Comparisons of Fish Species Traits from Small Streams to Large Rivers

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Abstract.—To examine the relations between fish community function and stream size, we classified 429 lotic freshwater fish species based on multiple categories within six species traits: (1) substrate preference, (2) geomorphic preference, (3) trophic ecology, (4) locomotion morphology, (5) reproductive strategy, and (6) stream size preference. Stream size categories included small streams, small, medium, and large rivers, and no size preference. The frequencies of each species trait category were determined for each stream size category based on life history information from the literature. Cluster analysis revealed the presence of covarying groups of species trait categories. One cluster (RUN) included the traits of planktivore and herbivore feeding ecology, migratory reproductive behavior and broadcast spawning, preferences for main-channel habitats, and a lack of preferences for substrate type. The frequencies of classifications for the RUN cluster varied significantly across stream size categories ($P = 0.009$), being greater for large rivers than for small streams and rivers. Another cluster (RIFFLE) included the traits of invertivore feeding ecology, simple nester reproductive behavior, a preference for riffles, and a preference for bedrock, boulder, and cobble–rubble substrate. No significant differences in the frequency of classifications among stream size categories were detected for the RIFFLE cluster ($P = 0.328$). Our results suggest that fish community function is structured by large-scale differences in habitat and is different for large rivers than for small streams and rivers. Our findings support theoretical predictions of variation in species traits among stream reaches based on ecological frameworks such as landscape filters, habitat templates, and the river continuum concept. We believe that the species trait classifications presented here provide an opportunity for further examination of fish species' relations to physical, chemical, and biological factors in lotic habitats ranging from small streams to large rivers.

Understanding and predicting the responses of stream fish communities to their environment often present major challenges to researchers. Poff (1997) noted that understanding the patterns of distribution and abundance of lotic species requires testing theoretical predictions about relations between species' functional attributes (species traits) and their environments. Many frameworks can provide theoretical predictions regarding the variation in fish communities among stream reaches, such as along longitudinal gradients of stream size. These frameworks include landscape filters (Poff 1997), habitat templates (Southwood 1977; Townsend and Hildrew 1994), and the river continuum concept (RCC; Vannote et al. 1980).

Landscape filters are based on the premise that environmental selective forces ''filter'' certain species traits at spatial scales ranging from river

basins to microhabitats (Poff 1997). Thus, a landscape filter framework could be used to predict species traits that vary among as opposed to within stream reaches. For example, Poff (1997) speculated that fish reproductive traits might be structured at the river basin scale and therefore would vary with stream size, whereas substrate preferences may be driven largely by within-reach microhabitat influences and thus would not vary with stream size. Although landscape filters provide predictions about which species traits vary with stream size, they provide little information about how these traits vary.

Habitat templates focus on the premise that two dimensions of stream habitat, temporal variability and spatial heterogeneity, provide a template for understanding fish communities and deriving predictions about species traits (Townsend and Hildrew 1994). The temporal dimension has been defined by Southwood (1977) as habitat durational stability. Thus, habitat template predictions in relation to stream size can be made on the assump-

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tion that temporal variability (habitat stability) decreases with increasing stream size. As stream size increases, the temporal variability in factors such as discharge decreases (Hynes 1970; Horwitz 1978). Habitat templates provide predictions about which species traits vary with stream size as well as information about how these traits vary. For example, habitat templates predict not only that reproductive traits will vary with habitat stability (stream size) but also more specifically that parental care will increase with increasing habitat stability or stream size (Townsend and Hildrew 1994).

Li et al. (1987) suggested that the RCC, a basin-scale framework for integrating geomorphic processes and organic matter loading, could be used to explain the longitudinal variation in fish species traits. The RCC is useful in predicting specific variations in trophic ecological traits with stream size. For example, Bayley and Li (1992) showed that according to the RCC, both zooplanktivorous and phytoplanktivorous species should increase as one moves downstream in a large river while benthic invertivores should decrease.

Testing theoretical predictions about fish species traits and how they vary along a longitudinal gradient presents some challenges. Knowledge of functional traits varies greatly by species and is often incomplete (Lamouroux et al. 2002). Also, Hughes and Gammon (1987) reported that studies of longitudinal variation in fish community structure and function have largely been based on the upstream and downstream reaches of relatively small streams. Reash (1999) noted that there is a general lack of understanding regarding biological expectations for large rivers relative to small rivers and headwater streams.

The goals of our study were to determine the distribution of species traits along a gradient of stream sizes and to assess how the observed patterns of distribution correspond to predictions based on theoretical ecological frameworks. Our hypothesis was that expectations for fish community function as defined by the frequency of species traits are different in small streams and large rivers. Specifically, our objectives were to (1) classify lotic fish species into categories of selected species traits within stream sizes; (2) describe fish communities for different stream sizes based on the frequencies of species trait categories; (3) examine relations among species trait categories within and among stream sizes; and (4) relate the findings to general theories of stream community structure and function.

Methods

Various classification systems have been devised to describe fish species traits. The most common are trophic classifications that separate species into trophic groups or guilds by dominant food source (Gerking 1994), but there are also classifications based on locomotion morphology (Webb and Weihs 1986) and reproduction (Balon 1975, 1981; Simon 1999). However, multiple classification schemes at varying scales of resolution often result in confusion over terminology (Goldstein and Simon 1999). The goal of any classification system should be to classify species traits according to a small number of components that permit better understanding (Harris 1995).

