

Trait-Based Approaches in the Analysis of Stream Fish Communities

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Abstract.—Species traits are used to study the functional organization of fish communities for a range of reasons, from simply reducing data dimensionality to providing mechanistic explanations for observed variation in communities. Ecological and life history traits have been used to understand the basic ecology of fishes and predict (1) species and community responses to habitat and climate alteration, and (2) species extinction, species invasion, and community homogenization. Many approaches in this arena have been developed during the past three decades, but they often have not been integrated with related ecological concepts or subdisciplines, which has led to confusion in terminology. We review 102 studies of species traits and then summarize patterns in traits being used and questions being addressed with trait-based approaches. Overall, studies of fish–habitat relationships that apply habitat templates and hierarchical filters dominate our sample; the most frequently used traits are related to feeding. We define and show the relationships among key terms such as fundamental and realized niches; functional traits, performance, and fitness; tactic, trait-state, syndromes, and strategies; and guilds and functional groups. We propose accelerating research to (1) quantify trait plasticity, (2) identify traits useful for testing ecological hypotheses, (3) model habitat and biotic interactions in communities while explicitly accounting for phylogenetic relationships, (4) explore how traits control community assembly, and (5) document the importance of traits in fish–community responses to anthropogenic change and in delivering ecosystem services. Further synthesis of these topics is still needed to develop concepts, models, and principles that can unify the disparate approaches taken in trait-based analysis of fish communities, link fish community ecology to general community ecology, and inform sustainable management of ecosystems.

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Glossary

Biological trait: A trait that reflects physiological requirements, morphological adaptations, and life histories innate to an organism.

Ecological trait: A trait that reflects an organism's environmental preferences and associated behaviors.

Functional group: A group of co-occurring species that perform a common ecosystem function by their mode of resource utilization.

Guild: A group of co-occurring species that exploit a common resource in a similar way.

Performance: The capacity of an organism to maintain biomass over many generations.

Syndrome: A suite of coevolved traits associated with an organism's performance and linked to multiple major activities (e.g., feeding, spawning, and resting).

Strategy: A suite of coevolved traits associated with an organism's performance and linked to a single major activity (e.g., feeding).

Tactic: The observed state of a trait expressed by an individual at a given time.

Trait: A well-defined and measurable morphological, physiological, behavioral, ecological, or life-history expression of an individual organism's adaptations to its environment that may also be regarded as a property of the taxon or population to which the individual belongs.

Trait-state: A species' or population's modal tactic of a given trait.

Introduction

Species traits provide a promising means to establish general rules in community ecology. It is widely concluded that such generalities exist, but mainly as expressed through traits along environmental or landscape gradients (Townsend and Hildrew 1994; Poff 1997; Lamouroux et al. 2002; McGill et al. 2006a). While the search for general patterns in traits within and among communities can be an end in itself (Gatz 1979), traits may also provide a lens through which solutions

to major challenges in fish management and conservation may be found. Trait-based approaches are common in both theoretical and applied fish ecology, addressing topics such as (1) responses of species and communities to habitat alterations (generally intertwined with biological assessment and monitoring) or climate change; (2) processes of species extinction, species invasion, and assemblage homogenization; and (3) underlying mechanisms of community assembly. General rules in community ecology could form the basis for management and conservation tools that

apply broadly across taxonomic groups and geographic areas.

With the wide and growing applications of traits in stream and fish community ecology (Poff et al. 2006; Vieira et al. 2006), there is also a divergence in terminology and concepts between stream community ecology, general community ecology, and plant community ecology in particular (Kearney and Porter 2006; McGill et al. 2006a, 2006b). The fast-growing research in habitat template-type models (Townsend and Hildrew 1994; Lamouroux et al. 2002; Goldstein and Meador 2004) has roots in terrestrial entomology and plant ecology (Southwood 1977; Southwood 1988). Therefore, fish ecologists have much to be gained by interacting with plant ecologists, as suggested by Matthews (1998). The literature on trait-based approaches in community ecology is extensive, which makes synthesis and synergy of ideas across taxa and habitats all the more necessary to guide future research.

For trait-based approaches to contribute to community ecology theories that are useful across taxa and ecosystems, existing knowledge and concepts need to be synthesized. In particular, we suggest that the rapidly expanding lexicon be streamlined, that data needs be clearly articulated, and that methodological limitations be recognized and addressed. Our objectives in this chapter are to (1) provide an overview of trait-based approaches in community ecology, with emphasis on parallels and contrasts between fish community ecology and plant community ecology; (2) synthesize existing knowledge and conceptual models applied in trait-based community analyses; (3) clarify selected terms used in the literature on trait-based analyses and their relationships with levels of ecological organization; and (4) develop a set of key research topics to advance trait-based approaches in stream fish community ecology. We address these objectives

in an integrated manner rather than as separate sections in this chapter. Because of space constraints, we focus on research directions rather than empirical results. Finally, although our literature review draws from concepts and empirical examples in fish ecology in general, our synthesis focuses on using trait-based approaches to advance our understanding of stream fish communities.

Stream Fish Community Ecology in a Broader Context

Trait-based approaches have multiple origins but little integration in community ecology. A recent review of community ecology argued in favor of seeking general rules for using traits (McGill et al. 2006a). Subsequent critique and rebuttal (Kearney and Porter 2006; McGill et al. 2006b) underscored the apparent disconnect between the literature on stream community ecology and that purported to represent community ecology in general. Kearney and Porter argued that the tools required to implement McGill et al.'s (2006a) proposed research agenda were already well developed and being applied under such guises as dynamic energy budget models, the geometrical framework of organismal stoichiometry, and biophysical ecology. Using references largely from plant ecology, McGill et al. (2006a) built their case for a "functional traits research program" focused on traits, environmental gradients, the interaction milieu, and performance currencies. They argued "these themes are linked by taking a more physiological approach, by using concepts that are measurable in well defined units and by avoiding short-term population dynamics." In their response to Kearney and Porter, McGill et al. (2006b) viewed Kearney and Porter's list of well-developed tools as restricted to the physiological (functional) component of their four-part research agenda:

McGill et al. (2006b) recommended that community ecologists should (1) pay more attention to and make greater use of, functional ecology; (2) emphasize quantitative measures of traits, performance currencies, and environment and explore relationships among these factors; (3) explore processes regulating both fundamental and realized niches (i.e., the interaction milieu or species interactions); and (4) shift from analysis of variance (ANOVA)-based approaches to analyses of mathematical relationships between quantitative measures of traits and environment. Although neither set of these authors clearly distinguished between physiological and functional ecology, we view functional ecology as much broader than physiological ecology.

