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[Article]

Seasonal and Ontogenic Shifts in Microhabitat Selection by Fishes in the Shallow Waters of the Detroit River, a Large Connecting Channel

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Abstract.—We examined the relationship between microhabitat variables and fish distributions in a large connecting channel, the Detroit River. Fishes were sampled by boat seine at 60 sites in shallow (<2.5 m) Canadian waters in May, July, and September 2004. Length-frequency distributions were used to separate species into small- and large-species size categories. Fish–microhabitat associations were examined by applying canonical correspondence analysis separately for each season. Small fishes were often more strongly associated with microhabitat variables than large conspecifics. For example, small centrarchids were more strongly associated with complex macrophytes than large centrarchids in the spring; however, this pattern varied among seasons. We attribute the stronger microhabitat associations of small fishes to predator avoidance. Small-bodied species also selected habitats that provided protection against predation: the spotfin shiner *Cyprinella spiloptera* preferred shallow water, and the round goby *Neogobius melanostomus* preferred coarse substrate. We observed a strong difference in microhabitat preferences between the small and large size categories of a species. Fish size played a greater role than season in determining fish–microhabitat associations. We found that macrophytes with a complex morphological structure were the most important factor in determining fish distributions in all seasons, while depth ranked second or third in importance. Fishes use an array of microhabitats in the Detroit River, and habitat heterogeneity is essential for promoting a diverse fish assemblage.

Few quantitative studies of the habitat requirements of fishes in large rivers were conducted before this decade, largely because of the challenges involved in sampling the deep, flowing waters of these systems. Despite the increased attention that large-river fishes now receive, little is known about the habitat requirements of fishes in large connecting channels. Such channels differ markedly from large rivers in that the headwaters are composed of large lakes rather than a network of tributaries, and because water levels and discharge remain relatively stable (Edwards et al. 1989). These characteristics result in a lack of floodplain habitat and low rates of hydraulic exchange between channels and protected backwaters. Thus, large connecting channels represent a unique ecosystem (intermediate between large rivers and lakes) for which fish–microhabitat associations have not been described.

Copp et al. (1994) and Grenouillet et al. (2000) suggested that large rivers contain distinct lentic and lotic fish assemblages. The inshore retention concept (Schiemer et al. 2001) supports this division of habitats in large rivers by proposing that young fishes use inshore areas as nurseries because of their shoreline structure, protection from washout during changing water levels, high retention of organic material, and unique temperature regimes. These characteristics primarily result from hydraulic retention and separation from flowing channel waters. The riverine productivity model (Thorp and Delong 1994) suggests that local carbon sources, such as autochthonous production and riparian imports, are important sources of nutrients in large rivers. Local nutrient sources are even more important in lentic regions that receive few nutrients from upstream waters. The separation of lentic and lotic habitats is especially appropriate for large connecting channels, where lentic areas exhibit relatively stable water levels and current velocities and, therefore, low rates of hydraulic exchange with lotic areas.

Little is known about fishes' habitat preferences in large connecting channels, although these are probably similar to their habitat preferences in large rivers; therefore, information may be drawn from the literature

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about large rivers. Grossman et al. (1987) and Copp (1997) showed that fishes tend to respond strongly to microhabitats in large rivers. For example, fishes are strongly associated with macrophytes in large rivers where aquatic vegetation is abundant (Grenouillet et al. 2000; Petry et al. 2003). Additionally, large-river fishes are associated with physical variables, such as substrate, depth, current velocity, slope, and cover (Cantu and Winemiller 1997; Fladung et al. 2003).

Although few studies have examined how habitat use changes with season and such studies tend to be at the macrohabitat scale (Pusey et al. 1993; Slavik and Bartos 2001), shifts in habitat use are expected in relation to seasonal events such as spawning and macrophyte growth. Thus, microhabitat preferences should be determined at each season. Examinations of microhabitat associations for fish assemblages are preferred over studies focused on individual species for ecosystem management and restoration (Lobb and Orth 1991; Barko et al. 2004). Habitat preferences should also be evaluated separately for size-classes of individual species, given that ontogenic shifts in habitat use often occur. In large rivers, for example, adult fishes prefer deeper waters with higher current velocity than do juvenile fishes (Lamouroux et al. 1999; Fladung et al. 2003). Our primary objective was to explore the microhabitat associations of fishes in the Detroit River, a large connecting channel, accounting for season and fish size. We asked two questions: Do small and large individuals of a species exhibit similar microhabitat preferences? Do microhabitat associations of species vary among seasons? We tested the null hypothesis that microhabitat variables, useful in structuring fish assemblages, do not differ among seasons.