We classified fish species based on categories within each of six species traits: (1) substrate preference, (2) geomorphic preference, (3) trophic ecology, (4) locomotion morphology, (5) reproductive strategy, and (6) stream size preference. The fish species list used for our classification was derived from and follows the nomenclature of Robins et al. (1991). We focused on lotic species from the Mississippi River basin east to the Atlantic and Gulf coasts. Diadromous species were included, but the classifications are applicable only to their freshwater stages. The classification applies to adults for all species except lampreys (family Petromyzontidae), where it applies to ammocoetes. Numerous references were consulted for species trait data (Hildebrand and Schroeder 1928; Scott and Crossman 1973; Trautman 1981; Becker 1983; Robison and Buchanan 1988; Page and Burr 1991; Etnier and Starnes 1993; Jenkins and Burkhead 1994; Rohde et al. 1994; Mettee et al. 1996; Pflieger 1997; Ross 2001). In cases where different authors assigned the same species to different classifications, the classification assigned most often was used. In cases of a tie, we used our best professional judgment.

Substrate trait categories included bedrock, boulder, cobble–rubble, gravel, sand, mud, vegetation, and variable. Mud included silt, clay, and detritus. Vegetation included aquatic macrophytes and algae. In some cases, the reference literature described substrate preferences as ''rocky''; these were classified as cobble–rubble. When references listed two substrate preference types (e.g., sand and gravel), preferences were classified as being in both categories. The eighth substrate trait category was designated as variable, indicating that the references reported a variety of substrate pref-

erences (three or more substrate types) or that no specific substrate preferences were mentioned.

Geomorphic trait categories included pool, riffle, run, backwater, and variable. Pools, riffles, and runs are commonly used geomorphic descriptors of channel shape and scour pattern (Fitzpatrick et al. 1998). Backwater was included to represent the use of habitat adjacent to but not within the main channel. Geomorphic preferences described in the reference literature as main channel were classified as run. In some cases, species were indicated as having two geomorphic preferences, such as pools and runs. As with substrate preferences, combinations of preferences were classified as being in both applicable groups. The fifth geomorphic trait category was designated as variable, indicating that the reference literature reported a variety (three or more) of geomorphic preferences or no specific geomorphic preference.

The trophic classification followed that of Goldstein and Simon (1999). This system uses mouth position, teeth, pharyngeal accessories, the ratio of gut length to body length, peritoneum color, and stomach morphology in conjunction with reported stomach contents to classify fish into five major trophic categories: herbivores, detritivores, planktivores, invertivores, and carnivores. In this classification, membership in a particular trophic category is not exclusive; a species may belong to more than one category. The classification of a species into multiple trophic categories is indicative of the variability in feeding ecology and is preferable to a generalist classification of omnivore whereby the scope and variability in feeding ecology is lost (Goldstein and Simon 1999).

To classify species based on locomotor morphology, we modified a classification system developed by Webb (1984a, 1984b) and Webb and Weihs (1986). These authors had identified four locomotion morphology categories for early life history stages: cruisers, accelerators, maneuverers, and a generalist group. We modified these four categories to encompass adult life stages. The resulting six locomotion categories in our classification were cruisers, accelerators, maneuverers, benthic high-velocity huggers, benthic low-velocity creepers, and specialists. We classified species into these six categories based on a descriptive body shape pattern and a taxonomic identity that emphasized the patterns in locomotion morphology associated with each category. The associated body shape descriptors and taxonomic archetypes for the six categories were as follows: cruisers (torpedo; Salmonidae), accelerators (ar-

row; Esocidae), maneuverers (disk; *Lepomis* spp.), benthic high-velocity huggers (arched; Cottidae), benthic low-velocity creepers (teardrop; Ictaluridae), and specialists (elongate; Anguillidae).

To assess our locomotion morphology classification system as a means of defining ecologically different groups, we applied the findings of Gatz (1979) that statistical differences in body morphology are equivalent to ecological differences. We used six morphometric characteristics similar to those used by Webb and Weihs (1986) to characterize the groups. The morphometric characteristics were expressed as ratios and included (1) body length/body depth (to define dorsoventral compression); (2) height of caudal fin/height of caudal peduncle (an indicator of swimming thrust generation); (3) distance from the snout to the anterior edge of the dorsal fin/total body length (to define the anterior position of the dorsal fin); (4) distance from the snout to the posterior edge of the dorsal fin/total body length (to define the posterior position of the dorsal fin); (5) distance from the snout to the base of the pectoral fin/total body length (to define the position of the pectoral fins); and (6) width of head/width of caudal peduncle (to define lateral compression). We measured three individuals of a representative species from 66 selected genera (26 families). Because the specialist category was limited to obvious "eel-like" fish (Petromyzontidae and Anguillidae), no individuals were measured to represent this category.

The reproductive strategy classification was derived from the reproductive guilds of Balon (1975, 1981) and Simon (1999) as well as information from Breeder and Rosen (1966). Our classification system included five categories that are not mutually exclusive: migratory, broadcaster, simple nester, complex nester–guarder, and bearer. The first category is based on spawning location and identifies species that employ a reproductive migration or movement. By definition, anadromous species undergo a spawning migration. Also included in this category were species that move from one habitat or resource to another, such as from a lake to a tributary or from a river to a lower-order stream, strictly for the purpose of reproduction.

The term "broadcaster" refers to species that release large numbers of gametes into the environment. With broadcasters, there may be prespawning behavior but no postspawning behavioral activity to increase the chances for survival of the young. The term "simple nester" refers to species that use a rudimentary nesting surface that

is excavated in the substrate (such as salmon redds) or constructed from substrate (such as the spawning mounds of many cyprinids). Cavity spawners, including species that bury their eggs during spawning and those that place their eggs in the nests of other species, were included in the simple nester category. The term ''complex nester–guarder'' refers to species that provide some level of parental care after spawning, usually guarding of fertilized eggs or fry by the male. Finally, the term ''bearer'' was used to designate species that provide the greatest amount of parental investment by bearing their young alive either internally or attached externally.