The foregoing research agenda does not seem as urgent for stream ecology as for plant ecology. A quick survey of the stream community ecology literature indicates that considerable relevant research had been conducted prior to McGill et al.'s (2006a) call to arms, which reflects a lack of integration of literature across taxa and habitats. In particular, the literature on species–habitat relationships is almost overwhelming (e.g., Pont et al. 2005). Though examples are not nearly as preponderant, traits are increasingly being used to link species to their environment in many applied research areas. These uses include explaining changes in assemblage composition due to habitat alteration (Berkman and Rabeni 1987; Poff and Allan 1995; Goldstein and Meador 2005; Hoeinghaus et al. 2006; Tedesco et al. 2008), explaining mechanisms of nonnative invasions and assemblage homogenization (Scott and Helfman 2001; Vila-Gispert et al. 2005; Olden et al. 2006; Garcia-Berthou 2007), modeling species response to climate change (Daufresne et al. 2003), and explaining and predicting species extirpations and extinctions (Angermeier 1995; Parent and Schriml 1995; Johnston 1999;

Reynolds et al. 2005; Olden et al. 2006, 2008). Aquatic biological monitoring and assessments, employing trait-based metrics (Karr 1981; Karr et al. 1986; Angermeier et al. 2000; Pont et al. 2006; Welcomme et al. 2006) and used by regulatory agencies across countries and continents (Karr and Chu 2000), are excellent examples of the maturity of trait-based approaches in some areas of McGill et al.'s proposed research agenda. Trait-based modeling and applications continue to grow concomitantly with the development of more sophisticated multivariate analysis techniques (Diniz-Filho et al. 1998; Dray et al. 2003; Dray and Legendre 2008; Jackson et al. 2010, this volume). With the foregoing examples as a backdrop, we believe stream and fish community ecology has made important progress in trait-based analysis (Figure 1). Below, we describe how trait-based approaches in stream and fish community ecology have progressed beyond some fundamental questions but still lag behind McGill et al.'s agenda in others. Ultimately, we hope to lay a conceptual foundation to advance trait-based approaches in stream fish community ecology while fostering connections with general community ecology.

Overview of Trait-Based Approaches in Stream and Fish Community Ecology

Initial Approaches

Trait-based approaches to community ecology emerged at least six decades ago with the description of ecological groups of fishes by Kryzhanovskii (1949). The term “guild,” a group of co-occurring species that exploit a common resource in a similar way (Root 1967; Blondel 2003), appeared almost two decades later. Although the guild concept is of terrestrial origin, the closely related term “functional group” originated from studies of macroinvertebrate

Proposed research agenda for community ecology		Progress/5
1. Make use of physiological ecology.		• •
2. Link traits, performance currencies, and the environment.	Trait–environment relationships	• • • •
	Trait–performance relationships	• • •
	Performance–environment relationships	• • •
	Trait–performance–environment relationships	• • •
3. Emphasize both fundamental and realized niche (or interaction) processes.	Fundamental niche (species–habitat relationships)	• • • •
	Realized niche (species–habitat–biotic interactions)	• •
4. Develop multivariate trait–environment models.		• • •

Figure 1. Stream fish community ecology evaluated qualitatively against McGill et al.’s (2006a, 2006b) proposed research agenda for finding general rules of community ecology. Progress is scored qualitatively on a scale of 0–5, where 5 implies that no major research questions are currently outstanding.

trophic relations in streams (Cummins 1973, 1974). The functional approach to stream ecology soon encompassed fishes in the context of the river continuum concept (RCC), which theoretically linked functional groups with the longitudinal gradients in river habitat configurations and production dynamics (Vannote et al. 1980).

Concurrent with the development of the RCC was continuing advancement of trait-based studies of fish ecology. Of particular importance was Balon’s (1975, 1981a) improvement and description of Kryzhanovskii’s (1949) ecological groups of fishes as “reproductive guilds,” which also included a synthesis of the comprehensive family-level accounts of fish reproductive modes compiled by Breder and Rosen (1966). Balon’s approach transcended taxonomy by more explicitly recognizing similarities in reproductive modes among unrelated species while accounting for evolutionary relationships among guilds. Under this scheme, fishes were organized by ethological and ecological traits. Ethological groups range from broadcast spawners with no parental care for eggs or larvae to live-bearers, some of which provide months of internal gestation. Ecological groups were defined primarily with respect to the spawning substrates (e.g., open water, mineral, or vegetation) required for egg broadcasting, attachment, or nesting. No-

tably, the description of reproductive groups as guilds appears to have been the first major departure in fish ecology from Root’s (1967) original meaning of the term. This usage has persisted despite efforts to correct the discrepancy with other uses of “guild.”

Another significant early contribution to trait-based community ecology is the *habitat template* concept (Southwood 1977, 1988), which called attention to the spatiotemporal and physicochemical contexts that determine the adaptiveness of species traits. Schlosser (1987, 1990) invoked a habitat template to explain organization of headwater fish communities. He used life history traits such as longevity and adult length, but also recognized the effect of biotic interactions (specifically, competition and predation) on species distributions. The major premise of Southwood (1988) was that trade-offs between tactics produce different life history strategies over ecological time and certain strategies are favored through effects on fitness at certain positions along habitat gradients. Two important habitat axes forming the “template” include frequency of disturbance and general harshness. Southwood (1988) discussed several conditions for applying the habitat template model: (1) habitat axes are scaled to match the temporal (e.g., generation time) and spatial (e.g., trivial range) scales of study or-

ganisms being considered, (2) tactical trade-offs are constrained by phylogenetic history, and (3) the template constrains the range of life history strategies but does not impose uniformity.

In the years intervening Southwood's work, a hierarchical framework for classifying stream habitat was proposed by Frissell et al. (1986). This work was as seminal for defining stream habitat as Balon's (1975) was for grouping fishes across taxonomic boundaries. Frissell et al.'s framework provided spatially and temporally explicit dimensions to stream habitat templates across multiple scales. The spatial hierarchy of habitat ranged from microhabitat to the stream network (watershed) and the temporal hierarchy ranged from days to millennia. These dimensions reflected the scope needed for organism-centered scaling of axes in habitat template models. The hierarchical scaling of stream habitat also superimposed patchiness and dynamism on the RCC and expanded beyond the riparian zone the view of linkages between watershed and stream. Definitions of channel geomorphic units in streams were later refined (Hawkins et al. 1993), making it easier to adopt the Frissell et al. (1986) framework in modeling species-habitat relationships at the spatial scales where stream fishes have been studied most. Given impetus by Frissell et al.'s (1986) work, Townsend and Hildrew (1994) provided the most comprehensive definition yet of the spatial and temporal axes of the habitat template for streams, and summarized the species traits that enhance fitness at the extremes of these axes. Subsequent empirical studies have shown that traits of fish species in local stream assemblages are organized along spatial habitat gradients (Goldstein and Meador 2004; Yorick et al. 2008).

A second major trait-habitat concept developed in fish ecology, *hierarchical filters*, was introduced originally as the "successive screen principle" with the publication of a study of the summer fish communities of Brier Creek,

Oklahoma (Smith and Powell 1971). Jackson and Harvey (1989), Tonn (1990), and Tonn et al. (1990) contributed additional empirical evidence of this principle with fishes of lake communities in Canada, Finland, and northern Wisconsin. Tonn (1990) introduced the term "filters" for the first time in the context of predicting fish community responses to climate change. The hierarchical filters concept was later elaborated for stream habitats and species traits (Poff 1997). A major distinction between filters and habitat templates is that the former accounts for the evolutionary and dispersal history required for a species to contact the habitat template. Poff (1997) used the Frissell et al. (1986) framework to define abiotic habitat filters so that a species' presence in a microhabitat, for example, is constrained by selective forces at the watershed-scale. However, hierarchical filters can be biotic or abiotic factors that regulate species presence in or absence from an assemblage. Studies of species and trait distribution interpreted through the concepts of habitat template and hierarchical filters have converged on the conclusion that scale, biotic, and abiotic factors interact to determine the structure of a local fish assemblage.

Habitat templates and hierarchical filters are closely related to earlier conceptions of the ecological niche. Characterizing fish-habitat relationships is a form of *fundamental niche* modeling if taxa (usually species) are the subjects being modeled (i.e., the response variables). Alternatively, if the response variables in fish-habitat relationships are traits possessed by species (or other taxa), such analysis is more appropriately considered habitat template and/or landscape filters modeling, depending on how the habitat units are defined and structured across space and time. Although not typically couched as such, using structural and functional attributes of fish communities to evaluate effects of habitat modifications (Karr 1981;

Schlosser 1982a) were early applications of the habitat template idea in stream fish community ecology. Although conceived without explicitly considering species traits (Tonn 1990), hierarchical filter models are a form of *realized niche* models that apply both biotic and abiotic filters to explaining species distributions.