Methods

Site Description

The 51-km Detroit River, an International Heritage River, is located along the Michigan–Ontario border and connects Lake St. Clair to Lake Erie. The International Joint Commission (Hartig 2003) classified the Detroit River as an Area of Concern because its beneficial uses have been impaired. Several technical reports have examined spawning and larval fish habitat and the interrelationships among the fish assemblages of these rivers and the Great Lakes (e.g., Goodyear et al. 1982; Haas et al. 1985; Hatcher et al. 1991; OMNR 1994); however, with few exceptions (Caswell et al. 2004), the primary literature on Detroit River fishes has focused on contaminant levels (e.g., Li et al. 2003). Average flushing time and discharge are 19 h and 5,300 m^3/s, respectively, although these rates can vary greatly as a result of seiches in Lake Erie that temporarily raise downstream water levels above those in Lake St. Clair (Edwards et al. 1989; Bolsenga and Herdendorf 1993). Shipping channels are maintained in the Detroit River by annual dredging (Manny and Kenaga 1991).

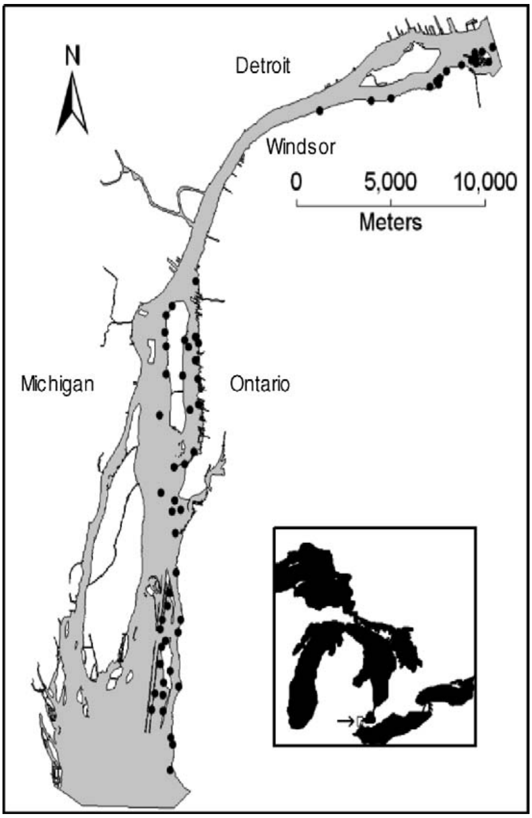


FIGURE 1.—Locations of fish sampling sites in shallow Canadian waters of the Detroit River.

Site Selection

Sixty sites were selected from the shallow (<2.5 m) Canadian waters of the Detroit River (Figure 1). A polygon shapefile (14.4 km^2) outlining all permanent, shallow Canadian waters of the river was created with ArcMap 8.3 (ESRI 2003). The Universal Transverse Mercator site coordinates were plotted in the area outlined by the polygon with randomization macros in ArcMap following a stratified random sampling design from a related macrohabitat study (Lapointe 2005). Half the sites were located along the shoreline (inshore), and the other half were placed offshore. These coordinates represented the centroids of the sites, which covered approximately 18 m^2 (i.e., the area enclosed by the seine). To avoid sampling nonresident fishes, tributary confluence regions were removed from the potential sampling area before site selection. Marinas and other small inlets were also removed, given that small channel width and increased depth prohibited proper seine use. To reduce the effects of spatial autocorrelation, a minimum distance of 200 m between sites was arbitrarily selected. Sites were verified in the field, and inappropriate points (e.g., deep water, high current velocity) were replaced with other randomly selected sites.