Stream size preferences were derived from Page and Burr (1991), who described individual fish species as occurring in four lotic environments: small streams, small rivers, medium rivers, and large rivers. For classification of stream size traits and to quantify these descriptive categories, we modified the stream size classification of Becker (1983) to include five categories: (1) small streams (generally 1–3 m wide), (2) small rivers (>3–15 m), (3) medium rivers (>15–50 m), (4) large rivers (>50 m), and (5) variable (representing a range of river sizes). When Page and Burr (1991) listed two stream size preferences (e.g., small streams and small rivers), preferences were classified as being in both categories. When preferences were reported that included three (or more) stream sizes (e.g., small streams to medium rivers), stream size preference was classified as being variable.

Data analysis.—To describe fish community function for each stream size category, the frequencies of classifications within each species trait category were determined for each stream size category. Chi-square tests of independence between trait and stream size categories were conducted for contingency tables for each species trait. An analysis of variance (ANOVA) with Tukey's comparisons was used to assess the differences in morphological ratios among the locomotion categories. Data normality was estimated by examination of probability plots prior to statistical analysis. The percentage frequencies of the classifications were arcsine-square-root transformed prior to ANOVA testing.

Cluster analysis was conducted to examine the relations among trait categories across all stream size categories combined. A correlation matrix of the frequencies of all 29 species trait categories combined from all stream size categories was constructed using Pearson coefficients. The Pearson correlation coefficients were used as measures of

similarity, and clusters were determined by means of unweighted pair-group averaging. The results of the cluster analysis were used to produce a dendrogram from which clusters of similar traits could be identified. Clusters of more than two trait categories were considered highly dissimilar when the Pearson coefficients were less than 0 and were considered highly similar when the coefficients were greater than 0.75. An ANOVA with Tukey's comparisons was used to assess the differences in clusters within and among stream size categories after the frequencies had been transformed to satisfy normality requirements. All differences were declared to be statistically significant when α was less than 0.05.

Results

Of the 429 fish species and life history stages selected for classification, data were lacking regarding a particular species trait in some cases and thus no classification could be made for that particular trait. Therefore, the total number of species classified varied within each of the five species traits though a river size classification was mandatory. An electronic file containing a list of the species and their respective trait classifications can be found at http://water.usgs.gov/nawqa/ecology/pubs/index.html.

For substrate classifications, a total of 426 of the 429 species and life history stages (99.3%) were classified on the basis of their substrate and stream size preferences. Of the 727 total classifications, 10.4% were variable as to preference for stream size and substrate category combined (Table 1). The percent frequencies of classified preferences for sand and gravel were greater than 15% for all five stream size categories. The percent frequency for cobble–rubble was greater than 17% for small streams, small rivers, and medium rivers. In the large-rivers category, the percent frequency for variable substrate preferences was 40.0%, which represents the single largest percent frequency of substrate preference across all substrate and steam size categories. Chi-square analysis indicated that substrate trait categories were significantly associated with stream size ($\chi^2 = 122.7$, df = 28, $P = 0.001$).

In all, 417 of the 429 species and life history stages (97.2%) were classified on the basis of geomorphic and stream size preferences. Of the 671 total preference observations, 0.8% were classified as variable for the stream size and geomorphic trait categories combined (Table 2). Pool was the most preferred geomorphic category for small streams

TABLE 1.—Percent frequencies of 727 classifications of species by substrate trait and stream size category for 426 North American fish species and life history stages. Some species have more than one substrate and stream size preference. Values in parentheses are the number of preference classifications.

Substrate trait category (727)	Stream size category				
	Small streams (155)	Small rivers (286)	Medium rivers (117)	Large rivers (35)	Variable (134)
Bedrock (15)	2.6	2.8	1.7	0.0	0.7
Boulder (43)	3.9	9.1	6.8	0.0	2.2
Cobble–rubble (162)	22.6	31.5	17.9	2.9	11.2
Gravel (158)	15.5	24.1	23.9	25.7	20.9
Sand (154)	22.6	18.9	21.4	20.0	24.6
Mud (77)	11.6	7.0	11.1	8.6	17.2
Vegetation (51)	11.6	3.8	3.4	2.9	12.7
Variable (67)	9.7	2.8	13.7	40.0	10.4

(50.3%), small rivers (36.3%), and the variable river size category (40.3%). Pool and run were the most preferred geomorphic categories in medium rivers (38.5% each). However, in large rivers, run (main channel) was the most preferred geomorphic category (42.3%). Chi-square analysis indicated that the geomorphic preference categories were significantly associated with stream size ($\chi^2 = 132.4$, df = 16, $P = 0.001$).

Trophic classification was accomplished for 359 of the 429 species and life history stages (83.6%). Of the 482 total classifications, 18.8% were variable in their preference for stream size category and trophic category combined (Table 3). The percent frequency of species classified as invertivores was greater than 54% for all stream size categories except large rivers (40.6%). Chi-square analysis indicated that the trophic ecology trait categories were significantly associated with stream size ($\chi^2 = 45.1$, df = 16, $P = 0.001$).

Locomotion and stream size classification was accomplished for 427 of the 429 species and life history stages (99.5%) (Table 4). Of these, 70 (16.4%) represented no reported stream size preference. Cruiser and creeper morphologies were the

most abundant, each representing more than 30% for each stream size category. The preferences for the other locomotion morphology categories ranged from 0% (specialists in small streams and large rivers) to 16.0% (maneuverers in large rivers). Chi-square analysis indicated that the locomotion morphology categories were significantly associated with stream size ($\chi^2 = 47.9$, df = 20, $P = 0.004$). Significant differences among locomotion morphology categories were detected for five of the six morphometric characteristics (Table 5). No significant differences were detected in the ratio of the height of the caudal fin to that of the caudal peduncle.

