories provide adequate approximation for swimming in these fish (e.g., Hoerner 1965; Blake 1983; Pedley and Hill 1999; Sfakiotakis et al. 1999; McHenry and Lauder 2006).

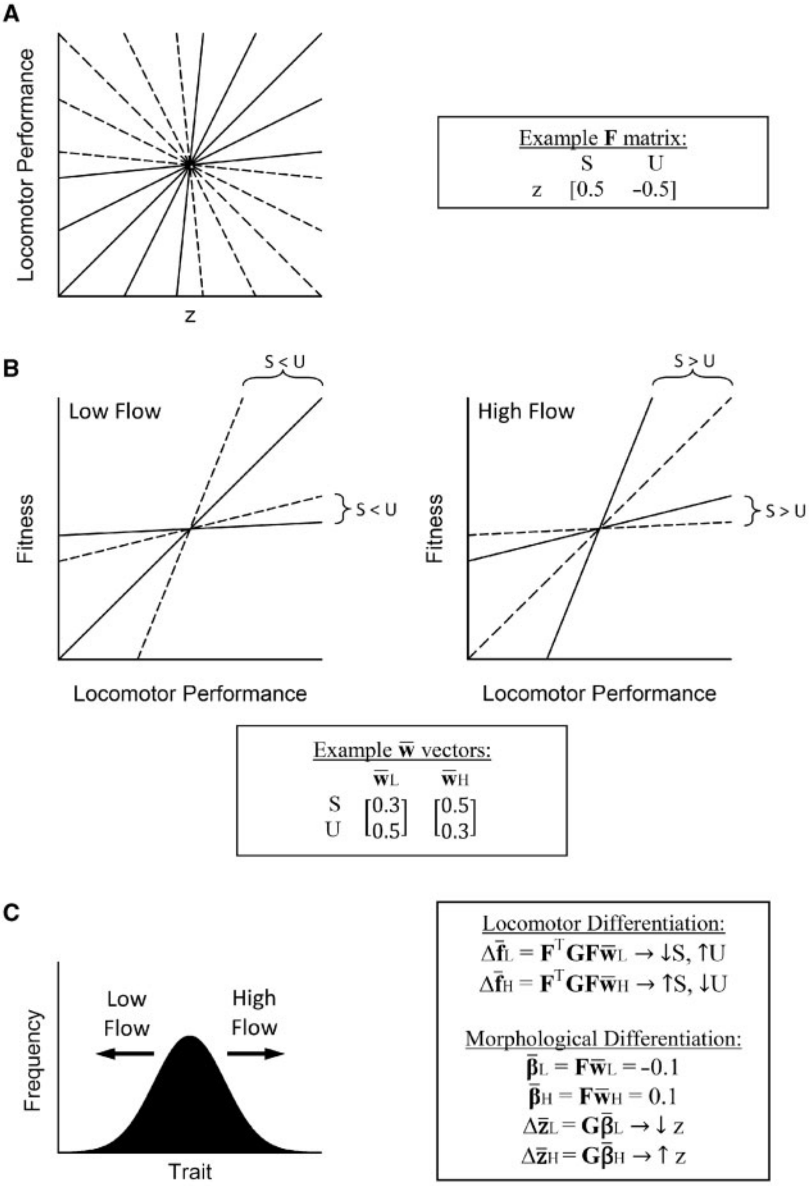

Fig. 1 Illustration of the model used to predict locomotor and morphological differentiation between flow regimes in fishes. (**A**) Functional trade off between steady (S) and unsteady (U) swimming, illustrated by one morphological trait (z) that positively influences steady swimming (solid lines) and negatively influences unsteady swimming (dashed lines). The assumed trade off is reflected by oppositely signed slopes across locomotor modes (described by the **F** matrix), or lines that cross (five hypothetical slopes illustrated for each mode). (**B**) Shift in the balance of selection between flow regimes (two hypothetical cases illustrated for each flow environment), where selection for unsteady swimming is stronger (steeper slope) than selection for steady swimming in low-flow environments, but vice versa in high-flow environments (described by a $\bar{\mathbf{w}}$ vector within each environment; L, low flow, H, high flow). (**C**) Predicted phenotypic trajectories in low-flow and high-flow environments. Based on the example **F** matrix and $\bar{\mathbf{w}}$ vectors, divergent selection is predicted to drive differentiation in locomotor performance ($\Delta\bar{\mathbf{f}}$) and morphology ($\Delta\bar{\mathbf{z}}$), pulling population means for traits toward different adaptive peaks.

Steady swimming is enhanced by a stiff, streamlined body, a high proportion of red muscle, and a caudal fin with a high aspect ratio. These features act to maximize thrust while minimizing energy losses due to drag and recoil. High unsteady performance is typically produced by a flexible, posteriorly deep body, a high proportion of white muscle, and a caudal fin with a low aspect ratio. These features maximize thrust and stability during rapid bouts of swimming activity. Thus, a functional trade off is hypothesized for each of these four morphological traits, where no single trait value can simultaneously optimize both steady and unsteady swimming abilities. Combined with divergent selection on locomotor modes across

Table 2 Predictions of phenotypic differences between flow regimes

	Predictions	
Trait	**Low flow**	**High flow**
Body shape	Posteriorly deeper	More streamlined
Caudal fin shape	Lower aspect ratio	Higher aspect ratio
Muscle architecture	Relatively more white	Relatively more red
Body flexibility	More flexible bodies	Stiffer bodies
Steady swimming	Lower performance	Higher performance
Unsteady swimming	Higher performance	Lower performance

flow regimes, this predicts divergence in body shape, caudal-fin shape, muscle architecture, and body flexibility for fish inhabiting different flow environments (Table 2). Note that although subtle, low-speed maneuvers also represent unsteady swimming activities, I focus here on rapid components of unsteady behaviors as their underlying morphological bases are better understood. A brief description of each prediction is provided below.

A streamlined body has a fusiform shape, approximating the form of an airfoil—deep/wide anterior body, tapering to a shallow/narrow caudal peduncle—and minimizes drag during steady swimming (Wu 1971; Lighthill 1975; Webb 1975, 1984; Blake 1983; Weihs 1989; Hobson 1991; Videler 1993; Vogel 1994; Boily and Magnan 2002; McHenry and Lauder 2006; Fisher and Hogan 2007). Posteriorly deep bodies—small head and large caudal peduncle, accomplished by the body or by median fins—enhance unsteady swimming activities, such as increased velocity and acceleration during fast-starts, and increased stability during rapid turns (Blake 1983, 2004; Webb 1983, 1984, 1986; Walker 1997; Langerhans et al. 2004).

A lunate caudal fin with a high aspect ratio—long span with a short chord, height^2/surface area—produces thrust more efficiently than do alternative fin shapes during body/caudal-fin steady swimming, leading to reduced locomotor costs; a low-aspect-ratio caudal fin—maximizing surface area, resulting in a rounded or squared fin—produces greater thrust during rapid maneuvers (Keast and Webb 1966; Lighthill 1975; Blake 1983; Webb 1984; Videler 1993; Vogel 1994; Boily and Magnan 2002; Blake 2004).

Fish possess two major types of muscle fibers, each providing power for either steady or unsteady swimming. Red muscle (aerobic, slow twitch) powers continuous swimming, and white muscle (anaerobic, fast twitch) powers rapid activities such as fast-starts and sprints (Greer-Walker and Pull 1975; Bone 1978; McLaughlin and Kramer 1991; Videler 1993; Jayne and Lauder 1994; Thys et al. 2001; Coughlin 2002; Müller and van Leeuwen 2006). Thus, to enhance performance in one locomotor mode, fish are expected to produce a relatively greater proportion of the appropriate type of muscle fiber.

Stiff bodies reduce recoil energy losses during steady swimming, and can exploit stored energy in the spring-like circumstances of stiff bodies; flexible bodies allow large-amplitude propulsive actions, resulting in tighter turning radii and enhanced turning rates and acceleration during fast-starts and rapid turns (Webb 1984; Videler 1993; Long and Nipper 1996; Pabst 1996; Brainerd and Patek 1998; Dickinson et al. 2000; Domenici 2003; Blake 2004).

Testing the model: meta-analysis

I employed a meta-analytic approach to test each of the model's predictions. This involved an intensive literature search designed to locate studies providing relevant tests of the predictions. My analyses address three primary questions: (1) what is the role of natural selection in driving predictable phenotypic differentiation among environments? (2) Do phenotypic outcomes typically derive from genetic divergence, phenotypic plasticity, or both? (3) What is the role of predictable differentiation between flow regimes in driving speciation and producing major microevolutionary and macroevolutionary patterns?