The concepts of fundamental niche and habitat template exclude effects of biotic interactions on species distributions. Some of the earliest attempts to incorporate species traits and biotic interactions into fish niche modeling were made through ecomorphological analyses. Gatz (1979) examined community organization of stream fishes through a morphological lens and concluded that patterns of species co-occurrence deviated from a random assortment. Ecomorphological research is reviewed elsewhere (Matthews 1998; Wootton 1998) and shows that morphology determines the autecology of feeding and microhabitat selection by fishes. However, advances in understanding realized niches of fishes through ecomorphological analyses have been limited by (1) the emphasis on feeding morphology and competition as the main biotic interaction, (2) the inevitably strong phylogenetic signal in morphological data, and (3) a lack of appropriate statistical and systematic tools to deal simultaneously with phylogenetic relationships in species pools and the multidimensionality of comparing all pairs of species (and life stages) in trait space. The limitation to modeling realized niches through pair-wise comparisons of all species for a region was acknowledged in the presentation of biotic factors as filters for species distributions (Poff 1997). Ibanez et al. (2007), in a recent study of the relationship between fish diet and morphology, referenced promising methods for accounting for phylogenetic inertia in ecomorphology and similar comparative studies. The development of eigenvector techniques for estimating and accounting for phylogenetic

inertia (Diniz-Filho et al. 1998) also offers several new avenues for dealing with phylogenetic constraints in multivariate data sets. However, these methods are useful only to the extent that hypothesized phylogenetic relationships are accurate, and obtaining trees that adequately represent quantitative phylogenetic relationships among fishes is still challenging.

Current Developments

Most of the concepts discussed herein have been expanded, refined, debated, or integrated with other concepts over the past 25 years. Following Kryzhanovskii's (1949) initial work and Balon's (1975) improvement of the reproductive-mode classification, major schemes for grouping fishes have continued to develop. Theories of ontogeny in fishes with different modes of reproduction led to the altricial (generalist)–precocial (specialist) classification of early life history of fishes based on physiology, morphology, and development (Balon 1981b, 1984, 1985; also see a synthesis by Diana 1995). The outcomes of this classification are similar to the outcomes of gradient models commonly used to organize species by their traits. Perhaps most familiar is the r versus K continuum of life history traits (Pianka 1970). A triangular gradient model for fishes, based primarily on fecundity, age-specific survivorship, and generation time, has been proposed (Winemiller 1989, 1992, 2005; Winemiller and Rose 1992) and applied initially to some tropical and North American fishes. This model splits r strategists into opportunistic (small, short-lived, high reproductive effort, and high demographic resilience) and periodic (long-lived, high fecundity, and high recruitment variation) groups, which together with the equilibrium (low fecundity, large egg size, and parental care) group define the endpoints in the triangular surface. The model predicts fish distributions across a range of habitats

and has applications in species conservation, biological assessments, and predicting invasive species effects (Winemiller 2005).

Winemiller's model has spurred much subsequent research. Ordinations of traits of 24 European freshwater fishes (Blanck et al. 2007) and 29 native and exotic fishes in Mediterranean streams (Vila-Gispert et al. 2005) also identified three major strategies that matched the three endpoints of Winemiller's model. Tedesco et al. (2008), using fishes in West African rivers, verified the utility of Winemiller's model, which predicts associations between (1) periodic species and predictable but seasonally fluctuating rivers and (2) equilibrium species and hydrologically stable rivers. Tedesco et al. (2008; West African rivers), Olden et al. (2006; Colorado River basin, USA), and Vila-Gispert et al. (2005; Iberian Peninsula) have shown the efficacy of the Winemiller model to predict fish distributions and invasion success in relation to hydrologic alterations such as damming of rivers. However, while Vila-Gispert et al. (2002) discovered strategy gradients matching the Winemiller endpoints, they concluded that there were strong taxonomic and geographic affiliations (across continents) of fish life history strategies. Similarly, Vila-Gispert and Moreno-Amich (2002) could identify only two of the main life history endpoints in their ordinations of 25 European freshwater fishes and concluded that there were no true equilibrium species among the European fishes used in that study. A cluster analysis of Australian fishes produced seven groups that mirrored the three major endpoints in Winemiller's model (Growth 2004). However, traits like egg adhesiveness and buoyancy and spawning migrations further subdivided the groups. Similar to observations from other studies, there was a strong influence of phylogeny on Growth's (2004) classification. Merigoux et al. (2001) in a test of the habitat

template model with floodplain fishes of the Sinnamary River in French Guiana, observed life history strategies matching equilibrium, periodic, and opportunistic groups but could not match life history distributions to habitat variability gradients as predicted by the template model, although many significant bivariate trait-habitat relationships were found. The authors suggested that future studies improve the description of the habitat axes, consider trade-off among traits, and extend the study period. Considering trade-offs among traits and phylogenetic effects on trait correlations seems to be a timely caution. Traits associated with a particular "strategy" by ordination methods may not necessarily be relevant to the strategy under consideration. Among existing reproductive and life history classifications, phylogeny, species pool, and the traits used as input strongly influence the outcome of classifications or ordination gradients.

Grouping fishes by feeding modes (trophic groups) may be the oldest attempted and most difficult nontaxonomic classification of fishes. The difficulties arise from the enormous variety of fish feeding modes both across taxa and within a species, due to ontogenetic, diurnal, seasonal, and habitat effects on feeding. Early comprehensive trophic schemes (Keenleyside 1979; Gerking 1994) encountered the challenges of accommodating feeding plasticity within habits while keeping the groupings simple enough to be meaningful. Detailed schemes are unwieldy for applied research and management; yet schemes based on very broad categories like herbivore, omnivore, carnivore, and insectivore (Karr 1981; Schlosser 1982b; Karr et al. 1986) may lack versatility for addressing some applied problems. Several recent trophic groupings converge toward basing groups on *what* is eaten (e.g., insects or detritus), *when* it is eaten (e.g., day or night), *where* it is eaten (e.g., benthic or water surface), *how* it is eaten (e.g., suction

or ambush), and *how much* is eaten (Matthews 1998; Wootton 1998; Goldstein and Simon 1999). We would add, at what life stage (e.g., larvae, juvenile, adult)? The number of permutations of these six criteria can be staggering, but they afford more flexibility for applied research (Orians 1980). Some successful classifications of species into functional feeding groups have been accomplished by focusing on regional or local species pools where detailed knowledge of the species feeding behavior and diet choices exists (Matthews 1998; Goldstein and Simon 1999). The use of morphological (e.g., relative mouth size, mouth position, mouth orientation, and barbels) and anatomical (e.g., relative length of intestines and pharyngeal teeth) features to classify fishes independent of observed feeding behavior remains underexploited. Such an approach could likely provide more robust, ecologically meaningful trophic groupings if phylogenetic relationships among species can be carefully controlled.

Species physiological limitations (e.g., temperature, dissolved oxygen, pH, and salinity) account for much of their geographic distribution and their longitudinal and lateral zonation within rivers. Zonation, however, reflects responses to multiple interacting variables, some of which are not directly physiological, such as hydrology, hydraulic, and substrate requirements (e.g., Lamouroux et al. 2002; Lamouroux and Cattaneo 2006). Therefore, zonation hardly provides an unconfounded basis for grouping fishes. Salinity tolerances for most North American freshwater fishes have been classified (Hocutt and Wiley 1986), and thermal classifications have been presented for lake fishes of the contiguous United States (Fang et al. 2004a, 2004b, 2004c). Although regional studies frequently classify species by their temperature and oxygen requirements, unified schemes for such classifications are lacking.