In all, 307 of the 429 species (71.6%) were classified on the basis of reproductive strategy and stream size preference. Of the 363 total preference observations, 68 (18.7%) represented no reported stream size preference (Table 6). Preferences in the broadcaster category ranged from 22.3% in small rivers to 61.3% in large rivers, whereas those for the simple nester category ranged from 6.5% in large rivers to 42.0% in small rivers. Preferences in the complex nester–guarder category ranged from 0% in large rivers to 38.2% in the variable-

TABLE 2.—Percent frequencies of 671 classifications of species by geomorphic trait and stream size category for 417 North American fish species and life history stages. Some species have more than one geomorphic and stream size preference. Values in parentheses are the number of preference classifications.

Geomorphic trait category (671)	Stream size category				
	Small streams (153)	Small rivers (256)	Medium rivers (117)	Large rivers (26)	Variable (119)
Riffle (108)	12.4	24.2	10.3	3.8	11.8
Pool (271)	50.3	36.3	38.5	30.8	40.3
Run (188)	19.6	29.7	38.5	42.3	21.8
Backwater (90)	13.7	8.2	12.0	15.4	25.2
Variable (14)	3.9	1.6	0.8	7.7	0.8

TABLE 3.—Percent frequencies of 482 classifications of species by trophic preference and stream size category for 359 North American fish species and life history stages. Some species have more than one trophic and stream size preference. Values in parentheses are the number of preference classifications.

Trophic category (482)	Stream size category				
	Small streams (104)	Small rivers (161)	Medium rivers (94)	Large rivers (32)	Variable (91)
Herbivore (48)	9.6	9.3	11.7	18.8	6.6
Planktivore (39)	11.5	3.1	8.5	21.9	7.7
Detritivore (28)	5.8	4.3	9.6	3.1	5.5
Invertivore (306)	67.3	75.2	54.3	40.6	56.4
Carnivore (61)	5.8	8.1	16.0	15.6	24.2

stream-size category. Bearers represented a small portion of classifications, ranging from 0% to 2.6%. Preferences for the migratory category ranged from 10.5% for small rivers to 32.3% for large rivers. Chi-square analysis indicated that the reproductive strategy categories were significantly associated with stream size ($\chi^2 = 70.1$, df $= 16$, $P = 0.001$).

Cluster analysis of the 29 species trait categories indicated the presence of two highly dissimilar clusters ($r = -0.38$) of at least 14 trait categories (Figure 1). The first cluster (GRAVEL, SAND, and MUD) consisted of 15 categories of all five species traits, namely, gravel, specialist, variable substrate, planktivore, herbivore, broadcaster, migratory, run, bearer, detritivore, cruiser, carnivore, backwater, sand, and mud. The second cluster (BOULDER, COBBLE, and BEDROCK) consisted of 14 categories of all five species traits, namely, variable geomorphology, creeper, accelerator, vegetation, pool, maneuverer, hugger, complex nester–guarder, simple nester, riffle, invertivore, bedrock, cobble–rubble, and boulder.

The frequency of occurrence of trait categories within each of these two clusters was compared within stream sizes. For large rivers, the frequency of occurrence of trait categories for the GRAVEL, SAND, and MUD cluster was significantly greater than the frequency of occurrence of trait categories in the BOULDER, COBBLE, and BEDROCK cluster ($P = 0.009$). For small rivers, the frequency of occurrence of trait categories in the BOULDER, COBBLE, and BEDROCK cluster was significantly greater than the frequency of occurrence of trait categories in the GRAVEL, SAND, and MUD cluster ($P = 0.046$). No other significant differences were detected between the two clusters within stream size categories. In comparisons of clusters across stream size categories, the frequency of occurrence of trait categories within the GRAVEL, SAND, and MUD cluster did not vary significantly among stream size categories ($P = 0.106$), as was true for the frequency of occurrence of trait categories within the BOULDER, COBBLE, and BEDROCK cluster ($P = 0.083$).

Cluster analysis also indicated the presence of five highly similar clusters of at least three trait categories with Pearson coefficients greater than 0.75 (Figure 1). Two of these clusters consisted of six trait categories each. Of these, one cluster

TABLE 4.—Percent frequencies of 427 classifications of species by locomotion morphology and stream size category for 427 North American fish species and life history stages. Values in parentheses are the number of preference classifications.

Locomotion morphology category[a] (427)	Stream size category				
	Small streams (98)	Small rivers (163)	Medium rivers (71)	Large rivers (25)	Variable (70)
Cruiser (157)	33.7	31.9	53.5	40.0	34.3
Accelerator (29)	13.3	4.3	2.8	3.9	8.6
Benthic high-velocity hugger (29)	6.1	8.0	2.8	0.0	11.4
Benthic low-velocity creeper (171)	39.8	44.2	35.1	40.0	35.7
Maneuverer (26)	7.1	8.0	0.0	16.0	8.6
Specialist (15)	0.0	3.7	5.6	0.0	1.4

[a] Examples of the fish species in the different categories are as follows: cruiser, Salmonidae; accelerator, Esocidae; benthic high-velocity hugger, Cottidae; benthic low-velocity creeper, Ictaluridae; maneuverer, *Lepomis* spp.; and specialist, Anguillidae.

TABLE 5.—Mean values of morphologic ratios that describe locomotion morphology categories. Means with the same letter are not significantly different (Tukey's test; $P > 0.05$). See Table 4 for examples of the different morphology categories.