Fish Sampling

Fishes were sampled in May (spring), July (summer), and September (fall) by boat seining because this technique is effective for capturing high fish-species richness (Lapointe et al. 2006). We used a 15-m-long, 2.5-m-tall seine net with a 2.5-m bag and 0.64-cm "ace" mesh. Five replicate hauls were taken for each sample (site and season). If a new species was discovered on the fourth or fifth haul, additional hauls were taken until two hauls were completed without capturing a new species for the sample. All fishes were identified to species, and up to 30 individuals of each species were measured (total length) for each sample. Fishes were released alive, except for vouchers that were anesthetized with clove oil and fixed with 10% formalin.

Microhabitat Measurements

Based on a review of 20 recent papers on fish–microhabitat associations in large rivers, the most commonly measured variables (in descending order of use) were depth, current velocity, macrophytes, substrate, temperature, turbidity, cover, and distance from shore (Lapointe 2005). Of these, we measured all but cover because coarse woody debris and other forms of cover were rarely found in the Detroit River. Microhabitat variables such as percent cover of macrophytes were estimated for the 18 m^2 enclosed by the seine, whereas variables such as water temperature, turbidity, and current velocity were measured at the centroid of each sample site. Turbidity was measured using a Secchi disk (only in deep water) and a turbidity tube (in shallow water). Current velocity (Z21 Ott current meter) was measured at 0.2% and 0.8% of the water column at sites with a mean depth of less than 1 m. In depths of 1 m or greater, current velocity was measured 1 m below the surface. Depth was measured to the nearest 0.05 m using markings on the seine brail. The percent cover of each taxonomic group of macrophytes and filamentous algae was estimated visually. Where turbidity made visual estimation difficult, percent cover estimates were made using macrophytes and algae attached to the anchor or in the seine. Percent composition of substrate classes was estimated in the field using a combination of Ekman grab samples, visual estimates, and underwater video. A single Ekman grab sample was taken near the centroid of each site, except when underwater video was used to examine coarse substrates. Substrate type estimates were supplemented by manual prodding of the channel bottom with the seine brail and by examination of sediments attached to the anchor to ensure that all substrate sizes in the sampling area were identified. Substrate classes were defined according to the Wentworth scale as coarse (>2 mm), sand (2–0.075 mm), and fine (<0.075 mm). Fish and microhabitat data are available online at www.uwindsor.ca/corkum.

Analysis

Fish data.—Length-frequency distributions and reported lengths (Scott and Crossman 1979) were used to differentiate the youngest age-class from older (large) fish for each species. Three species (spotfin shiner *Cyprinella spiloptera*, round goby *Neogobius melanostomus*, and tubenose goby *Proterorhinus marmoratus*) exhibited normally distributed length frequencies and, therefore, multiple size-classes could not be distinguished. In the analysis, small and large individuals of these three species were grouped into a single variable. Few young of year were found during spring; however, age-1 individuals (yearlings) were distinct in length from other age classes. Therefore, "small" generally represents yearlings in the spring, and "young of year" represents those in the summer and fall (as determined through length-frequency analysis). Small and large fishes of the same species were considered separate variables in all analyses and henceforth will be referred to as "species size categories."

Species size categories found in less than 5% of the samples in a season were considered uncommon and excluded from analysis (see Gauch 1982). We present the presence or absence of species for a site rather than the total abundance because seining differs in efficiency with substrate and species (Pierce et al. 1990; Bayley and Herendeen 2000). Sample outliers were identified by first calculating the Euclidean distance between samples for the species size categories by samples matrix. Outlier samples were then removed if their distance exceeded 2.5 deviations from the mean distance.

Microhabitat data.—Turbidity tube values were used at shallow sites when the Secchi disk was observed on the substrate. Where possible, missing or maximum turbidity tube values were calculated from Secchi disk values by means of a simple linear regression between all corresponding Secchi disk and turbidity tube measurements (i.e., turbidity value $= 19.8 + 0.48 \cdot$Secchi disk value; $R^2 = 0.63$, $P < 0.001$). We grouped macrophytes according to whether their morphological structure was simple or complex because the morphological structure of aquatic macrophytes affects the quality of habitat provided to fishes (Petry et al. 2003). A separate variable was used to represent the percent cover of filamentous algae. The bottom slope was calculated for offshore sites as $(D_a - D_i)/15$, where D_a is the maximum depth, D_i is the minimum depth, and 15 represents the maximum diameter of the site in meters (i.e., the length of the seine net). For inshore sites, slope was calculated as $(D_a - D_0)/d$, where D_0 is the depth at 0 m and d is the distance from shore at which the maximum depth was initially reached (3–15 m). Proportional variables (macrophyte and substrate classes, slope) were arcsine square root transformed, while all other variables were (log + 1) transformed to improve normality (McCune and Grace 2002).