For each study identified in the literature, I determined whether the results provided conclusive evidence either for or against any of the model's predictions. While many studies directly tested some of the model's predictions, a number of studies provided relevant results, without actually discussing them in this context. Whether a study explicitly tested a given prediction, or discussed that prediction in its text, was irrelevant for inclusion in analyses conducted here—if a conclusive result could be discerned regarding one or more predictions, it was included.

My literature search uncovered ~200 studies that addressed the general topic of the effects of water-flow regime on the diversity and diversification of fish. From this set of studies, 101 provided relevant results regarding the predictions; however, 15 of these did not provide unambiguous results and were thus excluded from analyses. Ambiguous results reflected inconsistencies, either between sexes or among age classes, or imprecise description of results precluding unambiguous interpretation.

All investigators addressed phenotypic differentiation across flow regimes at one of three possible scales: (1) among populations (or experimental treatments) within species, (2) among species, or (3) among fish assemblages. I excluded cases at the last scale (six studies), as these studies suffered from a lack of phylogenetic control, included species that commonly used nonlocomotor means of contending with water flow (e.g., regularly utilizing rock crevices or other refugia from high velocity of water flow), and had a low sample size (six tests for body shape, two tests for caudal fin aspect ratio). Moreover, it might even be argued that testing some of these predictions by comparing fish assemblages would be circular, as some of the original conceptions of these predictions may have been based on qualitative observations of differences among such assemblages (prior to theoretical and empirical work).

Using a total of 80 studies (115 tests of predictions), I conducted analyses separately for intraspecific and interspecific differentiation. Because results were similar across scales, I also performed pooled analyses to evaluate overall support for predictions. Studies exhibited a broad chronological span, illustrating the long-standing interest in the effects of water flow on fish diversification (Fig. 2A). The increase in number of publications since the turn of the century (50% of studies were published subsequent to 1999), likely reflects an overall increase in the volume of peer-reviewed literature. Studies covered a wide geographic range (Fig. 2B), including all continents but Antarctica—although, most studies were conducted in North America or Europe. Assessment of the magnitude of water flow varied among studies. Most studies compared fish phenotypes between low-flow and high-flow environments (e.g., lakes versus rivers), while 16 studies examined continuous variation in water flow across localities.

For each study, I tallied whether or not results matched predictions for each relevant trait. I used a one-tailed binomial test in each case to evaluate whether results provided significant support for the *a priori* predictions. The degree of correspondence between predictions and observations should provide insight into the accuracy with which the model describes and predicts the biomechanics and evolutionary ecology of fish inhabiting divergent flow regimes (Losos 1990; Lauder 1996; Wainwright 1996; Walker 1997; Koehl 1999; Domenici 2003). As a conservative approach, I included all species with relevant results that clearly experienced alternative flow regimes, rather than excluding those that violated some natural history assumptions (e.g., often resting on substrate rather than employing locomotion to maintain position). For the model to possess strong predictive applicability, it should prove robust to such violations. For this reason, and because results were similar whether or not I excluded species obviously violating assumptions, I only present results using the entire dataset. At the intraspecific scale, some species were represented by multiple tests for a given trait (Appendix Table A1). Because such tests are not independent, I conducted additional analyses at the intraspecific scale using species as replicates. For these analyses, I only included species for which all tests for a given trait were consistent.

Because I could find no study testing differentiation of body flexibility between flow regimes, I could not test this prediction. For all other traits, I found at least three studies providing relevant results. For caudal-fin shape, I included studies that measured either caudal-fin aspect ratio *per se*, or caudal fin height as a surrogate for aspect ratio. Taller caudal-fins should generally reflect higher aspect ratios, as squared tail height forms the numerator of the metric (i.e., spurious self-correlation; Kenney 1982). Empirical data from an African cyprinid ($r = 0.64$, $P < 0.0001$, data from Langerhans et al. 2007a) and New World mosquitofishes ($r = 0.87$, $P < 0.0001$; unpublished data across six species) suggest the two variables are indeed significantly correlated in natural fish populations. For analyses conducted here, I assumed that taller caudal fins reflected higher aspect ratios.

I further evaluated whether the observed findings generally resulted from genetic divergence or phenotypic plasticity by examining all cases within the dataset that provided laboratory tests of these potential sources of phenotypic variation (i.e., common garden experiment, plasticity experiment).

Results of meta-analysis

At the intraspecific scale, I found 60 studies, comprising 87 relevant tests of predictions. These studies spanned a diverse group of fishes (Appendix Table A1), including 10 orders, 15 families, and 35 species. Overall, 69 of 87 cases (79%) matched *a priori* predictions of phenotypic differentiation across flow regimes (one-tailed $P < 0.0001$; Fig. 3A). Using species as replicates, and including only those for which results were consistent across all traits, I found that 23 of 25 species (92%) exhibited differences matching predictions (one-tailed $P < 0.0001$). Evaluating each trait separately, I found significant support for predictions for body shape, caudal-fin shape, and steady-swimming performance; while results for muscle architecture suffered low sample size and were ambiguous for unsteady locomotion (Table 3). Treating species as replicates yielded similar results for each trait (Table 3).

I found 21 studies, representing 28 relevant tests, at the interspecific scale (Appendix Table A2). Across all traits, 24 of 28 cases (86%) matched predictions

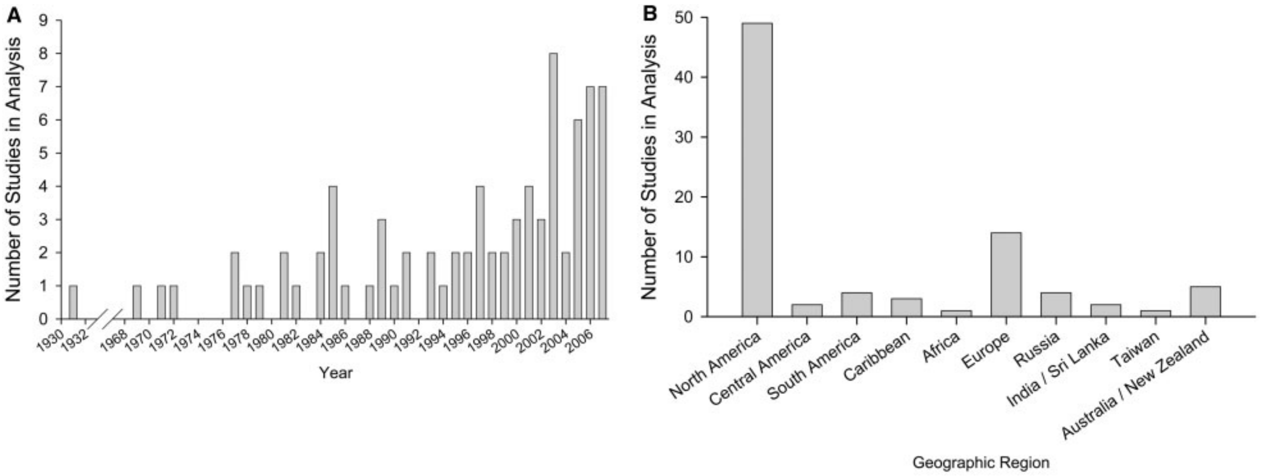

Fig. 2 Summary of the (**A**) chronological span and (**B**) geographic range encompassed by the publications included in the meta-analysis.