It is also common, especially in biologi-

cal assessments, to classify fishes by “tolerance.” This concept of tolerance is often not well defined and is prone to inconsistency across studies and for a given species across its geographic range because of changes in the environmental stresses to which species exhibit tolerance. A recent effort uses field observations to quantitatively assign tolerance indicator values (TIVs) to fishes for selected physicochemical variables (Meador and Carlisle 2007). TIVs may be more precise than expert judgment for some stressors, but they have not been applied to the many anthropogenic impacts on fishes that lack clear physiological response (e.g., alteration of physical habitat, flow regime, predation risk, and production dynamics), and care must be taken to avoid circularity in assessing tolerance based strictly on physicochemical variables.

Species are often classified by their habitat preferences and geographic distribution patterns. Zoogeographic patterns and species traits are commonly used as variables in studies of extinction or invasion risk (Garcia-Berthou 2007). Latitudinal range is a common surrogate for temperature tolerance. For narrowly distributed species, regional species accounts usually provide maps of distribution and descriptions of habitat use at resolutions sufficient for most research questions. Information on the distribution of most North American fishes has been collated to be suitable for many research needs (Lee et al. 1980; Hocutt and Wiley 1986; Page and Burr 1991).

Expansion of Research Questions

In order to determine trends and patterns in the use of traits in stream and fish community analysis, we reviewed 102 peer-reviewed studies published from 1980 to 2008 (List is quite long but would be provided on request). We used our personal libraries and also conducted keyword searches on Web of Science/Science

Citation Index using the queries “fish AND trait” and “fish AND (guild OR functional group).” We selected studies that were about fish, focused on at least two species, and addressed at least one objective related to fish ecology, conservation, or management. Studies that focused exclusively on development or description of biotic indices were excluded, but those that aggregated attributes of communities to test hypotheses were included. We consider the 102 studies representative but not exhaustive. We tallied the number of species involved, research questions, and traits used to address these questions. In our presentation, we group questions as (1) species–habitat relationships or responses to habitat alterations, (2) biological assessments and monitoring, (3) species introductions or invasiveness, and (4) species extinctions or extirpations. We found only two studies on climate change so they were excluded from this analysis. We also grouped traits as (1) morphological or hydrodynamic, (2) life history, (3) mode of reproduction, (4) habitat association, (5) food habit (trophic), (6)

physiological or undefined tolerance, and (7) geographic distribution. Some studies addressed more than one question and many used traits from multiple groups.

Individual studies considered from 2 to an estimated 1,200 species (mean = 100; median = 40; mode = 22; Figure 2). Studies in the high end of the range involved comparisons of species across communities or regions. The challenge of pairwise species comparisons is illustrated by the number of species included in a typical study: 22 species yield 231 possible comparisons, 40 species yield 780 comparisons, and 100 species yield 4,950 comparisons! Trait-based approaches reduce dimensionality and overcome the unwieldiness of multispecies comparisons.

Not only has there been a tremendous increase in trait-based approaches over time (true for all types of community ecology research), but the breadth of questions addressed has also expanded. Trait-based studies in the 1980s occurred in only species–habitat and bioassessment categories. In the 1990s and 2000s, studies of species invasion and ex-

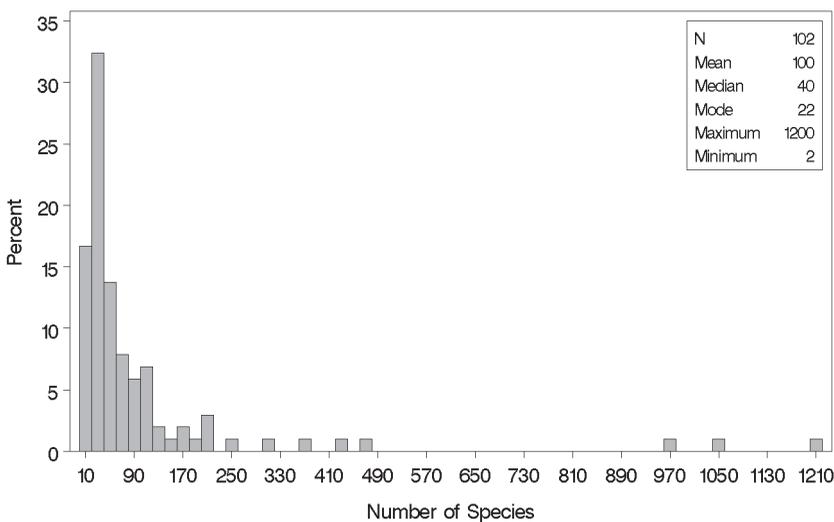


Figure 2. Distribution of number of fish species analyzed in a sample of 102 studies in trait-based fish community ecology between 1980 and 2008.

inction appeared, with species–habitat studies still predominating trait-based approaches (Figure 3). In terms of traits used, other than an absence of morphological/hydrodynamic and geographic distribution traits in studies of the 1980s, there is remarkable constancy in the variety of traits used since the 1990s (Figure 4). Trophic traits are used most frequently, followed by habitat associations, life history, and mode of reproduction. A cross-tabulation of frequency of traits used by study objective shows that geographic distributions are used more commonly with studies of species invasion and extinction (Table 1). However, the underrepresentation of extinction/extirpation studies makes any generalization somewhat speculative. Notably, widespread trait usage need not imply great utility or appropriateness in testing a particular hypothesis. We observed that rationales for trait selection were usually not provided and often appeared to weight availability (ease of measurement) and previous usage at least as much as appropriateness, as might be based on ecological knowledge or concepts. It would be instructive to examine the hypotheses under which individual traits seemed to advance understanding of fish community organization. Such information, which is beyond our scope here, would strengthen study designs, traits

reporting, and rationales for choosing traits in future studies.

General Conceptual Underpinnings of Trait-Based Approaches

In our overview of trait-based approaches, we have avoided the linkages (or conceptual bridges [Orians 1980]) between individual, population, and community ecology. Our discussion was greatly simplified by not explicitly referring to these linkages; the implicit assumption is that there is a single conceptual framework, even if not clearly articulated. However, the lack of an explicit general framework produces the increasing confusion in the formulation and communication of these approaches. In this section we interface the trait-based work in stream fish ecology with general ecology and propose a framework for trait-based approaches in fish ecology. We define all terms used in this context and explain relationships among them. First, we define traits, performance, and individual fitness; then, we discuss tactics, trait-states, strategies, and syndromes as essential concepts for measuring and working with correlated traits. Finally, we consider how traits are expressed at different levels of ecological organization and the implications for organizing traits information to test community-level hypotheses.

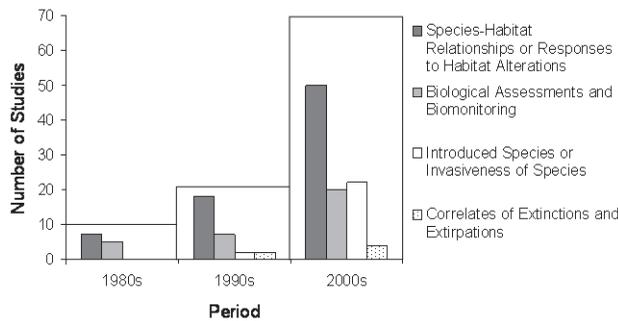


Figure 3. Trends in the types of questions addressed with species traits between 1980 and 2008. Outer histogram represents the total number of peer-reviewed studies examined from each decade.