Principal components analyses (PCA) based on a correlation matrix were performed on microhabitat variables measured at sites for all seasons combined. An exploratory PCA scatterplot showed that inshore and offshore samples were separated in multivariate space (even when distance from shore was not included as a variable), suggesting that inshore microhabitats were distinct from those found offshore. Accordingly, separate analyses were performed on inshore and offshore samples.

Species–microhabitat relationships.—The relationship between species size categories and microhabitat variables was explored separately for each season applying canonical correspondence analysis (CCA) with CANOCO 4.53 (Ter Braak and Smilauer 2004). For all analyses, we chose biplot scaling focused on interspecies distances and manual stepwise selection of environmental variables. Monte Carlo permutations (9,999 permutations) were used to test the stepwise significance of adding microhabitat variables to the model and, therefore, their usefulness in determining the species size category data (Ter Braak and Smilauer 1998). Variables were retained if the *P*-value was less than 0.05.

Species size categories were grouped to determine whether distinct assemblages were associated with specific microhabitat variables. Hierarchical cluster analysis was performed separately for each season using flexible beta linkage ($\beta = -0.25$) based on a Sorenson distance matrix. Four groups were defined in each season, and group membership was overlaid onto the CCA biplots.

Seasonal microhabitat use.—Only species size categories common in all three seasons were used to test the null hypothesis that microhabitat variables, useful in structuring the fish assemblage, do not differ among seasons. Species size categories common in only one season may prefer unique habitats and thus bias comparisons among seasons. Forward selection of environmental variables in CANOCO was used to identify which microhabitat variables explained species size category data for each season. Monte Carlo permutation tests were used as indicated above. Microhabitat variables were considered important in a season at $P < 0.05$.

TABLE 1.—Species captured by seining in the Detroit River, 2004, and codes used to represent them. Abundance is the total abundance across seasons.

Species	Code	Abundance
Alewife *Alosa pseudoharengus*	ALPS	131
Rock bass *Ambloplites rupestris*	AMRU	374
White sucker *Catostomus commersonii*	CACO	9
Spotfin shiner *Cyprinella spiloptera*	CYSP	276
Common carp *Cyprinus carpio*	CYCA	9
Gizzard shad *Dorosoma cepedianum*	DOCE	2,663
Johnny darter *Etheostoma nigrum*	ETNI	28
Brook silverside *Labidesthes sicculus*	LASI	219
Pumpkinseed *Lepomis gibbosus*	LEGI	201
Bluegill *Lepomis macrochirus*	LEMA	487
Striped shiner *Luxilus chrysocephalus*	LUCH	302
Smallmouth bass *Micropterus dolomieu*	MIDO	73
Largemouth bass *Micropterus salmoides*	MISA	397
White perch *Morone americana*	MOAM	404
White bass *Morone chrysops*	MOCH	468
Round goby *Neogobius melanostomus*	NEME	898
Hornyhead chub *Nocomis biguttatus*	NOBI	92
Golden shiner *Notemigonus crysoleucas*	NOCR	87
Emerald shiner *Notropis atherinoides*	NOAT	17,376
Spottail shiner *Notropis hudsonius*	NOHU	2,171
Sand shiner *Notropis stramineus*	NOST	25
Mimic shiner *Notropis volucellus*	NOVO	1,172
Rainbow smelt *Osmerus mordax*	OSMO	134
Yellow perch *Perca flavescens*	PEFL	1,781
Logperch *Percina caprodes*	PECA	69
Trout-perch *Percopsis omiscomaycus*	PEOM	12
Bluntnose minnow *Pimephales notatus*	PINO	911
Fathead minnow *Pimephales promelas*	PIPR	4
Black crappie *Pomoxis nigromaculatus*	PONI	15
Tubenose goby *Proterorhinus marmoratus*	PRMA	22