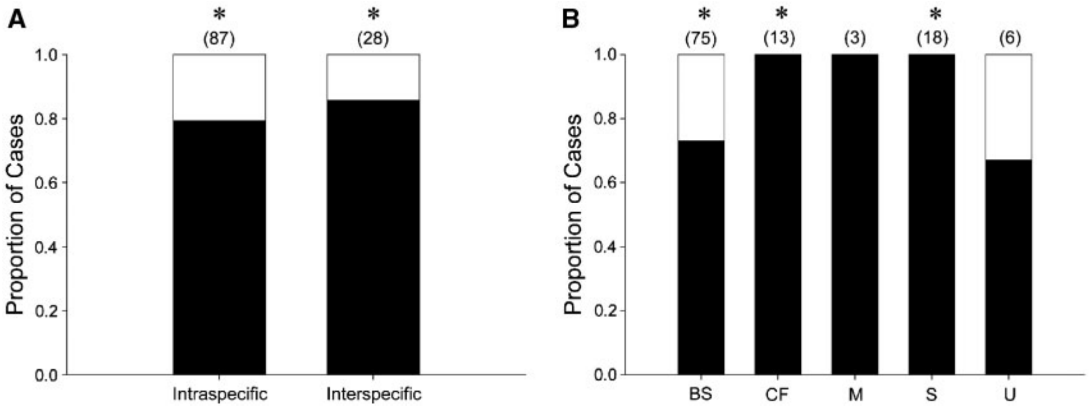

Fig. 3 Results of the meta-analysis (**A**) across all traits for intraspecific and interspecific scales of analyses, and (**B**) across both scales for each of the five traits. Each bar represents 100% of cases, where the filled portion indicates the proportion of cases matching predictions, and the open portion provides the proportion of cases not matching predictions. Sample sizes are given in parentheses above each bar. *Significant support for predictions (one-tailed $P \leq 0.0001$). BS, body shape; CF, caudal-fin shape; M, muscle architecture; S, steady swimming; U, unsteady swimming.

(one-tailed $P < 0.0001$; Fig. 3A). Examining each trait separately, significant support for predictions was found for the two traits with adequate sample sizes, body shape, and steady locomotion; while sample sizes were small for caudal-fin shape and unsteady-swimming performance, and nonexistent for muscle architecture (Table 3).

Results were reasonably similar across both scales of analysis, indicating general support for the model's predictions (Table 3). Pooling results across scales to evaluate overall support for each prediction reveals significant support for body shape (one-tailed $P < 0.0001$), caudal-fin shape (one-tailed $P = 0.0001$), and steady swimming (one-tailed $P < 0.0001$); muscle architecture matched predictions in all cases, but did not reach statistical significance due to small sample size (one-tailed $P = 0.1250$), while results for unsteady locomotion were nonsignificant (one-tailed $P = 0.3438$), also suffering from small sample size (Fig. 3B). Overall, results for each trait confirmed predictions more often than not (ranging from 67% to 100% of cases).

To assess whether phenotypic differentiation across flow regimes might typically result from genetic divergence or phenotypic plasticity, I examined all cases within the dataset that provided relevant results. At the intraspecific scale, 17 studies, providing 34 relevant tests, examined the role of either genetic divergence or phenotypic plasticity as putative source(s) of phenotypic differentiation. These cases included 10 species from three families, with eight of the 10 species being salmonids (the others being livebearing fish, family Poeciliidae, and rainbow fish, family Melanotaeniidae). Although data were sparse

Table 3 Summary of phenotypic differences across flow regimes in fishes at both intraspecific and interspecific scales

	Intraspecific					Interspecific				
Family	**Body shape**	**Caudal fin**	**Muscle**	**Steady**	**Unsteady**	**Body shape**	**Caudal fin**	**Muscle**	**Steady**	**Unsteady**
Blenniidae	0/1									
Centrarchidae	5/6					1/1			1/1	
Characidae	2/2									
Cichlidae	1/1									
Cobitidae						1/1				
Cottidae	1/1					1/1				
Cottocomephoridae	1/1									
Cyprinidae	4/5	1/1		1/1		1/2	1/1		2/2	
Cyprinodontidae	1/1									
Galaxiidae	2/2					1/1				
Gasterosteidae	1/1			1/1	1/1					
Lotidae	0/1									
Melanotaeniidae	0/2		2/2	1/1	1/2					
Percidae						1/3				
Poeciliidae	1/3			2/2		1/1				
Retropinnidae	1/1		1/1							
Salmonidae	22/30	9/9		6/6	1/2	1/1			2/2	1/1
Multiple families						5/6	2/2		2/2	
Cases as replicates	**42/58**	**10/10**	3/3	**11/11**	3/5	**13/17**	3/3	0/0	**7/7**	1/1
Species as replicates	**20/25**	**8/8**	3/3	**8/8**	3/5					

Tallies indicate the number of cases matching predictions out of the total number of cases found in the literature review. Totals along the bottom represent the sum of all cases for a given trait. The additional row at the bottom of the intraspecific results provides the findings when species are treated as replicates (see text). Bold text indicates significant support for the *a priori* predictions (one-tailed binomial test, $P < 0.05$).

Table 4 Summary of tests for the role of genetic divergence and phenotypic plasticity in phenotypic differences among fish experiencing divergent flow regimes

	Body shape		Caudal fin		Muscle		Steady		Unsteady	
	Genetic	**Plasticity**	**Genetic**	**Plasticity**	**Genetic**	**Plasticity**	**Genetic**	**Plasticity**	**Genetic**	**Plasticity**
Cases as replicates	11/11	8/8	1/2	5/5	0/1	0/0	3/3	2/2	1/2	0/0
Species as replicates	6/6	7/7	1/2	4/4	0/1	0/0	3/3	2/2	1/2	0/0

All tests were conducted at the intraspecific scale. Tallies indicate the number of cases finding significant evidence for either genetic differentiation or environmentally-induced phenotypes out of the total number of cases conducting such tests. Across all traits, there is significant evidence for both genetic divergence and phenotypic plasticity (see text).

for all traits other than body shape, evidence suggests that both sources of phenotypic variation play significant roles (Table 4). Overall, I found significant support for a genetic basis for phenotypic divergence, as in 16 of 19 cases (84%) laboratory-reared offspring in a common environment exhibited significant differences (one-tailed $P = 0.0022$). However, there was also strong support for an environmental influence on phenotypic differentiation, as in 15 of 15 cases (100%) there was significant evidence of phenotypic plasticity (one-tailed $P < 0.0001$). When treating species as replicates, results are similar, as both genetic divergence (one-tailed $P = 0.0287$) and phenotypic plasticity (one-tailed $P = 0.0001$) received significant support. Differences at the interspecific scale likely, at least partially, reflect genetic differentiation, although only four studies included in the analyses actually provided such information (all four confirmed a genetic basis; three for body shape, one for steady-swimming performance).

Discussion

Virtually all fish routinely move through their fluid medium to perform tasks critical for survival and reproduction. Consequently, locomotor abilities of fish are presumably under strong selection, and the nature of this selection might vary across time and space. This study used a general model describing divergent selection on locomotor performance across flow regimes to predict morphological and locomotor differentiation, and then tested the predictions by synthesizing previous data and conducting meta-analysis. The model described here, based on an understanding of the biomechanics and ecology of fish inhabiting divergent flow regimes, produced some accurate predictions regarding phenotypic differentiation in the wild. Results were largely consistent among studies examining variation either within or between species, and suggest that microevolutionary processes responsible for intraspecific differentiation might often generate broader interspecific patterns. In summary, the findings offer insight into the predictability of phenotypic differentiation between flow regimes in fishes, point to several areas deserving increased attention, and highlight the utility of a general predictive framework for gaining a better understanding of the ecological causes of phenotypic diversity.

Predicting phenotypic differentiation

For species tested so far, strongest support for the *a priori* predictions was found for steady-swimming performance and caudal-fin shape—100% of tests matched predictions (31 tests). This suggests that the model's assumptions regarding these traits may hold true for disparate fishes. Indeed, selection for increased steady-swimming abilities in environments with greater intensity of water flow may be a widespread phenomenon in fishes, driving repeatable and predictable phenotypic outcomes in many different groups of fish. The pattern of increased steady locomotor abilities in high-flow environments was repeatedly observed across studies, regardless of whether steady-swimming performance was assessed using critical swimming speed, endurance, or other methodology. Selection favoring increased steady-swimming performance in high-flow situations seems straightforward, as fish must regularly swim simply to maintain position and perform routine tasks. As water flow increases, the frequency of substantial drag experienced by fish almost certainly increases. Fish must then use some means, such as steady locomotion, to overcome this increased drag and avoid being swept wherever the current might take them. In the absence of strong selection for steady locomotion, as predicted for low-flow environments, it is less important to conserve energy during steady locomotion. This allows selection favoring alternative locomotor activities (e.g., fast-starts, complex maneuvering) to drive phenotypic responses. One of the simplest biomechanical predictions for increasing steady-swimming performance in fish using body/caudal-fin propulsion is to produce a lunate caudal fin with a high aspect ratio. This shape should reduce swimming costs compared to caudal fins with lower aspect ratios, and presumably explains the observation that most fish exhibited the predicted shift in caudal-fin shape across flow regimes. Note, however, that many studies did not directly measure caudal-fin aspect ratio *per se*, but rather measured only height of the caudal fin. Future studies should directly test this prediction by explicitly measuring the salient feature (e.g., height^2/surface area).