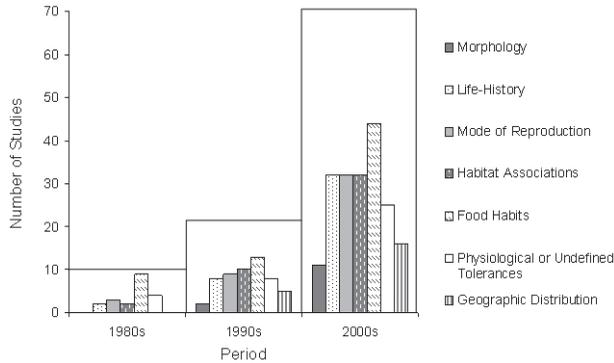


Figure 4. Patterns of frequencies of use of traits and attribute types for addressing questions in community ecology between 1980 and 2008. Outer histogram represents the total number of peer-reviewed studies examined from each decade.

Traits, Performance, and Fitness

Although central to this paper, the following sample of definitions (in increasing order of precision) shows that the very definition of trait is not settled and one's definition can profoundly change how a trait-based analysis is conceptualized. A trait has been defined simply as (1) the morphological, physiological, or behavioral expressions of an organism's adaptations to its environment (Goldstein and Meador 2005). Implicit in this definition are expressions of ecological and life history adaptations as well. According to McGill et al. (2006), a trait is (2) a well-defined, measurable property of an organism, usually measured for individuals and used comparatively across species. The most restrictive definition is (3) any morphological, physiological, or phenological feature measurable for individuals, from the cell to the whole organism, without reference to environmental context or any other level of [ecological] organization (Violle et al. 2007).

All three definitions encompass distinctive suites of traits. Measurability largely distinguishes definitions 2 and 1. To analyze definition 3, we must first distinguish the trait types recognized by Vieira et al. (2006). They defined *biological traits* as those that reflect

physiological requirements, morphological adaptations, and life histories innate to an organism and *ecological traits* as those that reflect an organism's environmental preferences and associated behaviors. In fish community ecology, it is obvious from our review of trait-based approaches that both types of traits are in common use. Adopting definition 3 would make ecological traits such as diet preferences, feeding locations, habitat association, and spawning substrate illegitimate traits. An advantage of ecological traits is that they are less constrained by phylogeny and therefore more responsive to proximate environmental factors, whereas biological traits, reflecting responses to ultimate evolutionary factors, are more phylogenetically constrained (Vieira et al. 2006).

However, definition 3 also has merit: because ecological traits are defined by species' observed behaviors, preferences, and lethal tolerances (e.g., diet and temperature selections), it seems tautological to apply these traits in tests of responses of species to environmental gradients that defined the traits (Vieira et al. 2006). To elicit mechanistic interpretations in trait-based approaches, one research focus should be finding innovative ways to measure the biological traits (genetic, physiological, and

Table 1. Percentages of usage for selected types of species traits and attributes in answering questions in trait-based fish community ecology between 1980 and 2008. Total number of studies sampled was 102. Some studies addressed multiple objectives and/or used multiple trait/attribute types. Number of studies involving each objective is in parentheses and used in the denominator for that row.

Study objective	Trait of attribute type						
	Morphological or hydrodynamic	Life history	Mode of reproduction	Habitat associations	Food habits	Physiological or undefined tolerances	Geographic distribution
Species-habitat relationships or responses to habitat alterations (75)	14.7	34.7	42.7	46.7	62.7	30.7	13.3
Biological assessments and monitoring (32)	9.4	21.9	43.8	40.6	75.0	68.8	9.4
Introductions or invasiveness of species (24)	8.3	62.5	33.3	37.5	58.3	41.7	37.5
Species extinctions or extirpations (6)	33.3	66.7	66.7	83.3	66.7	16.7	50.0

morphological) for which ecological traits have served as proxies. A corollary is to refine existing traits and develop more quantitative methods for handling phylogenetically constrained data. An additional strength of definition 3 is that no information at higher levels of ecological organization (population, community, or ecosystem) is needed to define a trait. This assertion is necessary to avoid the confusion of describing community-level attributes such as guilds and functional groups as traits. Rather than create a new definition, we note the following essentials of any definition of a trait: (1) measurable, (2) measured on the individual, and (3) applicable to a species or population.

Functional trait is used nearly as commonly as trait itself. McGill et al. (2006) defined *functional trait* as a trait that strongly influences organismal *performance* (the capacity of an organism to maintain biomass over many generations). Although this definition refers explicitly to linkage between individuals and populations, its open-endedness allows every trait to be viewed as functional, which is close to how functional traits have been viewed in stream and fish community ecology. Violle et al. (2007) suggested a narrower definition (for plants) as

morpho-physio-phenological traits that impact *fitness* indirectly via effects on growth, reproduction, and survival, the three components of individual performance. This definition stems from a conceptual framework linking traits, performance, and fitness (lifetime reproductive success). Arnold (1983) developed a conceptual framework to argue that selection can be measured in wild populations by responses in measurable phenotypic characters. He argued that measuring the effect of morphology (i.e., shorthand for any measurable aspect of structure, physiology, and behavior) on fitness can be simplified by decomposing the relationship into its morphology→performance and performance→fitness parts. Because individual fitness is difficult to measure, this decomposition enables researchers to focus measurements instead on the morphology→performance relationship and infer effects of morphology on fitness from effects on performance. Details of such relationships can be diagrammed (Figure 5) to show direct and indirect effects of multiple traits on performance and, consequently, fitness.

The three components (growth, reproduction, and survival) of performance can be mea-

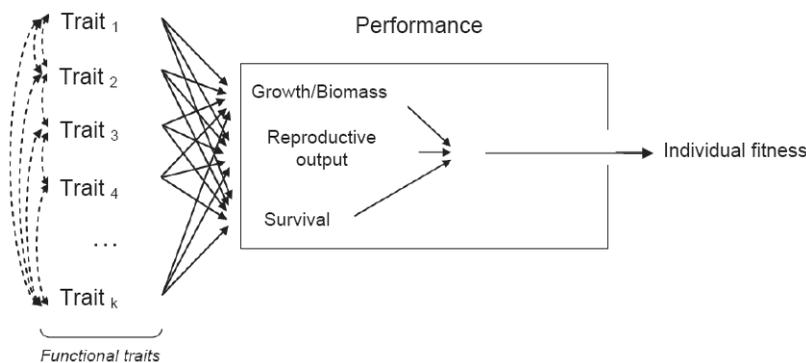


Figure 5. A framework for relationships among traits, performance, and fitness (modified from Arnold [1983] and Violle et al. [2007]). Functional traits affect each other indirectly (broken arrows) and each trait is involved in one or more of the three components of individual performance. Performance in turn affects fitness.

sured in numerous parts and ways. For example, fish swimming ability may enhance escape from predators, which in turn affects survival and reproduction. Several morphological and physiological traits contribute to swimming ability, including tail and caudal peduncle morphology and oxygen utilization efficiency. Other traits related to survival might include cryptic coloration or stinging ability, which result from combinations of morphological, physiological, and behavioral traits. To understand how traits affect performance, we need a common *performance currency* with physical units comparable across species and along environmental gradients (McGill et al. 2006a). Laboratory measures of performance typically have physical units (e.g., proportion of eggs surviving or hatching, with and without parental care), but field measures often lack physical units, excluding them from McGill et al.'s definition of performance.