Character	Locomotion morphology category				
	Cruiser	Accelerator	Benthic low-velocity creeper	Benthic high-velocity hugger	Maneuverer
Body length/body depth	5.0 yx	7.1 z	5.2 yx	6.4 y	3.3 x
Width of head/width of caudal peduncle	6.1 y	5.9 y	7.7 z	7.1 zy	5.6 y
Height of caudal fin/height of peduncle	2.3 z	2.0 z	2.1 z	2.5 z	2.1 z
Distance from snout to anterior of dorsal fin/total length	0.41 y	0.53 z	0.36 y	0.39 y	0.31 x
Distance from snout to posterior of dorsal fin/total length	0.61 y	0.73 z	0.63 y	0.61 y	0.74 z
Distance from snout to base of pectoral fin/total length	0.22 y	0.24 y	0.22 y	0.21 y	0.28 z

(RUN) included the categories variable substrate, planktivore, herbivore, broadcaster, migratory, and run ($r = 0.84$). The other cluster (RIFFLE) included the categories simple nester, riffle, invertivore, bedrock, cobble–rubble, and boulder ($r = 0.89$). The other three clusters consisted of three trait categories each. The BACKWATER cluster consisted of the categories backwater, sand, and mud ($r = 0.85$). The POOL cluster consisted of the categories accelerator, vegetation, and pool ($r = 0.81$), while the MANEUVERER cluster consisted of the categories maneuverer, hugger, and complex nester–guarder ($r = 0.86$).

The frequency of occurrence of trait categories within each of these five clusters was also compared within stream sizes, for which it varied significantly ($P = 0.002$) for large rivers. For that stream size category, the frequency of occurrence of trait categories within the RUN cluster was significantly greater than those for other clusters, with the exception of the BACKWATER cluster (Figure 2). The frequency of occurrence of trait categories within the five clusters did not vary significantly for medium rivers ($P = 0.372$), small rivers ($P = 0.374$), small streams ($P = 0.939$), or for the variable stream size category ($P = 0.891$).

In comparisons of clusters among stream size categories, the frequency of occurrence of trait cat-

egories within the RUN cluster varied significantly across stream size categories ($P = 0.009$). The frequency of occurrence of trait categories within the RUN cluster were significantly greater for large rivers than for other clusters except for medium rivers (Figure 3). No significant differences in the frequency of occurrence of trait categories among stream size categories were detected for the RIFFLE ($P = 0.328$), BACKWATER ($P = 0.244$), POOL ($P = 0.869$), or the MANEUVERER cluster ($P = 0.057$).

Discussion

Among the most significant limitations to any species trait classification system are the quantity and quality of the underlying data regarding life histories for individual species. Our ability to classify a species based on a trait category and an associated stream size category was relatively high for locomotion morphology (99.5%), substrate preference (99.3%), geomorphic preference (97.2%), and trophic ecology (83.6%). However, we were able to categorize only 71.6% of the 429 species based on combined reproductive and stream size categories. North America has one of the richest fish faunas in the world, with about 800 native species in Canada and the United States (Walsh et al. 1995). These species are not evenly

TABLE 6.—Percent frequencies of 363 classifications of species by reproductive strategy and stream size category for 307 North American fish species. Values in parentheses are the number of preference classifications.

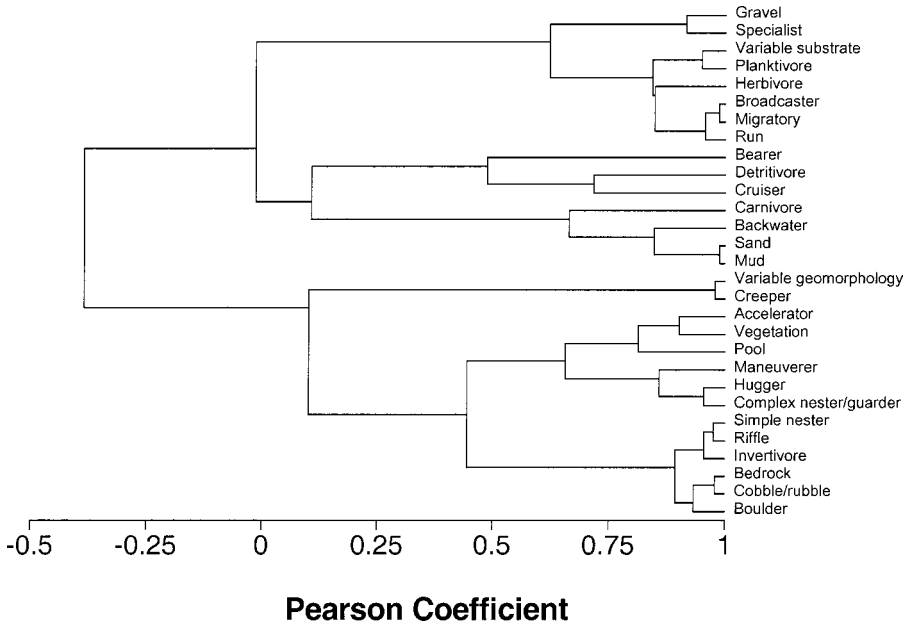| Reproductive strategy category (363)	Stream size category				
	Small streams (76)	Small rivers (112)	Medium rivers (76)	Large rivers (31)	Variable (68)
Broadcaster (122)	30.3	22.3	44.7	61.3	30.9
Simple nester (90)	21.0	42.0	18.4	6.5	14.7
Complex nester–guarder (90)	35.5	24.1	13.6	0.0	38.2
Bearer (3)	2.6	0.0	1.3	0.0	0.0
Migratory (58)	10.5	10.7	22.4	32.3	16.2

Pearson Coefficient

FIGURE 1.—Cluster analysis dendrogram of the frequencies of classification of 29 species trait categories representing five species traits: substrate preference, geomorphic preference, trophic ecology, locomotion morphology, and reproductive strategy. Cluster analysis was conducted for all stream size categories combined.

distributed but tend to concentrate in drainages of the Mississippi River basin. Thus, the data in this study represent 429 species largely occurring in the Mississippi River basin and east to the Atlantic coast. Though the freshwater fishes of the United States have arguably received more study than any fish fauna of comparable scope in the world, large gaps still exist in the study of life history traits (Heins and Matthews 1987; Walsh et al. 1995), especially with respect to reproductive behavior and ontogenetic information (Simon 1999).