The largest volume of evidence related to body shape, and results significantly supported predictions; however, results were less than perfectly consistent with predictions (73% of tests matched predictions). Thus, while the model accurately predicted differences in body shape in most cases, a nontrivial proportion of cases did not conform to predictions. This suggests that links between body shape, locomotor performance, and fitness may not always meet assumptions of the model. For instance, compensatory mechanisms (e.g., use of median or pectoral fins in steady swimming) likely weaken predicted locomotor trade-offs in some fish by reducing the degree of coupling between morphology and various locomotor activities. Decoupling of traits within a functional complex can lead to many-to-one mapping (e.g., equivalent swimming performances might be achieved by a number of underlying morphologies) and consequently this can lead to increased phenotypic diversity and to a reduction in morphology-performance correlations across populations or species (Liem 1973; Lauder 1981; Emerson 1988; Lauder 1990; Wainwright and Turingan 1993; Schaefer and Lauder 1996; Domenici 2003; Wainwright et al. 2005; Collar and Wainwright 2006; Wainwright 2007). Additionally, the accuracy of biomechanical models linking morphology to steady swimming based on theories of rigid bodies (e.g., airship design) may not be highly appropriate for fish that use their body (rather than strictly their tail) to generate thrust (Schultz and Webb 2002)—although, no clear alternative theory yet exists. Moreover, body shape is surely influenced by a number of factors other than natural selection on locomotor abilities as described by the model (e.g., genetic drift, life histories, sexual selection, other selective agents such as predators and competitors), and these might sometimes overwhelm the strength of divergent selection across flow regimes, even when present.

Only three studies examined differences in the proportion of red or white muscle in fish inhabiting divergent flow regimes. While all three cases were consistent with predictions, it would be premature to draw any strong conclusions from such limited results. Cleary, this prediction deserves future attention if we are to understand the general effects of water velocity on muscle architecture in fishes.

The prediction of greater unsteady-swimming performance in low-flow environments was not strongly supported, although a majority of cases did match predictions. This observation might have resulted from a number of causes. First, it might simply reflect low statistical power, as sample size was quite small ($n=6$). If so, then either the true percentage of cases matching *a priori* predictions in the wild is higher (i.e., sampling artifact) or the observed value (67%) is accurate, and merely lacked statistical significance due to low power. Second, it could derive from violations of the model. For instance, the functional trade off between steady and unsteady locomotion may be weak or nonexistent in some fish due to some degree of decoupling in locomotor systems. That is, a fish might be capable of simultaneously optimizing components of both steady and unsteady swimming by independently modifying various underlying traits—e.g., some fish might enhance steady swimming in high-flow environments without compromising their unsteady-swimming abilities by producing appropriate combinations of morphological traits (see discussion of trait decoupling and many-to-one mapping above). Further, selection on locomotor performance might not be divergent in some cases (e.g., selection on steady-swimming performance might be stronger than selection on unsteady performance in all environments). Finally, lack of strong support for the predicted divergence in unsteady-swimming performance might be methodological in nature. The two studies that found evidence inconsistent with predictions examined burst-swimming performance as the unsteady locomotor component of interest (Peake et al. 1997; McGuigan et al. 2003). It is possible that the methods—raceway sprints and high-speed flow within a flume—included some amount of aerobic swimming abilities, rather than explicitly addressing anaerobic capacities. However, if these methods did not adequately address unsteady performance, it is difficult to explain why confirmation of the prediction for unsteady locomotion occurred for other species examined within the same studies. Note, however, that the only two studies that directly examined C-start performance (undoubtedly a uniquely unsteady activity) found results consistent with predictions (Taylor and McPhail 1985b; Taylor and McPhail 1986). Moreover, inter-individual variation in general quality or motivation could have masked true differences in unsteady locomotor performance (Losos et al. 2002; Van Damme et al. 2002). Both species that failed to support the unsteady-swimming prediction did match the steady-swimming prediction (i.e., these fish exhibited higher steady swimming performance in high-flow habitats without suffering the cost of reduced unsteady performance). The issue of "general quality" (*sensu* Van Damme et al. 2002) might be important here: fish from one environment could simply be more "athletic" (e.g., overall larger muscle mass, better health), requiring the control of confounding factors to detect functional trade offs. Regardless of all this speculation for unsteady-swimming abilities, more research is necessary to answer the question of whether the model accurately predicts differentiation in unsteady locomotion across flow regimes in fishes.

Flow regime, plasticity, microevolution, and macroevolution

Phenotypic differences among populations and species result from some combination of genetic divergence (differences in fixed, genetically-determined phenotypes) and phenotypic plasticity (environmentally-contingent phenotype production). Either source of phenotypic variation can reflect adaptive evolutionary responses to divergent natural selection across heterogeneous environments, and facilitate microevolutionary change and speciation (Levins 1968; Schlichting and Pigliucci 1998; Schluter 2000; Pigliucci and Murren 2003; West-Eberhard 2003; Schlichting 2004; Pigliucci et al. 2006; Crispo 2007; Ghalambor et al. 2007). Both genetic divergence and phenotypic plasticity appear to play important roles in phenotypic differentiation across flow regimes in fishes. It thus seems likely that the phenotypic differences examined here often reflect both sources of variation simultaneously. A central question in the study of phenotypic variation concerns the relative importance of genetic divergence and phenotypic plasticity (Day et al. 1994; Robinson and Wilson 1996; Chapman et al. 2000; Ruehl and DeWitt 2005; Keeley et al. 2007). However, without explicitly addressing both potential sources of phenotypic variation within a common experimental context, one cannot address this question. Unfortunately, only one study included in analyses here simultaneously addressed both genetic and environmental influences on phenotypic differentiation (Keeley et al. 2007). That study found evidence for both genetic divergence and plasticity in body shape differences; however, genetic differentiation explained much more morphological variance (52.7%) than did phenotypic plasticity (7.3%). Only by simultaneously testing both possibilities can such information be attained. In all other cases, we simply know whether or not genetic divergence or plasticity plays *some* role in generating phenotypic differences. Moreover, most studies on this topic have examined salmonids, leaving the question entirely open for most groups of fish. Thus, we clearly do not yet possess a realistic understanding of the relative importance of genetic differences and environmentally-induced phenotypes in producing the patterns observed here. Future research should expand beyond salmonids and address the simultaneous roles of genetic divergence and phenotypic plasticity in generating phenotypic differences across water-velocity gradients.

Most studies to date examined intraspecific differences among flow regimes, with about one-quarter of the studies included here addressing interspecific patterns. This is fortunate in one respect, as revealing cause-and-effect in the relationships between selective agents and phenotypic responses is most straightforward at the intraspecific scale—avoiding major confounding variables often present in more distantly related groups of organisms. Thus, results matching predictions within species provides strong support for natural selection's role in driving predictable phenotypic outcomes. While far less evidence exists for interspecific differentiation, results do match predictions in the vast majority of cases. This suggests that the general model described here may prove accurate in predicting major evolutionary patterns among species. However, these studies typically did not quantitatively account for phylogenetic relationships among species when assessing phenotypic patterns. Although most studies focused on relatively closely related species (e.g., within the same family), this does not avoid the problems inherent to the nonindependence of species (e.g., Felsenstein 1985; Harvey and Pagel 1991; Martins 2000). So far, only one study has investigated the effects of water flow on phenotypic differentiation among species explicitly within a phylogenetic context (Langerhans and Reznick, in press). No study has examined locomotor performance across flow regimes using a phylogenetic framework. Moreover, despite the evidence that water velocity can drive phenotypic variation both within and among species, no study to date has directly investigated the role of divergent flow regimes in speciation. Clearly, more work is required if we are to understand the role of water flow in driving speciation and generating broad, macroevolutionary patterns.

Conclusions

Meta-analysis provides a powerful approach to testing general hypotheses. For instance, a recent study used meta-analysis to reveal strong evidence for adaptive phenotypic plasticity in northern fishes (Robinson and Parsons 2002), and another demonstrated a general role of ecology in driving speciation (Funk et al. 2006). This study described a generalized model, producing testable hypotheses across diverse fishes, and tested the predictions using meta-analysis. Overall, I found general correspondence between predictions and observations, indicating that water flow plays a substantial and predictable role in influencing phenotypic diversity of fish. However, the analysis also revealed a number of gaps in our knowledge of the effects of water velocity on phenotypic differentiation: no study has yet directly tested the hypothesis of greater body stiffness in high-flow environments; few studies have examined differentiation of muscle architecture across flow gradients; we have little evidence bearing directly on the relative roles of genetic divergence and phenotypic plasticity in generating phenotypic differences, or the role of water flow on speciation and major macroevolutionary patterns; and we need more empirical tests of the assumptions linking morphology, locomotor performance, and fitness in diverse fishes.