Results

Fish Data

A total of 30,943 fish (16 families, 46 species) were captured in 1,141 seine hauls (Table 1); 19,657 fish (15 families, 41 species) were captured in spring, 6,654 (13 families, 35 species) in summer, and 4,632 (13 families, 33 species) in fall. Spawning emerald shiners contributed to 78% of the spring catch. No species exhibited such strong numerical dominance in the summer or fall. There were 31, 28, and 30 common (>5% of samples) species size categories in the spring, summer, and fall, respectively. In total, 43 species size categories were common in at least one season;

however, only 17 were common in all seasons. Some early season spawners (e.g., rainbow smelt, trout-perch, white sucker) were abundant only in spring, whereas species that continue spawning into the summer (e.g., common carp, brook silverside) were common in spring and summer. Some young of year were common in both summer and fall (e.g., gizzard shad, *Micropterus* spp.), whereas others were not common until fall (e.g., alewife, mimic shiner, bluegill).

Microhabitat Data

Water temperature (11–27°C), turbidity tube (17–120 cm), Secchi disk (15–225 cm), current velocity (0–1.4 m/s), mean depth (32.7–254 cm), and slope (0–23.3%) measurements varied throughout the sampling period. River water levels did not vary by more than 15 cm among seasons. Each substrate class varied between 0 and 100% composition by site.

Macrophytes found included bulrush *Scirpus* spp.; coontail *Ceratophyllum demersum*; elodea *Elodea canadensis*; milfoil *Myriophyllum* spp.; pondweeds *Potamogeton* spp.; stonewart *Chara* spp.; water stargrass *Heteranthera dubia*; waterlily *Nymphaea* spp.; and wild celery *Vallisneria americana*. Two morphological groups were identified: simple macrophytes (wild celery and water stargrass) with grasslike long, narrow leaves, and complex macrophytes (coontail, elodea, milfoil, pondweed) with branching stems and featherlike or linear leaves (Janecek 1988). Some plants were excluded from analysis because of difficulties in estimating abundance (*Chara*) or because of infrequent occurrence (bulrush and water lily). Complex macrophytes were common in spring and increased in abundance in summer and fall. Simple macrophytes were rare in spring but common in summer and fall.

Principal components analysis.—Only the first two axes of the inshore and offshore ordinations of sample sites were interpreted because they explained the greatest amount of variability in the data (Table 2). No strong seasonal patterns in microhabitat variables were observed at inshore or offshore sites, given that seasons were not separate in multivariate space (Figure 2). The first inshore axis described an increasing gradient between deep sites with complex macrophytes and shallow, sandy beaches (Figure 2a). The second axis described a gradient between sites with high current velocity, high turbidity, and coarse substrates, and other sites with clear water, low flow, fine substrates, and simple macrophytes. The first offshore axis described a gradient between sites with deep water, low flow, fine substrate and complex macrophytes, and sites with coarse substrates and high flow (Figure 2b). The second axis described an increasing gradient between sites with sandy substrate and simple macrophytes, and sites with filamentous algae. The amount of variance explained by two axes was low for both inshore (42%) and offshore (46%) ordinations, suggesting weak linear relationships among microhabitat variables.

TABLE 2.—Inshore and offshore microhabitat PCA results, including eigenvectors for microhabitat variables.

	Inshore		Offshore	
PCA element	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	2.72	2.32	3.01	1.65
Cumulative percentage variance	24.7	45.8	27.4	42.4
Microhabitat variables eigenvectors				
Turbidity	−0.26	−0.34	−0.21	0.13
Current velocity	0.10	−0.42	0.32	0.12
Water temperature	−0.10	0.19	−0.20	−0.33
Depth	−0.42	−0.11	−0.40	0.10
Slope	−0.44	−0.13	−0.12	0.24
Fine substrate	−0.23	0.49	−0.39	−0.06
Sand substrate	0.42	0.07	0.37	−0.41
Coarse substrate	−0.20	−0.52	0.35	0.28
Complex macrophytes	−0.41	0.17	−0.45	0.15
Simple macrophytes	−0.25	0.31	−0.16	−0.51
Filamentous algae	0.22	−0.05	0.02	0.51

Canonical correspondence analysis.—When combined, all axes explained significantly more of the variation in the fish–microhabitat data than expected by chance ($P < 0.001$) for each season. Only the first two axes are presented for each season because they explained most of the variance in the species size category–microhabitat relationship in spring (65%), summer (68%), and fall (72%) (Table 3). In spring, the first axis primarily described an increasing gradient from sites with filamentous algae to other sites with fine substrates and complex macrophytes. Deep sites loaded positively on the second axis. In summer, the first axis described an increasing gradient between offshore sites with macrophytes and nonvegetated inshore sites. The second axis described an increasing gradient between shallow, turbid sites and deep, clear sites. In fall, the first axis described an increasing gradient between sites with high current velocity and sites with complex macrophytes. Deep sites and sites with fine substrates were highly negatively loaded on the second axis.