In addition to species trait information, the abil-

ity to classify species traits is related to factors such as the number of categories for each trait and within-species variation in traits throughout life stages. The number of categories per trait in our classification is relatively low compared with other classifications (e.g, Goldstein and Simon 1999). As a result, our trait categories tend to be more general than those of classification schemes with

FIGURE 3.—Mean percent frequency of classification of a cluster of species traits consisting of planktivore and herbivore feeding ecology, migratory reproductive behavior and broadcast spawning, a preferences for runs (main-channel habitats), and no preferences for specific substrate types. Means with the same letter are not significantly different ($P > 0.05$) across stream size categories.
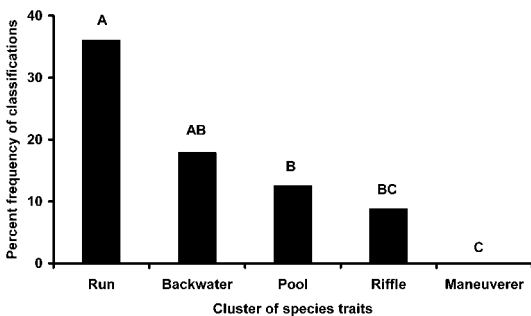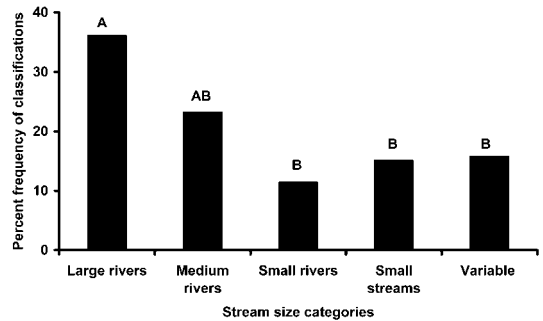

FIGURE 2.—Mean percent frequency of classification of five clusters of species traits associated with large rivers. Means with the same letter are not significantly different ($P > 0.05$).

a larger number of trait categories, which would allow for finer classifications. Although a greater number of trait categories may increase one's ability to distinguish longitudinal variation in species traits, the ability to classify trait categories may be reduced by limited data.

Our approach to classifying was to include multiple trait categories for species when indicated by the literature. For example, in our classification, membership in a particular trophic category is not exclusive: a species may belong to more than one category. However, with the exception of lamprey ammocoetes, our classification applied to adult life stages. The literature may not represent variation in traits across life history stages, and some species may exhibit certain trait preferences that are exclusive to certain life history stages. Thus, the results of this study may not accurately reflect the diversity of traits in streams where juvenile traits vary significantly from adult traits.

We used species presence to determine the frequencies of traits in a stream size-class. The geographic scale of the analysis encompasses a large part of the United States. Hence, the scale of resolution is by necessity gross. More geographically confined studies may choose to use relative abundance rather than species presence for determining the frequencies of species traits. In areas where fish communities are not subject to large zoogeographic differences, relative abundance may produce more precise species trait frequencies. However, given the issues concerning the stability and consistency of sampling fish communities in large rivers (Simon and Sanders 1999), using relative abundances to determine the frequencies of species traits in such systems should be done with caution.

This study indicated that the relations between species traits and stream size categories were most pronounced when comparing the categories small streams and small rivers with the categories medium rivers and large rivers. Definitions and thus quantifiable distinctions between words like "stream" and "river" are often difficult to determine. Generally, the only distinction that can be made is that a stream is "smaller" and a river that is "larger." Further, we used a single dimension (channel width) to quantify distinctions among stream size categories. Clearly, stream size is multidimensional, and factors such as channel depth, discharge, and drainage area are all related components of "size." We used a single measure in an attempt to easily translate a subjective measure of size from the literature (e.g., small stream) to an empirical measure (e.g., a channel width of 1–

3 m). More detailed quantification of stream size may shed additional light on the relations between species traits and stream size.

The results of this study confirm our hypothesis that expectations for fish community function are different for large rivers than for small streams and rivers. However, expectations for fish community function in large and medium rivers may be similar. Fish community function based on four of the five fish species traits (substrate preference, geomorphic preference, trophic ecology, and reproductive strategy) appeared to be unique to large and medium rivers. Specifically, fish community function in large and medium rivers tended to be characterized by species exhibiting the traits of planktivore and herbivore feeding ecology, migratory and broadcast spawning reproductive strategies, preferences for runs (main-channel habitats), and a lack of preferences for specific substrate types.

Whereas our observations of species traits along a longitudinal gradient were generally consistent with the predictions provided by theoretical frameworks, there were some contrasts. For example, the habitat template and landscape filter frameworks predict that fish community function based on reproductive traits would be different for large rivers and small streams, as we observed (Table 7). The landscape filter framework predicts that reproductive traits will vary with flow and substrate variability. Habitat template frameworks predict a reduction in the number of reproductive strategies and an increase in parental care. We also observed a reduction in the number of reproductive strategies. Of the four reproductive strategies in our classification, only two were noted in large rivers whereas at least three were observed in all other stream size categories. However, in contrast to habitat template predictions, broadcast spawners exhibiting no parental care dominated in large rivers, as did migratory traits. Energetically, broadcast spawning behaviors and spawning movements or migrations would seem to be related since broadcast spawners are more likely to accumulate the energy stores needed to make spawning movements (Moyle and Herbold 1987).