Field proxies for individual performance comparable across species and sites include, in increasing order of information content: (1) species presence (indicates ability to survive under existing abiotic and biotic conditions), (2) abundance (density) or proportional abundance of species in the community (indicates relative ability to utilize resources and survive the myriad biotic interactions), (3) number of age-classes represented in each population (may indicate multiyear reproductive success and survival), and (4) proportion of the population represented by multiple age-classes (reflects the population growth parameter λ , and so the temporal trajectory of a population under existing conditions; Smith and Powell 1971; Power 2007). Of course, these performance proxies need to be assessed in the context of a species' entire trait composition. For example, very large fishes would not be expected to be very abundant and short-lived fishes would not be expected to have many

age-classes (Vamosi and Vamosi 2007). In any case, strong correlations (positive or negative) between traits of individuals found or expected at a site and any of these performance measures enable researchers to infer effects of traits on fitness. Other performance measures that might be sensitive in the field are individual growth rate, various condition factors, and population biomass per unit of habitat.

Tactics, Strategies, and Syndromes

It is clear from our discussion of traits, performance, and fitness that finding the trait(s) most strongly related to performance or fitness from among the many potential traits could be very time-consuming (Figure 5). We argue that trait-by-trait analyses of species distribution or community organization is inefficient and not necessarily supported by evolutionary theory. The thousands of measurable traits possessed by an organism have evolved to function together to ensure survival, growth, and reproduction—the components of performance. A fish's daily activities can be partitioned into major categories such as foraging, reproduction, and evasion or resting (Wootton 1998), with time allocations depending on age and physiological state. Because fish evolution has been shaped by the special demands on morphology and physiology of a water environment, only those fishes whose hydrodynamic, physiological, trophic, reproductive, and behavioral traits are largely integrated and adaptive will reside in a given location (Matthews 1998). We can map any trait onto these dimensions of a fish's life cycle and daily activity, producing highly collapsed suites of traits. Thus, thousands of traits can be represented by perhaps fewer than 10 groups of important activities and processes related to a fish's performance (e.g., see the seven major headings in Appendix A).

Traits do not evolve independently of each other but, more importantly, neither do strategies (i.e., suites of traits associated with fish performance, linked to a single major activity [e.g., feeding] and characteristic of individuals in the same gene pool). A benthic-feeding fish may also be adapted to spawning and hiding or resting in the substrate and may exhibit traits such as small body size and large pectoral fins that facilitate all three activities. Moreover, executing one adaptive activity affects execution of others and natural selection primarily acts on the strategies emerging from interactions among traits. For example, a population making opportunistic life history choices (evolutionarily speaking), with small body size and short generation time, may simultaneously evolve traits that enhance efficiency for substrate spawning and benthic invertivory (for example, see Figure 6). We would expect traits that simultaneously support multiple strategies across different major activities to cluster in multivariate trait-space and appear as a syndrome. Thus, *syndromes* (i.e., suites of traits associated with fish performance and linked to

multiple major activities [e.g., feeding, spawning, and resting]) appear in the same organism because of their adaptive contribution to inter-related strategies. In a study of plant herbivory defenses, Agrawal and Fishbein (2006) found all pairwise correlations among measured traits to be positive but found significant negative correlations between defense and palatability traits, which indicated that the evolutionary trade-off is between strategies, not individual traits. Such strategy trade-offs remain largely unexplored for fish traits.

A new synthetic conceptual framework is needed to (1) objectively define strategies and syndromes based on trait composition, (2) group fish taxa by these strategies and syndromes, and (3) link strategies and syndromes to environmental templates where a given fish taxon or group would be expected to succeed or fail. Such a framework would also predict species responses to environmental change based on their observed strategies. There are fewer axes in strategy- and syndrome-space than in trait-space, which enables reduced data dimensionality, similar to the way shared traits

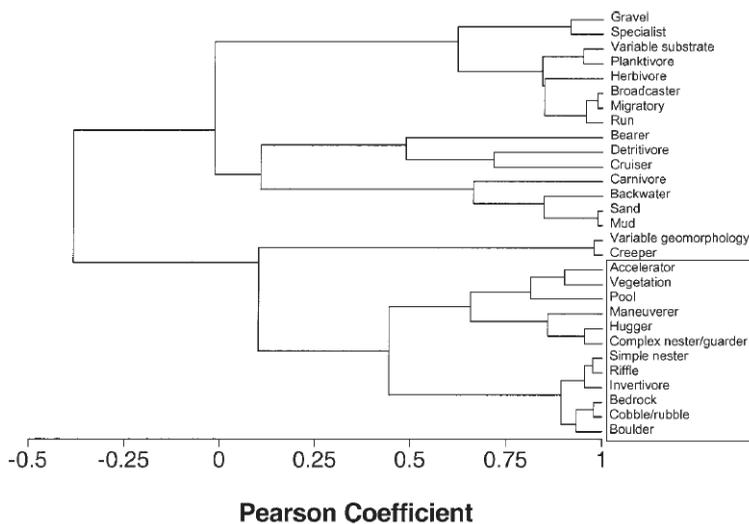


Figure 6. A phenogram of traits of 429 fish species of the United States, showing clusters of traits from Goldstein and Meador (2004). We label the bottom cluster of traits (boxed) as a benthic syndrome.

reduce dimensionality of species data. For example, based on about 20 traits, Winemiller and Rose (1992) defined three life history axes, each representing a gradient of strategies, for 216 fish species. Furthermore, mechanistic interpretations of species–environment relationships are enhanced by modeling multiple traits in the strategies and syndromes to which those traits contribute. Even if strategies and syndromes cannot be defined unequivocally for a pool of species, we believe applying these concepts will make trait selection more meaningful for hypothesis testing and will advance ecological understanding more efficiently than current ad hoc trait selection, which is commonly driven by data availability.

How does one define strategies and syndromes and assign species to them? Wootton’s (1998) conceptual framework for reproductive strategies seems applicable to other strategies.

An individual fish possesses traits constrained by its genotype, a product of its evolutionary history. Each trait has a range of possible phenotypic expressions, but an individual can express only a subset of these. For each of traits 1, 2, ..., i that contribute to a strategy, the actual value expressed by an individual at a given time is its *tactic* for that trait (Figure 7). Thus, tactics can vary among individuals in the same and different populations or in the same individual at different times and as a function of proximate environmental factors. The range of variation due to these sources is a measure of a trait’s *phenotypic plasticity*. To objectively assign species to strategies and syndromes, it is often necessary to partition the possible range of expressions for each trait into categorical, mutually exclusive *states* or *modalities* (Poff et al. 2006; Vieira et al. 2006). The difficult task of assigning a species to a *trait-state* should be based on a comprehensive

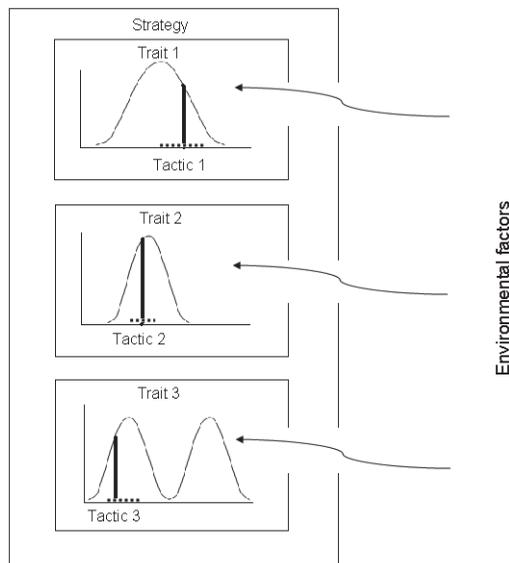


Figure 7. A framework for relationships among strategies, traits, tactics, and the environment (modified from Wootton [1998]). A strategy comprises multiple traits. Each trait has a possible range of expression among all fishes, represented by the horizontal spread of the curve for that trait. The broken line along the horizontal axis represents the genotypic range of an individual and the vertical line marks the tactic expressed at a given time. Many tactics for each trait are possible. Ultimate environmental factors (e.g., long-term minimum water temperature) shape the distribution of each trait in a given taxon, and proximate factors (e.g., average temperature over the past 30 d) affect the tactic expressed.

review of the species' biology and operational definition of trait-states suitable for the research hypothesis of interest. Where knowledge of species' biology and ecology are extensive, fuzzy coding (involving ranked assignment of a single species or population to multiple trait-states; e.g., Persat et al. 1994) may provide a more realistic framework for partitioning the range of variation of a trait.