Prior studies lacked a general, unified framework for testing specific hypotheses of morphological and locomotor differentiation across water flow regimes in fishes. This study attempted to provide such a framework, and to guide studies in fruitful directions to enhance our understanding of the predictability of phenotypic variation in nature. Future work might benefit from employing, and extending/refining, the general model described here. Hopefully, this study will spur more interest in the questions concerning ecological causes of phenotypic diversity and their predictability—whether in fish or other taxa across our planet.

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Appendix

Table A1 Summary of results for each species included in the intraspecific analysis

Family	Species	BS	CF	M	S	U	Reference
Blenniidae	*Salaria fluviatilis*	0/1					Neat et al. (2003)
Centrarchidae	*Ambloplites rupestris*	1/1					Brinsmead and Fox (2002)
	Lepomis auritis	1/1					Gatz (1979)
	Lepomis cyanellus	1/1					Gatz (1979)
	Lepomis gibbosus	1/2					Brinsmead and Fox (2002), Bhagat et al. (2006)
	Pomoxis nigrom.	1/1					Gatz (1979)
Characidae	*Bryconops caudomaculatus*	1/1					Langerhans et al. (2003)
	Bryconops sp. cf. melanurus	1/1					Sidlauskas et al. (2006)
Cichlidae	*Biotodoma wavrini*	1/1					Langerhans et al. (2003)
Cottidae	*Cottus carolinae*	1/1					Kerfoot and Schaefer (2006)
Cottocomephoridae	*Paracottus kneri*	1/1					Bogdanov (2007)
Cyprinidae	*Abramis ballerus*	1/1					Szlachciak (2005)
	Barbus neumayeri	1/1	1/1				Langerhans et al. (2007)
	Notropis volucellus	1/1					Trautman (1931)
	Rhinichthys atratulus				1/1		Nelson et al. (2003)
	Rutilus rutilus	1/2					Baranyi et al. (1997), Šprem et al. (2001)
Cyprinodontidae	*Cyprinodon tularosa*	1/1					Collyer et al. (2005)
Galaxiidae	*Galaxias maculatus*	2/2					Pollard (1971), McDowall (1972)
Gasterosteidae	*Gasterosteus aculeatus*	1/1			1/1	1/1	Taylor and McPhail (1986)
Lotidae	*Lota lota*	0/1					Nelichik (1978)
Melanotaeniidae	*Melanotaenia duboulayi*	0/1		1/1	1/1	0/1	McGuigan et al. (2003)
	Melanotaenia eachamensis	0/1		1/1		1/1	McGuigan et al. (2003)
Poeciliidae	*Poecilia reticulata*	0/2			2/2		Nicoletto (1996), Nicoletto and Kodric-Brown (1999), Hendry et al. (2006)
	Poeciliopsis turrabarensis	1/1					Zúñiga-Vega et al. (2007)
Retropinnidae	*Retropinna retropinna*	1/1		1/1			Northcote and Ward (1985), Meyer-Rochow and Ingram (1993)
Salmonidae	*Coregonus nasus*		1/1				Chudobiak et al. (2002)
	Oncorhynchus kisutch	1/2			1/1	1/1	Taylor and McPhail (1985a, 1985b), Swain and Holtby (1989)
	Oncorhynchus mykiss	1/3			1/1		Thomas and Donahoo (1977), Keeley et al. (2005, 2007)
	Oncorhynchus nerka	8/10	1/1[a]		2/2		Taylor and Foote (1991), Blair et al. (1993), Hendry and Quinn (1997), Taylor et al. (1997), Hamon et al. (2000), Hendry et al. (2000), Quinn et al. (2001), Lee et al. (2003), Winans et al. (2003), Crossin et al. (2004), Ramstad (2006)
	Oncorhynchus tshawytscha		1/1[a]				Beacham et al. (1989)
	Salmo salar	3/5	1/1[a]		2/2	0/1	Riddell and Leggett (1981), Riddell et al. (1981), Claytor et al. (1991), Peake et al. (1997), McDonald et al. (1998), Pakkasmaa and Piironen (2000), Solem et al (2006)
	Salmo trutta	2/2	1/1[a]				Yevin (1977), Pakkasmaa and Piironen (2000)
	Salvelinus alpinus	1/1	1/1[a]				Peres-Neto and Magnan (2004)
	Salvelinus fontinalis	4/5	3/3[a]				McLaughlin and Grant (1994), Imre et al. (2002), Peres-Neto and Magnan (2004), Fraser and Bernatchez (2005), Morinville and Rasmussen (2008)
	Thymallus thymallus	2/2					Salonen (2005)

BS, body shape; CF, caudal-fin shape; M, muscle architecture; S, steady swimming; U, unsteady swimming. [a]Caudal-fin shape measured by caudal-fin height.

Table A2 Summary of results for each study included in the interspecific analysis

Family	BS	CF	M	S	U	Reference
Centrarchidae	1/1			1/1		Schaefer et al. (1999)
Cobitidae	1/1					Vasil'eva et al. (2003)
Cottidae	1/1					Andreasson (1969)
Cyprinidae	0/1					Felley (1984)
	1/1			1/1		Chuang et al. (2006)
		1/1		1/1		Chan (2001, Ch. 4)
Galaxiidae	1/1					Pollard (1971)
Percidae	0/1					Guill et al. (2003)
	0/1					Paine et al. (1982)
	1/1					Matthews (1985)
Poeciliidae	1/1					Langerhans and Reznick (in press)
Salmonidae	1/1					Bisson et al. (1988)
				1/1		Hawkins and Quinn (1996)
				1/1	1/1	Peake et al. (1997)
Multiple families				1/1		Mitchell (1989)
	0/1					Chan (2001, Ch.1)
	1/1	1/1				Mahon (1984)
	1/1					Wikramanayake (1990)
	1/1					Poff and Allan (1995)
	1/1	1/1[a]				Bhat (2005)
	1/1			1/1		Sagnes and Statzer (unpublished manuscript)

Abbreviations follow Appendix 1. [a]Caudal-fin shape measured by caudal-fin height.

References

Andreasson S. 1969. Interrelations between *Cottus poecilopus* Heckel and *C. gobio* L. (Pisces) in a regulated north Swedish river. Oikos 20:540–6.

Arnold SJ. 1983. Morphology, performance and fitness. Am Zool 23:347–61.

Baranyi C, Gollmann G, Bobin M. 1997. Genetic and morphological variability in roach *Rutilus rutilus*, from Austria. Hydrobiologia 350:13–23.

Beacham TD, Murray CB, Withler RE. 1989. Age, morphology, and biochemical genetic variation of Yukon River chinook salmon. Trans Am Fish Soc 118:46–63.

Bhagat Y, Fox MG, Ferreira MT. 2006. Morphological differentiation in introduced pumpkinseed *Lepomis gibbosus* (L.) occupying different habitat zones in Portuguese reservoirs. J Fish Biol 69:79–94.

Bhat A. 2005. Ecomorphological correlates in tropical stream fishes of southern India. Environ Biol Fishes 73:211–25.

Bisson PA, Sullivan K, Nielsen JL. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans Am Fish Soc 117:262–73.

Blair GR, Rogers DE, Quinn TP. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak river system, Bristol Bay, Alaska. Trans Am Fish Soc 122:550–9.

Blake RW. 1983. Fish locomotion. Cambridge: Cambridge University Press.

Blake RW. 2004. Fish functional design and swimming performance. J Fish Biol 65:1193–222.

Bogdanov BE. 2007. Variation of stone sculpin *Paracottus knerii* (Cottidae, Scorpaeniformes) of Baikal and Waters of Baikal region. J Ichthy 47:162–74.

Boily P, Magnan P. 2002. Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). J Exp Biol 205:1031–6.

Bone Q. 1978. Locomotor muscle. In: Hoar WS, Randall DJ, editors. Fish physiology. London: Academic Press. p 361–424.