In contrast to predictions provided by landscape filters, substrate traits varied with stream size. Landscape filter predictions suggest that substrate preferences are driven largely by microhabitat scale factors (Poff 1997). Thus, these predictions would suggest that the variation in substrate preferences is greater within than among stream reaches. However, the present study indicates that it is

TABLE 7.—Generalized theoretical predictions and empirical findings from the present study of variation in fish species traits along a longitudinal stream gradient from a small stream to a large river. The term ''little variation'' indicates that the trait does not vary along the gradient (or among stream reaches) but may vary within a stream reach. Landscape filter predictions are from Poff (1997) and are used to predict species traits that vary among as opposed to within stream reaches. Habitat template predictions, derived from Townsend and Hildrew (1994) and Lamouroux et al. (2002), focus on locomotion morphology and reproductive strategy and are based on the assumption that temporal variability in discharge and riffle habitat decreases with increasing stream size. Predictions for the river continuum concept (RCC) are from Vannote et al. (1980) and focus on trophic ecology traits.

Species trait	Landscape filter	Habitat template	RCC	Present study findings
Substrate preference	Little variation			More to less diverse
Geomorphic preference	Varies with habitat characteristics among reaches			Increase in preferences for main-channel habitats
Trophic ecology	Varies with food resource base among stream reaches	Increase in number of trait categories	Fewer invertivores; more planktivores and herbivores	Invertivores remained constant; increase in planktivores and herbivores
Locomotion morphology	Little variation	Increase in diverse body shapes; increase in non benthic forms		Little variation
Reproductive strategy	Varies with substrate and flow characteristics among stream reaches	More reproductive strategies to fewer; increase in parental care		More reproductive strategies to fewer; more to less parental care
Migration	Decreases with increasing barriers to movement			Less to more migratory

possible to make generalizations about the variation in substrate preferences with increasing stream size, there being no single substrate preference for fish in large rivers.

Our findings support landscape filter predictions of the variation in geomorphic preferences with stream size (Table 7). This study underscored the importance of functional relations to backwater areas linked to large rivers. Stalnaker et al. (1989) noted that although backwaters represent less than 10% of the total surface area of large rivers, they support up to 90% of the fish biomass. Stalnaker et al. (1989) also indicated that large-river fish species show a greater tendency toward habitat zonation than species in small streams.

Although predictions based on the landscape filter, habitat template, and RCC frameworks suggest variation in trophic ecology among stream reaches, the RCC can be used to contrast predictions and observations in greater detail. The RCC predicts an increase in planktivores and herbivores with increasing stream size. Schlosser (1982, 1987) proposed a longitudinal progression in fish trophic ecology based on the RCC that begins in small streams with species that can be classified as generalized invertivores and ends in large rivers with primarily detritivores and herbivores. Our findings support the RCC predictions and the findings of Schlosser (1982, 1987). However, our findings for

the variation in invertivores related to stream size are in contrast to predictions based on the RCC. Our results indicated that the frequency of classification of a cluster of species trait categories that included invertivores did not vary with stream size. Whereas the RCC is concerned with the longitudinal movement of energy and the corresponding responses by biota, the flood-pulse concept (FPC) is concerned with the transverse movement of energy and the responses by biota, particularly in large-floodplain rivers (Junk et al. 1989). Thus, in large-floodplain rivers, the FPC may supplement or replace the RCC. The FPC suggests that organic matter from upstream may not be as important as that from along the floodplain. Similarly, Thorp and Delong (1994) proposed the riverine productivity model, which hypothesizes that carbon derived from allochthonous and localized riparian zone production is the primary energy source for macroinvertebrates in large rivers. Thus, the limited longitudinal variation of invertivores may be related more to the importance of the aquatic–terrestrial transitional zone across all stream size categories.

Our findings suggest that the factors influencing the variation in locomotion morphology among stream size categories are complex. Cluster analysis indicated that the frequency of occurrence of locomotion morphology trait categories did not

vary significantly with stream size. Examination of measured morphometric ratios indicated that the locomotion morphology classification that we used reflected real ecological separation of morphological categories. Thus, our findings would seem to support the predictions of landscape filters that suggest that fish body morphology is most influenced by microhabitat scale factors such as hydraulic stress (Poff 1997). In contrast to landscape filter predictions, habitat template predictions suggest that the variation in locomotion morphology types occurs with an increase in specialized body shapes and nonbenthic forms with increasing stream size. Examination of individual locomotion morphology trait categories indicated that the frequencies of streamlined cruisers and dorsoventrally flattened huggers and creepers did not change greatly; however, the frequency of classification of the more specialized, nonbenthic maneuverers for large rivers was nearly double that for small stream and rivers.

Conclusions

Our results suggest that fish community function varies among stream size categories, that it is different in large rivers than in small streams and rivers, and that it provides information on biological expectations for large rivers. These differences are evident in the variations in trophic ecology, reproductive behavior, and preferences for substrate and geomorphic habitat types. In general, our findings support the theoretical predictions of the landscape filter and RCC frameworks. A notable contrast is the RCC prediction of a decrease in invertivores with increasing stream size. Our finding that invertivores remained relatively constant across stream sizes may reflect an increased ecological importance of the aquatic–terrestrial transitional zone with increasing stream size. Comparisons and contrasts with template predictions may be affected by the applicability of the habitat template to large rivers and the assumptions of temporal variability and spatial heterogeneity along a gradient of stream sizes. Our results serve as a generalized model of fish community function along a longitudinal gradient. Whereas conceptual frameworks such as habitat templates can be used to predict species trait distributions along longitudinal gradients, these frameworks are secondary to and overlay existing evolutionary histories driven by factors such as glaciation. We believe that the classifications presented in this study provide an opportunity for further examination of fish species' relations to physical, chemical, and biological factors at multiple spatial scales.

References

Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. Journal of the Fisheries Research Board of Canada 32:821–864.