The four assemblages defined by cluster analysis varied with season. In each season, an assemblage dominated by centrarchids (represented by circles) appeared to be positively associated with complex macrophytes (Figure 3a–c). Another assemblage dominated by *Notropis* spp., small yellow perch, spotfin shiner, and round goby (open triangles), was generally associated with average microhabitat variables in each season. Other assemblages (plus signs and filled

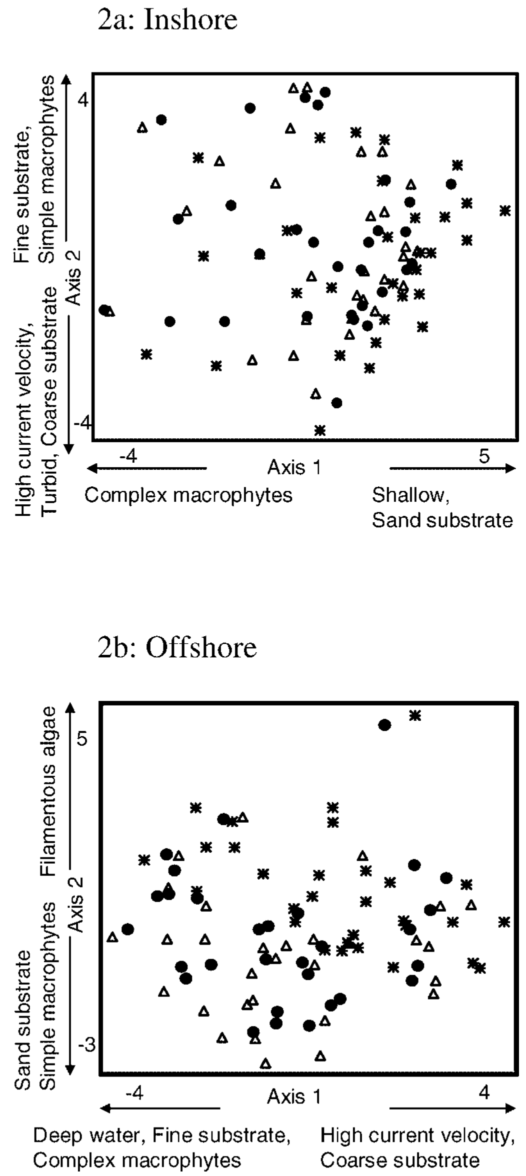


FIGURE 2.—Scatterplots of **(a)** 30 inshore and **(b)** 30 offshore sites where microhabitat variables were measured in all three seasons on principal component axes 1 and 2 (n = 90). Variables with the most positive and negative loadings on axes 1 and 2 are shown. Points represent sites in ordination space and are coded by season (circles = spring, triangles = summer, and asterisks = fall).

inverted triangles) varied with season in terms of species composition and microhabitat associations.

Ontogenic Shifts in Microhabitat Selection

In spring, small and large fish of the same species had similar habitat preferences, while preferences differed markedly among species (Figure 3a). With the exception of yellow perch and white perch, small fish were more strongly associated with microhabitat variables than were large fish of the same species. For example, small rock bass were more strongly associated with complex macrophytes than were large conspecifics.

In summer, the habitat preferences of small fishes typically differed from those of large conspecifics, but no pattern was observed among species. Small centrarchids and striped shiner preferred deeper sites with more macrophytes than did large fishes of the same species (Figure 3b). Small gizzard shad and white bass had a strong preference for sites with low turbidity. Small golden shiner and smallmouth bass were less strongly associated with microhabitat variables than were large conspecifics.