For widely distributed species, a species can span more than one defined state for some traits. The same problem may arise for a species exhibiting especially great phenotypic plasticity. The best traits for testing ecological hypotheses are those that vary along environmental gradients and for which interspecific variation exceeds intraspecific variation. Although some work has addressed these problems (Blanck et al. 2007), much remains unknown regarding phenotypic plasticity of traits and its role in defining strategies and syndromes.

A substantive discussion of the statistical tools available (including respective strengths and weaknesses) to explore relationships among traits is beyond the scope of this chapter, but we mention a few key points here. When trait-states are clearly defined and assigned, ordination methods such as nonmetric multidimensional scaling or clustering can be instructive. However, intermediate analytical steps accounting for phylogenetic relationships in the species pool are also necessary (Felsenstein 1985). Hierarchical clustering of traits produces a trait (phenotype) dendrogram called a *phenogram* (Agrawal and Fishbein 2006). Goldstein and Meador (2004) produced a phenogram for 429 fishes based on traits from all major activities. Such phenograms could be used to identify strategies and perhaps syndromes. For example, the lower part of Figure 6 shows a "benthic syndrome" involving traits such as maneuvering movements, invertivorous diet, cobble/rubble substrate association, and nest-

ing in the substrate. Statistical techniques to rigorously delineate the boundaries of such a syndrome have been developed and used in other fields but largely remain unrecognized by ecologists (Jackson et al. 2010).

Aggregating Traits in Communities: Guilds and Functional Groups

Stream and fish ecologists frequently compare communities by summarizing proportional composition based on numbers or biomass of individuals that share traits, strategies, or syndromes. This approach has been described as moving from micro- to macroanalysis (Orians 1980) or "scaling up" from organisms to higher organizational levels (Violle et al. 2007). In aggregating individual, population, or species attributes to describe communities, we attempt to capture the essence (*sensu* Orians 1980) of a community in fewer dimensions than represented by its component species. However, this is one area where trait terminology has been very confusing. Summing individuals by traits to represent a community is an application of *additive integration functions* (Violle et al. 2007). We are not aware of the use of other more complex integration functions in fish community ecology but that could be a direction for future research (see McGill et al. [2006] and Violle et al. [2007]). Our focus here is to clarify the terms used to describe communities so they are not confused with traits.

The notions of guild and functional group, introduced above, warrant further distinction. Because guilds are structured primarily by resource availability and use, members are expected to respond similarly (e.g., increase or decrease abundance) to changes in the resources (e.g., food or substrate) defining the guild (Austen et al. 1994). This is the basic tenet of assessments of changes in the envi-

ronment based on fish communities (Karr 1981). Cummins (1973) did not present functional groups as a redefinition of guilds, but as a process-oriented complementary concept. Individuals of a functional group perform an ecosystem function by their mode of resource utilization (Matthews 1998; Blondel 2003). For example, shredders (macroinvertebrates, Cummins 1973) break down pieces of organic matter, whereas substrate disturbers (fishes, Matthews 1998) resuspend organic matter; both groups facilitate nutrient cycling. Because of the common resources involved, guild members may also share membership in a functional group, but that is not always the case (Blondel 2003).

Guilds and functional groups are subsets of all potentially useful species groupings in an assemblage. For example, community-level life history descriptors, such as percentage of individuals that are opportunistic, do not describe a guild or functional group. An all-encompassing term to describe multispecies groups defined by traits, strategies, or syndromes is lacking and may not be necessary to advance development of trait-based concepts or analyses. However, we emphasize that membership in guilds, functional groups, or other trait-based groups need not be mutually exclusive. For example, central stonerollers *Camptostoma anomalum* may belong simultaneously to three trophic guilds (e.g., algivore, invertivore, and benthic feeder), a functional group that includes benthic feeders, substrate nesters, and brood-hiders (i.e., substrate disturber), and a life history group (i.e., opportunist).

Finally, it may be instructive to compare suites of communities based on their prevalent strategies and syndromes. Such comparisons may shed light on how drivers of community organization vary geographically (e.g., along hydrologic or predation-risk gradients). For example, although he did not describe com-

munities in terms of strategies and syndromes, Schoener (1987) ordered 15 community-types based on aggregated species traits such as body size, generation time, and number of life stages. Tedesco et al. (2008) showed that West African river fishes aggregated by Winemiller's endpoint strategies were distributed predictably along geographic and habitat gradients of hydrologic variability. Similar analyses, based on rigorous aggregations of sets of traits, could facilitate development and testing of theories germane to fish community ecology as well as general community ecology.

Research Gaps

We conclude by offering thoughts on the most pressing and instructive directions for future study of stream fish traits. We roughly divide these into topics to enhance basic ecological knowledge and to inform aquatic conservation programs, although these two directions frequently intersect and overlap.

Much has been done in trait-based fish ecology to link species distributions to habitat suitability, but a major gap remains in our understanding of how trait breadth and/or plasticity enables fish populations to persist in the face of dynamic lotic environments. In essence, we need to document how realized niches shift in response to different abiotic environments. This echoes gaps in ecological knowledge identified by McGill et al. (2006) and recommendations from a National Science Foundation workshop on population and community ecology (Agrawal et al. 2007). Current knowledge of stream fish species traits is based largely on a haphazard set of studies, with many taxa, regions, and system types still unexplored. Studies carefully designed to examine how traits vary over time, space, and phylogeny would tell us a great deal about the ecological and evolutionary importance of traits and help us build

a more predictive framework of principles and models.

Species traits offer a potentially powerful lens for understanding outcomes of biotic interactions, beyond predation and competition for food, across a broad spectrum of abiotic contexts. The traits controlling interactions such as competition for spawning substrate, mutualism, commensalism, and parasitism have barely been studied, let alone how those traits might figure into fish community responses to anthropogenic impacts or restorative actions. Studies of how biotic interactions, phylogeny, and habitat needs can be integrated simultaneously into trait-based community models merit a more comprehensive review, with the goal of developing more quantitative models. Such a review would necessarily discuss the adequacy or adaptability of available and emerging modeling tools such as RLQ analysis (Doledec et al. 1996), co-inertia analysis (Dray et al. 2003), the improved fourth-corner analysis (Dray and Legendre 2008), and phylogenetic eigenvector (Diniz-Filho et al. 1998) techniques and outline how those tools need to be enhanced. Jackson et al. (2010) is the beginning of such an effort.

Another research topic that warrants careful review and analysis is how species traits constrain or facilitate community assembly and nestedness, in both early and late stages of assembly. This is a fast-growing topic in plant community ecology (e.g., Fukami et al. 2005; Ackerly and Cornwell 2007; Kraft et al. 2007), but examples in stream fish community ecology are lacking (but see Cook et al. 2004; Eros et al. 2009). The statistical tools and conceptual models associated with the study of community assembly may be especially instructive in managing decimated fish communities or restoring streams.