Balon, E. K. 1981. Additions and amendments to the classification of reproductive styles in fishes. Environmental Biology of Fishes 6:377–389.

Bayley, P. B. and H. W. Li. 1992. Riverine fishes. Pages 251–281, *in* P. Calow and G. E. Petts, editors, The rivers handbook: hydrological and ecological principles, volume 1. Blackwell Scientific Publications, Oxford.

Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.

Breeder, C. M., Jr., and D. E. Rosen. 1966. Modes of reproduction in fishes. T. F. H. Publications, Jersey City, New Jersey.

Etnier, D. A., and W. C. Starnes. 1993. The fishes of Tennessee. University of Tennessee Press, Knoxville.

Fitzpatrick, F. A., I. R. Waite, P. D'Arconte, M. R. Meador, M. A. Maupin, and M. E. Gurtz. 1998. Revised methods for characterizing stream habitat in the National Water-Quality Assessment Program. U.S. Geological Survey, Water-Resource Investigations Report 98-4052. Raleigh, North Carolina.

Gatz, J. A., Jr. 1979. Community organization in fishes as indicated by morphological features. Ecology 60: 711–718.

Gerking, S. D., 1994. Feeding ecology of fish. Academic Press, San Diego.

Goldstein, R. M., and T. P. Simon. 1999. Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. Pages 123–202 *in* T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Harris, P. M. 1995. Are autecologically similar species also functionally similar? A test in pond communities. Ecology 76:544–552.

Heins, D. C., and W. J. Matthews. 1987. Historical perspectives on the study of community and evolutionary ecology of North American stream fishes. Pages 3–7 *in* D. C. Heins and W. J. Matthews, editors. Community and evolutionary ecology of

North American stream fishes. University of Oklahoma Press, Norman.

Hildebrand, S. F., and W. C. Schroeder. 1928. Fishes of Chesapeake Bay. U.S. Bureau of Fisheries Bulletin, Document No. 1024, volume 53, part 1.

Horwitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecological Monographs 48:307–321.

Hughes, R. M., and J. R. Gammon. 1987. Longitudinal changes in fish assemblages and water quality in the Willamette River, Oregon. Transactions of the American Fisheries Society 116:196–209.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood-pulse concept in river–floodplain ecosystems. Canadian Special Publication of Fisheries and Aquatic Sciences 106:110–127.

Lamouroux, N., N. L. Poff, and P. L. Angermeier. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. Ecology 83(7):1792–1807.

Li, H. W., C. B. Schreck, C. E. Bond, and E. Rexstad. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. Pages 184–192 in D. C. Heins and W. J. Matthews, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Mettee, M. F., P. E. O'Neil, and J. M. Pierson. 1996. Fishes of Alabama and the Mobile basin. Oxmoor House, Inc., Birmingham, Alabama.

Moyle, P. B., and B. Herbold. 1987. Life history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe. Pages 25–32 in D. C. Heins and W. J. Matthews, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Page, L. M., and B. M. Burr. 1991. A field guide to freshwater fishes north of Mexico. Houghton Mifflin, Boston.

Pflieger, W. L. 1997. The fishes of Missouri, revised edition. Missouri Department of Conservation, Jefferson City.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16(2):391–409.

Reash, R. J. 1999. Considerations for characterizing midwestern large-river habitats. Pages 463–473 in T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1991. Common and scientific names of fishes from the United States and Canada, 5th edition. American

Fisheries Society, Special Publication 20, Bethesda, Maryland.

Robison, H. W., and T. M. Buchanan. 1988. Fishes of Arkansas. University of Arkansas Press, Fayetteville.

Rohde, F. C., R. G. Arndt, D. G. Lindquist, and J. F. Parnel. 1994. Freshwater fishes of the Carolinas, Virginia, Maryland, and Delaware. University of North Carolina Press, Chapel Hill.

Ross, S. T. 2001. The inland fishes of Mississippi. University of Mississippi Press, Oxford.

Schlosser, I. J. 1982. Fish community structure and function along two geomorphologic gradients in a headwater stream. Ecological Monographs 52:395–414.

Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17–24 in W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology in North American stream fishes. University of Oklahoma Press, Norman.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa.

Simon, T. P. 1999. Assessment of Balon's reproductive guilds, with application to midwestern North American freshwater fishes. Pages 97–121 in T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Simon, T. P., and R. E. Sanders. 1999. Applying an IBI based on great-river fish communities: considerations in sampling and interpretation. Pages 475–505 in T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Southwood, T. R. E. 1977. Habitat: the template for ecological strategies? Journal of Animal Ecology 46:337–365.

Stalnaker, C. B., R. T. Milhous, and K. D. Bovee. 1989. Hydrology and hydraulics applied to fishery management in large rivers. Canadian Special Publication of Fisheries and Aquatic Sciences 106:13–30.

Thorp, J. H., and M. D. Delong. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large-river ecosystems. Oikos 70:305–308.

Townsend, C. R., and A. G. Hildrew. 1994. Species traits in relation to a geomorphologic templet for river systems. Freshwater Biology 31:265–275.

Trautman, M. B. 1981. The fishes of Ohio with illustrated keys, revised edition. Ohio State University Press, Columbus.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Journal of the Fisheries Research Board of Canada 37:130–137.

Walsh, S. J., N. M. Burkhead, and J. D. Williams. 1995. Southeastern freshwater fishes. Pages 144–147 in

E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Webb, P. W. 1984a. Body form, locomotion, and foraging in aquatic vertebrates. American Zoologist 24:107–120.

Webb, P. W. 1984b. Form and function in fish swimming. Scientific American 251:58–68.

Webb, P. W., and D. Weihs. 1986. Functional morphology of early life history stages of fishes. Transactions of the American Fisheries Society 115:115–127.