Brainerd EL, Patek SN. 1998. Vertebral column morphology, C-start curvature, and the evolution of mechanical defenses in tetraodontiform fishes. Copeia 1998:971–84.

Brinsmead J, Fox MG. 2002. Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. J Fish Biol 61:1619–38.

Chan MD. 2001. Fish ecomorphology: predicting habitat preferences of stream fishes from their body shape

[Dissertation]. Department of Fisheries and Wildlife Sciences. Blacksburg: Virginia Polytechnic Institute and State University.

Chapman LJ, Galis F, Shinn J. 2000. Phenotypic plasticity and the possible role of genetic assimilation: hypoxia-induced trade-offs in the morphological traits of an African cichlid. Ecol Lett 3:387–93.

Chuang LC, Lin YS, Liang SH. 2006. Ecomorphological comparison and habitat preference of two cyprinid fishes, *Varicorhinus barbatulus* and *Candidia barbatus*, in Hapen Creek of northern Taiwan. Zool Stud 45:114–23.

Chudobiak DH, Tallman RF, Abrahams MV. 2002. Variation in the morphology of two populations of Arctic broad whitefish (*Coregonus nasus* Pallas), in the Mackenzie River. In: Todd TN, Flerscher G, editors. Biology and management of coregonid fishes - 1999: Archiv für Hydrobiologie Special Issues 57:291–305.

Claytor RR, Maccrimmon HR, Gots BL. 1991. Continental and ecological variance components of European and North American Atlantic salmon (*Salmo salar*) phenotypes. Biol J Linnean Soc 44:203–29.

Clifton KB, Motta PJ. 1998. Feeding morphology, diet, and ecomorphological relationships among five Caribbean labrids (Teleostei, Labridae). Copeia 1998:953–66.

Colgate JE, Lynch KM. 2004. Mechanics and control of swimming: a review. IEEE J Oceanic Eng 29:660–73.

Collar DC, Wainwright PC. 2006. Discordance between morphological and mechanical diversity in the feeding mechanism of centrarchid fishes. Evolution 60:2575–84.

Collyer ML, Novak JM, Stockwell CA. 2005. Morphological divergence of native and recently established populations of White Sands Pupfish (*Cyprinodon tularosa*). Copeia 2005:1–11.

Coughlin DJ. 2002. Aerobic muscle function during steady swimming in fish. Fish Fish 3:63–78.

Couñago R, Chen S, Shamoo Y. 2006. In vivo molecular evolution reveals biophysical origins of organismal fitness. Mol Cell 22:441–9.

Crispo E. 2007. The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. Evolution 61:2469–79.

Crossin GT, Hinch SG, Farrell AP, Higgs DA, Lotto AG, Oakes JD, Healey MC. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J Fish Biol 65:788–810.

Day T, Pritchard J, Schluter D. 1994. A comparison of two sticklebacks. Evolution 48:1723–34.

Dickinson MH, Farley CT, Full RJ, Koehl MAR, Kram R, Lehman S. 2000. How animals move: an integrative view. Science 288:100–6.

Domenici P. 2003. Habitat, body design and the swimming performance of fish. In: Bels VL, Gasc J-P, Casinos A, editors. Vertebrate biomechanics and evolution. Oxford: BIOS Scientific Publishers Ltd. p 137–60.

Domenici P, Blake RW. 1997. The kinematics and performance of fish fast-start swimming. J Exp Biol 200:1165–78.

Emerson SB. 1988. Testing for historical patterns of change: a case study with frog pectoral girdles. Paleobiology 14:174–86.

Felley JD. 1984. Multivariate identification of morphological-environmental relationships within the Cyprinidae (Pisces). Copeia 1984:442–55.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Fisher R, Hogan JD. 2007. Morphological predictors of swimming speed: a case study of pre-settlement juvenile coral reef fishes. J Exp Biol 210:2436–43.

Fraser DJ, Bernatchez L. 2005. Adaptive migratory divergence among sympatric brook charr populations. Evolution 59:611–24.

Funk DJ, Nosil P, Etges WJ. 2006. Ecological divergence exhibits consistently positive associations with reproductive isolation across disparate taxa. Proc Natl Acad Sci USA 103:3209–13.

Gatz AJJ. 1979. Ecological morphology of freshwater stream fishes. Tulane Stud Zool Bot 21:91–124.

Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407.

Ghalambor CK, Walker JA, Reznick DN. 2003. Multi-trait selection, adaptation, and constraints on the evolution of burst swimming performance. Integr Comp Biol 43:431–8.

Gould SJ. 2002. The structure of evolutionary theory. Cambridge, MA: Harvard Univeristy Press.

Grant PR, Grant BR. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707–11.

Greer-Walker M, Pull GA. 1975. Survey of red and white muscle in marine fish. J Fish Biol 7:295–300.

Guill JM, Hood CS, Heins DC. 2003. Body shape variation within and among three species of darters (Perciformes: Percidae). Ecol Freshw Fish 12:134–40.

Hamon TR, Foote CJ, Hilborn R, Rogers DE. 2000. Selection on morphology of spawning wild sockeye salmon by a gill-net fishery. Trans Am Fish Soc 129:1300–15.

Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press.

Hawkins DK, Quinn TP. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. Can J Fish Aquat Sci 53:1487–96.

Hendry AP, Kelly ML, Kinnison MT, Reznick DN. 2006. Parallel evolution of the sexes? Effects of predation and habitat features on the size and shape of wild guppies. J Evol Biol 19:741–54.

Hendry AP, Quinn TP. 1997. Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations in relation to habitat features and ancestral affinities. Can J Fish Aquat Sci 54:75–84.

Hendry AP, Wenburg JK, Bentzen P, Volk EC, Quinn TP. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science 290:516–8.

Hobson ES. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: Sale PF, editor. The ecology of fishes on coral reefs. San Diego: Academic Press. p 69–95.

Hoerner SF. 1965. Fluid-dynamic drag. Midland Park (published by the author).

Hubbs CL. 1940. Speciation of fishes. Am Nat 74:198–211.

Hubbs CL. 1941. The relation of hydrological conditions to speciation in fishes. In: Needham JG, Sears PB, Leopold A, editors. A symposium on hydrobiology. Madison: University of Wisconsin Press. p 182–95.

Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 287:308–9.

Hynes HBN. 1970. The ecology of running waters. Toronto: University of Toronto Press.

Imre I, McLaughlin RL, Noakes DLG. 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. J Fish Biol 61:1171–81.

Jayne BC, Lauder GV. 1994. How swimming fish use slow and fast muscle-fibres: implications for models of vertebrate muscle recruitment. J Comp Phys A 175:123–31.

Keast A, Webb D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J Fish Res Board Can 23:1845–74.

Keeley ER, Parkinson EA, Taylor EB. 2005. Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia. Can J Fish Aquat Sci 62:1523–39.

Keeley ER, Parkinson EA, Taylor EB. 2007. The origins of ecotypic variation of rainbow trout: a test of environmental vs. genetically based differences in morphology. J Evol Biol 20:725–36.

Kenney BC. 1982. Beware of spurious self-correlations! Water Resour Res 18:1041–8.

Kerfoot JR, Schaefer JF. 2006. Ecomorphology and habitat utilization of *Cottus* species. Environ Biol Fishes 76:1–13.

Koehl MAR. 1996. When does morphology matter? Annu Rev Ecol Syst 27:501–42.

Koehl MAR. 1999. Ecological biomechanics of benthic organisms: life history mechanical design and temporal patterns of mechanical stress. J Exp Biol 202:3469–76.

Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. Evolution 33:402–16.

Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. Evolution 37:1210–26.

Langerhans RB. 2006. Evolutionary consequences of predation: avoidance, escape, reproduction, and diversification. In: Elewa AMT, editor. Predation in organisms: a distinct phenomenon. Heidelberg, Germany: Springer-Verlag. p 177–220.

Langerhans RB, Chapman LJ, Dewitt TJ. 2007a. Complex phenotype-environment associations revealed in an East African cyprinid. J Evol Biol 20:1171–81.

Langerhans RB, DeWitt TJ. 2004. Shared and unique features of evolutionary diversification. Am Nat 164:335–49.

Langerhans RB, Gifford ME, Joseph EO. 2007b. Ecological speciation in *Gambusia* fishes. Evolution 61:2056–74.

Langerhans RB, Knouft JH, Losos JB. 2006. Shared and unique features of diversification in Greater Antillean *Anolis* ecomorphs. Evolution 60:362–9.