Species traits are used increasingly to describe the functional organization of fish com-

munities and to understand mechanisms of biotic responses to anthropogenic changes in stream ecosystems. Such studies help reveal how imperilment occurs and which taxa are most/least vulnerable (Angermeier 1995; Olden et al. 2006) but usually cannot tell us which management actions are most/least effective in solving a given conservation problem (e.g., species recovery). More carefully designed and monitored field experiments are needed to document links from stream management actions to the physicochemical environment to population responses, as mediated through species traits. Such experiments can facilitate development of general models to help managers choose cost-effective projects and actions for implementation (Kondolf et al. 2008). More specifically, we might seek predictive associations between specific suites of species traits and common biotic responses to tactics used to restore flow regime, water quality, or imperiled species or to reduce abundance of nonnative species. In a recent pilot analysis (Frimpong and Angermeier 2009) we found that the three-matrix fourth-corner analysis technique (Dray and Legendre 2008) developed for linking species to habitat through traits could be adapted to link similar stressor types associated with disparate human activities directly to traits that are vulnerable to imperilment. Further refinements of such approaches are promising for not only explaining causes of species imperilment, but also anticipating the effects of novel threats to species and tailoring remedial management and conservation tactics to specific situations.

Ecosystem services are an emerging nexus between ecology and economics in the context of managing natural resources and landscapes. Because of their explicit link to human well-being, ecosystem services provide a new currency for evaluating conservation priorities and building public support for conserva-

tion. Nevertheless, little is known about how stream fishes contribute to ecosystem services (but see Holmlund and Hammer 1999). These services include fishes' roles in maintaining desirable ecosystem structure and function (Flecker et al. 2010, this volume) but certainly go beyond that to catalyze delivery of a wide range of provisioning, regulating, and cultural services. Moreover, we expect the species traits studied by fish ecologists to be tightly linked to the ecosystem services provided by streams. There is much fertile ground for future work to explore the extent to which the collective species traits of fish communities (i.e., the balance of guilds and functional groups) can predict the social value of ecosystem services, such as harvestable food, nutrient regulation, and recreation, in which fishes play key roles.

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Appendix A. Sample of traits and species attributes that have been used in fish community ecology studies.

Morphological/anatomical and hydrodynamic traits

Shape/locomotion/mobility
 Aspect ratio of caudal fin (caudal fin length to depth)
 Aspect ratio of pectoral fin (ratio of length and depth of pectoral fin)
 Relative insertion height of pectoral fin
 Dorsal insertion distance
 Maximum body depth
 Maximum caudal fin depth
 Minimum depth of caudal peduncle
 Relative body height
 Ratio of head width to caudal peduncle width
 Shape factor (ratio of length to body depth)
 Swim factor
 Streamlined
 Flattened
 Cylindrical
 Cruiser
 Accelerator
 Maneuverer
 Benthic high velocity hugger
 Benthic low velocity creeper
 Fluvial generalist
 Fluvial specialist
 Sedentary
 Territorial
 Highly mobile or migratory/roving

Size/length
 Total length
 Standard length
 Fork length
 Distance from snout to the anterior edge of dorsal fin
 Distance from snout to the base of the pectoral fin
 Distance from snout to the posterior edge of dorsal fin

Trophic potential
 Mouth size
 Oral gap
 Mouth position/oral gap position
 Inferior
 Superior
 Terminal
 Mouth angle
 Horizontal
 Oblique
 Eye diameter
 Pharyngeal accessories
 Gill raker depth
 Gut length/relative gut length
 Peritoneum color

Appendix A. Continued.

Protrusion length
 Presence or absence of barbels
 Presence or absence of teeth
 Stomach morphology
 Lateral stripe
 Mottled or vertical stripe
 Silvery body coloration

Mode of reproduction

Spawning substrate
 Lithopsammophil
 Lithophil
 Lithopelagophil
 Phytophil
 Phytolithophil
 Psammophil
 Ostracophil
 Ariadnophil
 Pelagophil
 Speleophil/crevice spawning
 Polyphil

Ethology
 Nester
 Saucer building
 Mound building
 Pit building
 Pit-ridge building
 Nest associate
 Egg broadcaster/open substratum spawner
 Brood hiders
 Guarder
 Egg tender
 Nonguarder
 External bearer
 Internal (live) bearer
 Simple
 Complex
 Egg-clumping
 Egg-clustering
 School spawning
 Distance traveled to spawn
 Spawning flow (velocity) preference
 Spawning connectivity requirement

Physiological/tolerance

Tolerance
 Turbidity
 Sediment
 Silt
 Organic pollution
 Warm water
 High oxygen
 Low oxygen
 Acidification
 Eutrophication

Appendix A. Continued.

- Conductivity/specific conductance
- Catchment/stream alteration
- Ventilation response
- Ammonia
- Chloride
- Nitrite/nitrate
- Phosphorus
- Sulfate
- Reduced flow
- EPA (U.S. Environmental Protection Agency)–RBP (rapid bioassessment protocols) tolerance
- Euryhaline
- Thermal preference
 - Cool water
 - Warm water
 - Cold water
 - Stenotherm
 - Eurytherm
- Tolerant
- Sensitive

Life-history traits (including invariants)

- Asymptotic (potential) length
- Maximum observed body length
- Larval size upon hatching
- Larval adhesiveness
- Longevity/generation time
- Annual population size fluctuation
- Pioneering/colonizing
- Fecundity
 - Maximum
 - Average
 - Batch/clutch
 - Age specific
 - Size specific
- Egg
 - Adhesiveness
 - Size/diameter
 - Pelagic
 - Demersal
- Age at maturity
- Length at maturity
- Length at first reproduction
- Spawning and seasonal migration
 - Anadromous
 - Catadromous
 - Potamodromous
 - Marine adventitious visitors
 - Marine juvenile migrants
 - Freshwater adventitious visitors
 - Marine seasonal migrants
- Spawning temperature
- Lowest temperature at which spawning begins
- Length of spawning season
- Semelparous
- Iteroparous

Appendix A. Continued.

- Batch/serial spawner
- Total/single spawner
- Degree of parental care
- Juvenile survival
- Incubation time (from fertilization to hatching)
- Growth rate
- Fractional adult growth rate
- Juvenile growth rate
- Larval growth rate
- Adult growth rate
- von Bertalanffy K
- Ratio of length at maturity to asymptotic length
- Ratio of adult mortality to K
- Product of adult mortality and age at mortality

Food habits (trophic)

- Diet
- Insectivore
- Invertivore
- Planktivore
- Piscivore
- Parasitic
- Algivore
- Periphytivorous
- Phytivorous
- Detrivore
- Benthophagous
- Zoobenthivorous
- Zooplanktivorous
- Carnivore
- Piscivore
- Feeding location/habitat
 - benthic feeding
 - pelagic feeding
- Vegetation
- Prey size
- Feeding in schools
- Feeding velocity preference
- Diet breadth

Geographic distribution

- Single drainage
- Multiple drainages
- Single physiography
- Multiple physiographies
- Coastal
- Range size
- Latitudinal range
- Rate of change in distribution
- Distance to native range

Habitat associations

- Velocity and microhabitat preference
 - Riffle/fast
 - Riffle/run

Appendix A. Continued.

Run

Pool

Rheophilic/prefer lotic

Limnophilic/prefer lentic

Backwater

Banks

Vegetation

Cover

Raceway

Depth preference

Benthic/demersal

Surface/pelagic

Mid-water

Deep

Shallow

Stream size

Creeks

Medium river

Large river

Elevation

Upland

Lowland

Montane

Estuaries

Substratum

Prefer gravel

prefer sand

Prefer silt

Eurytopic