Langerhans RB, Layman CA, Langerhans AK, Dewitt TJ. 2003. Habitat-associated morphological divergence in two Neotropical fish species. Biol J Linn Soc 80:689–98.

Langerhans RB, Layman CA, Shokrollahi AM, DeWitt TJ. 2004. Predator-driven phenotypic diversification in Gambusia affinis. Evolution 58:2305–18.

Langerhans RB, Reznick DN. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. In: Domenici P, Kapoor BG, editors. Fish locomotion: an etho-ecological perspective. Enfield: Science Publishers. In Press.

Lauder GV. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology 7:430–42.

Lauder GV. 1990. Functional morphology and systematics: studying functional patterns in an historical context. Annu Rev Ecol Syst 21:317–40.

Lauder GV. 1996. The argument from design. In: Rose MR, Lauder GV, editors. Adaptation. San Diego: Academic Press. p 55–92.

Lauder GV. 2005. Locomotion. In: Evans DH, Claiborne JB, editors. The physiology of fishes. Boca Raton: CRC Press. p 3–46.

Lauder GV, Drucker EG. 2002. Forces, fishes, and fluids: hydrodynamic mechanisms of aquatic locomotion. News Physiol Sci 17:235–40.

Lee CG, Farrell AP, Lotto A, MacNutt MJ, Hinch SG, Healey MC. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. J Exp Biol 206:3239–51.

Levins R. 1968. Evolution in changing environments. NJ: Princeton University Press.

Liem KF. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Syst Zool 22:425–41.

Lighthill MJ. 1969. Hydromechanics of aquatic animal propulsion: a survey. A Rev Fluid Mech 1:413–46.

Lighthill MJ. 1970. Aquatic animal propulsion of high hydromechanical efficiency. J Fluid Mech 44:265–301.

Lighthill MJ. 1975. Mathematical biofluiddynamics. Philadelphia: Society for Applied and Industrial Mathematics.

Long JH, Nipper KS. 1996. The importance of body stiffness in undulatory propulsion. Am Zool 36:678–94.

Losos JB. 1990. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. Evolution 44:1189–203.

Losos JB, Creer DA, Schulte JA. 2002. Cautionary comments on the measurement of maximum locomotor capabilities. J Zool 258:57–61.

Losos JB, Jackman TR, Larson A, de Queiroz K, Rodriguez-Schettino L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–8.

Mahon R. 1984. Divergent structure in fish taxocenes of north temperate streams. Can J Fish Aquat Sci 41:330–50.

Martins EP. 2000. Adaptation and the comparative method. Trends Ecol Evol 15:296–9.

Matthews WJ. 1985. Critical current speeds and microhabitats of the benthic fishes *Percina roanoka* and *Etheostoma flabellare*. Environ Biol Fishes 12:303–8.

McDonald DG, Milligan CL, McFarlane WJ, Croke S, Currie S, Hooke B, Angus RB, Tufts BL, Davidson K. 1998. Condition and performance of juvenile Atlantic salmon (*Salmo salar*): effects of rearing practices on hatchery fish and comparison with wild fish. Can J Fish Aquat Sci 55:1208–19.

McDowall RM. 1972. The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxias maculatus* (Jenyns). J Roy Soc NZ 2:325–67.

McGuigan K, Franklin CE, Moritz C, Blows MW. 2003. Adaptation of rainbow fish to lake and stream habitats. Evolution 57:104–18.

McHenry MJ, Lauder GV. 2006. Ontogeny of form and function: locomotor morphology and drag in zebrafish (*Danio rerio*). J Morphol 267:1099–109.

McLaughlin RL, Grant JWA. 1994. Morphological and behavioral differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow-running vs fast-running water. Environ Biol Fishes 39:289–300.

McLaughlin RL, Kramer DL. 1991. The association between amount of red muscle and mobility in fishes: a statistical evaluation. Environ Biol Fishes 30:369–78.

Meyer-Rochow VB, Ingram JR. 1993. Red-white muscle distribution and fiber growth dynamics: a comparison between lacustrine and riverine populations of the Southern smelt *Retropinna retropinna* Richardson. Proc R Soc Lond Ser B-Biol Sci 252:85–92.

Mitchell CP. 1989. Swimming performances of some native freshwater fishes. NZ J Mar Freshw Res 23:181–7.

Morinville GR, Rasmussen JB. 2008. Distinguishing between juvenile anadromous and resident brook trout (*Salvelinus fontinalis*) using morphology. Environ Biol Fishes 81:171–84.

Müller UK, van Leeuwen JL. 2006. Undulatory fish swimming: from muscles to flow. Fish Fish 7:84–103.

Neat FC, Lengkeek W, Westerbeek EP, Laarhoven B, Videler JJ. 2003. Behavioural and morphological differences between lake and river populations of *Salaria fluviatilis*. J Fish Biol 63:374–87.

Nelichik VA. 1978. Morphometric features of the burbot, *Lota lota*, of the Upper Tuloma Reservoir. J Ichthy 18:756–64.

Nelson JA, Gotwalt PS, Snodgrass JW. 2003. Swimming performance of blacknose dace (*Rhinichthys atratulus*) mirrors home-stream current velocity. Can J Fish Aquat Sci 60:301–8.

Nicoletto PF. 1996. The influence of water velocity on the display behavior of male guppies, *Poecilia reticulata*. Behav Ecol 7:272–8.

Nicoletto PF, Kodric-Brown A. 1999. The relationship among swimming performance, courtship behavior, and carotenoid pigmentation of guppies in four rivers of Trinidad. Environ Biol Fishes 55:227–35.

Northcote TG, Ward FJ. 1985. Lake resident and migratory smelt, *Retropinna retropinna* (Richardson), of the lower Waikato River system, New Zealand. J Fish Biol 27:113–29.

Pabst DA. 1996. Springs in swimming animals. Am Zool 36:723–35.

Paine MD, Dodson JJ, Power G. 1982. Habitat and food resource partitioning among four species of darters (Percidae, *Etheostoma*) in a southern Ontario stream. Can J Zool 60:1635–41.

Pakkasmaa S, Piironen J. 2000. Water velocity shapes juvenile salmonids. Evol Ecol 14:721–30.

Peake S, McKinley RS, Scruton DA. 1997. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. J Fish Biol 51:710–23.

Pedley TJ, Hill SJ. 1999. Large-amplitude undulatory fish swimming: fluid mechanics coupled to internal mechanics. J Exp Biol 202:3431–8.

Peres-Neto PR, Magnan P. 2004. The influence of swimming demand on phenotypic plasticity and morphological integration: a comparison of two polymorphic charr species. Oecologia 140:36–45.

Pigliucci M, Murren CJ. 2003. Genetic assimilation and a possible evolutionary paradox: can macroevolution sometimes be so fast as to pass us by? Evolution 57:1455–64.

Pigliucci M, Murren CJ, Schlichting CD. 2006. Phenotypic plasticity and evolution by genetic assimilation. J Exp Biol 209:2362–67.

Plaut I. 2001. Critical swimming speed: its ecological relevance. Comp Biochem Physiol A-Mol Integr Physiol 131:41–50.

Poff NL, Allan JD. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76:606–27.

Pollard DA. 1971. Biology of a landlocked form of normally catadromous salmoniform fish *Galaxias maculatus* (Jenyns) II. Morphology and systematic relationships. Aust J Mar Fresh Res 22:125–37.

Quinn TP, Wetzel L, Bishop S, Overberg K, Rogers DE. 2001. Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. Can J Zool 79:1782–93.

Ramstad KM. 2006. Colonization and local adaptation of sockeye salmon (*Oncorhynchus nerka*) of Lake Clark, Alaska [Dissertation]. Department of organismal biology and ecology. Missoula: University of Montana.

Reidy S, Kerr S, Nelson J. 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod J Exp Biol 203:347–57.

Reznick DN, Shaw FH, Rodd FH, Shaw RG. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934–7.

Riddell BE, Leggett WC. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 38:308–20.

Riddell BE, Leggett WC, Saunders RL. 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon (*Salmo salar*) native to tributaries of the S.W. Miramichi River, N.B. Can J Fish Aquat Sci 38:321–33.

Robinson BW, Parsons KJ. 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. Can J Fish Aquat Sci 59:1819–33.

Robinson BW, Wilson DS. 1994. Character release and displacement in fishes: a neglected literature. Am Nat 144:596–627.

Robinson BW, Wilson DS. 1996. Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (*Lepomis gibbosus*). Evol Ecol 10:631–52.

Roff DA. 2002. Life history evolution. Sunderland, MA: Sinauer Associates Inc.

Ruehl CB, DeWitt TJ. 2005. Trophic plasticity and fine-grained resource variation in populations of western mosquitofish, *Gambusia affinis*. Evol Ecol Res 7:801–19.

Sagnes P, Statzner B. Hydrodynamic abilities of riverine fish: a functional link between morphology and physical habitat use. Unpublished manuscript.

Salonen A. 2005. Behavioural and morphological variation in European grayling, *Thymallus thymallus*, populations [Dissertation]. Department of biological and environmental sciences. Helsinki: University of Helsinki.

Schaefer SA, Lauder GV. 1996. Testing historical hypotheses of morphological change: biomechanical decoupling in loricarioid catfishes. Evolution 50:1661–75.

Schaefer JF, Lutterschmidt WI, Hill LG. 1999. Physiological performance and stream microhabitat use by the centrarchids *Lepomis megalotis* and *Lepomis macrochirus*. Environ Biol Fishes 54:303–12.

Schlichting CD. 2004. The role of phenotypic plasticity in diversification. In: DeWitt TJ, Scheiner SM, editors. Phenotypic plasticity. Functional and conceptual approaches. New York: Oxford University Press. p 191–200.

Schlichting CD, Pigliucci M. 1998. Phenotypic evolution: a reaction norm perspective. Sunderland, MA: Sinauer Associates, Inc.

Schluter D. 2000. The ecology of adaptive radiation. Oxford: Oxford University Press.

Schultz WW, Webb PW. 2002. Power requirements of swimming: do new methods resolve old questions? Integr Comp Biol 42:1018–25.

Sfakiotakis M, Lane DM, Davies JBC. 1999. Review of fish swimming modes for aquatic locomotion. IEEE J Oceanic Eng 24:237–52.

Shadwick RE, Lauder GV. 2006. Fish biomechanics. San Diego: Elsevier Academic Press.

Sidlauskas B, Chernoff B, Machado-Allison A. 2006. Geographic and environmental variation in *Bryconops* sp cf. *melanurus* (Ostariophysi: Characidae) from the Brazilian Pantanal. Ichthyol Res 53:24–33.

Solem O, Berg OK, Kjosnes AJ. 2006. Inter- and intra-population morphological differences between wild and farmed Atlantic salmon juveniles. J Fish Biol 69:1466–81.

Šprem N, Piria M, Treer T. 2001. Morfološke osobine i dužinsko-maseni odnosi triju populacija bodorki (*Rutilus rutilus*) u sjeverozapadnoj Hrvatskoj. Ribarstvo 59:99–106.

Swain DP, Holtby LB. 1989. Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. Can J Fish Aquat Sci 46:1406–14.

Szlachciak J. 2005. Morphological features of zope, *Abramis ballerus*, from the middle stretch of the Odra River, Poland. Acta Ichthy Piscat 35:93–101.

Taylor EB, Foote CJ. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). J Fish Biol 38:407–19.

Taylor EB, Harvey S, Pollard S, Volpe J. 1997. Postglacial genetic differentiation of reproductive ecotypes of kokanee *Oncorhynchus nerka* in Okanagan Lake, British Columbia. Mol Ecol 6:503–17.

Taylor EB, McPhail JD. 1985a. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can J Fish Aquat Sci 42:2020–8.

Taylor EB, McPhail JD. 1985b. Variation in burst, & prolonged swimming performance among British Columbia populations of coho salmon, Oncorhynchus kisutch. Can J Fish Aquat Sci 42:2029–33.

Taylor EB, McPhail JD. 1986. Prolonged and burst swimming in anadromous and freshwater threespine stickleback, *Gasterosteus aculeatus*. Can J Zool 64:416–20.

Thomas AE, Donahoo MJ. 1977. Differences in swimming performance among strains of rainbow trout (*Salmo gairdneri*). J Fish Res Board Can 34:304–7.

Thys TM, Blank JM, Coughlin DJ, Schachat F. 2001. Longitudinal variation in muscle protein expression and contraction kinetics of largemouth bass axial muscle. J Exp Biol 204:4249–57.

Trautman MB. 1931. *Notropis volucellus wickliffi*, a new subspecies of cyprinid fish from Ohio and upper Mississippi rivers. Ohio J Sci 31:468–74.

Travisano M, Mongold JA, Bennett AF, Lenski RE. 1995. Experimental tests of the roles of adaptation, chance, and history in evolution. Science 267:87–90.

Triantafyllou MS, Triantafyllou GS, Yue DKP. 2000. Hydrodynamics of fishlike swimming. A Rev Fluid Mech 32:33–53.

Van Damme R, Wilson RS, Vanhooydonck B, Aerts P. 2002. Performance constraints in decathletes. Nature 415:755–6.

Vasil'eva ED, Vasil'ev VP, Skomorokhov MO. 2003. Loaches (*Misgurnus*, Cobitidae) of the Russian Asia. II. Morphology, synonymy, diagnoses, biology, and distribution. J Ichthy 43:501–10.

Videler JJ. 1993. Fish swimming. London: Chapman & Hall.

Vogel S. 1994. Life in moving fluids. Princeton: Princeton University Press.

Wainwright PC. 1996. Ecological explanation through functional morphology: the feeding biology of sunfishes. Ecology 77:1336–43.

Wainwright PC. 2007. Functional versus morphological diversity in macroevolution. Annu Rev Ecol Evol Syst 38:381–401.

Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD. 2005. Many-to-one mapping of form to function: a general principle in organismal design? Integr Comp Biol 45:256–62.

Wainwright P, Carroll AM, Collar DC, Day SW, Higham TE, Holzman RA. 2007. Suction feeding mechanics, performance, and diversity in fishes. Integr Comp Biol 47:96–106.

Wainwright PC, Reilly SM. 1994. Ecological morphology: integrative organismal biology. Chicago: University of Chicago Press.

Wainwright PC, Richard BA. 1995. Predicting patterns of prey use from morphology of fishes. Environ Biol Fishes 44:97–113.

Wainwright PC, Turingan RG. 1993. Coupled versus uncoupled functional systems: motor plasticity in the queen triggerfish *Balistes vetula*. J Exp Biol 180:209–27.

Walker JA. 1997. Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. Biol J Linn Soc 61:3–50.

Walker JA. 2007. A general model of functional constraints on phenotypic evolution. Am Nat 170:681–9.

Webb PW. 1975. Hydrodynamics and energetics of fish propulsion. Bull Fish Res Board Canada 190:1–159.

Webb PW. 1982. Locomotor patterns in the evolution of Actinopterygian fishes. Am Zool 22:329–42.

Webb PW. 1983. Speed, acceleration and manoeuvrability of two teleost fishes. J Exp Biol 102:115–22.

Webb PW. 1984. Body form, locomotion, and foraging in aquatic vertebrates. Am Zool 24:107–20.

Webb PW. 1986. Locomotion and predator-prey relationships. In: Lauder GV, Feder ME, editors. Predator-prey relationships. Chicago: University of Chicago Press. p 24–41.

Webb PW, Weihs D. 1983. Fish biomechanics. New York: Praeger.

Weihs D. 1989. Design features and mechanics of axial locomotion in fish. Am Zool 29:151–160.

West-Eberhard MJ. 2003. Developmental plasticity and evolution. Oxford: Oxford University Press.

Westneat MW. 1995. Feeding, function, and phylogeny: analysis of historical biomechanics in Labrid fishes using comparative methods. Syst Biol 44:361–83.

Wikramanayake ED. 1990. Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. Ecology 71:1756–64.

Winans GA, Pollard S, Kuligowski DR. 2003. Two reproductive life history types of kokanee, *Onchorynchus nerka*, exhibit multivariate morphometric and protein genetic differentiation. Environ Biol Fishes 67:87–100.

Wu TY. 1971. Hydromechanics of swimming propulsion. Part 1. Swimming of a two-dimensional flexible plate at variable forward speeds in an inviscid fluid. J Fluid Mech 46:337–55.

Yevsin VN. 1977. Morphological characteristics and variability of the summer sea trout (*Salmo trutta*) from the Pulmg'a and Malaya Kumzhevaya rivers. J Ichthy 17:350–6.

Zúñiga-Vega JJ, Reznick DN, Johnson JB. 2007. Habitat predicts reproductive superfetation and body shape in the livebearing fish *Poeciliopsis turrubarensis*. Oikos 116:995–1005.