In fall, many small and large fish of the same species (yellow perch, emerald shiner, and spottail shiner) were not strongly correlated with any variable (Figure 3c). The habitat requirements of large centrarchids differed from those of small individuals of the same species; however, no directional pattern was observed. Other species showed stronger microhabitat preferences for small individuals. For example, small mimic shiner preferred deeper sites with lower current velocity and finer substrate than did large conspecifics, whereas small hornyhead chub and bluntnose minnow preferred complex macrophytes compared with large fishes of the same species.

Seasonal Microhabitat Selection

Habitat associations did not differ among seasons for most species. In all seasons, two species (large mimic shiner, round goby) avoided complex macrophytes, while spotfin shiner preferred shallow water. The only species that exhibited opposite habitat preferences among seasons were large bluegill, which associated negatively with complex macrophytes and deep waters in the spring but strongly and positively associated with these variables in the fall; large largemouth bass, which associated negatively with complex macrophytes in the summer but positively in the fall; and tubenose goby, which strongly and negatively associated with complex macrophytes in the spring and summer but positively associated with complex macrophytes in the fall. Many common large species size categories (rock bass, pumpkinseed, spottail shiner, mimic shiner, emerald shiner, yellow perch) showed a preference for greater depths in the fall than in earlier seasons.

For the 17 species size categories common in all three seasons, forward selection of environmental variables in three CCA ordinations revealed that

TABLE 3.—Summary of seasonal canonical correspondence analysis (CCA) results showing eigenvalues, species–environment correlations, and the percentage of variance explained by each axis for each season.

	Spring		Summer		Fall	
CCA element	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.24	0.13	0.23	0.17	0.20	0.13
Species–environment correlation	0.80	0.77	0.81	0.73	0.79	0.79
Cumulative percentage variance						
Species data	8.0	12.2	7.8	13.3	7.8	12.7
Species–environment correlation	42.4	65.1	39.7	67.6	44.0	72.0

complex macrophytes was the most important variable in structuring fish data in all seasons (Table 4). Depth ranked second most important in spring and summer and third in fall; however, no other variable explained significantly more of the fish data than expected by chance in all three seasons. Filamentous algae and coarse substrate were significant only in spring, whereas turbidity and distance from shore were significant only in summer.

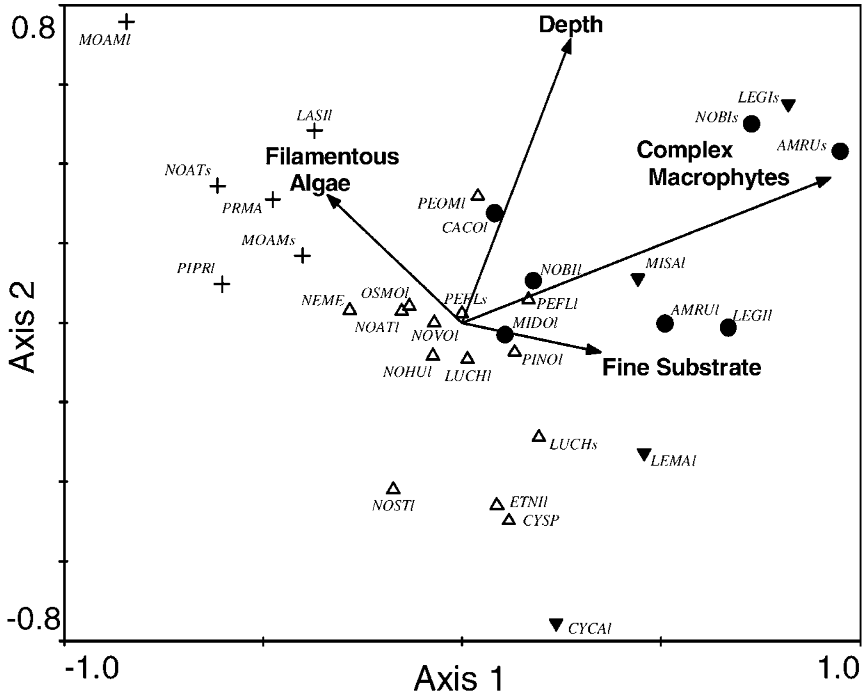
Discussion

Our study supports the delineation of large connecting channels into lotic and lentic habitats; habitats with low current velocities, fine substrates, and macrophytes supported a fish assemblage dominated by centrarchids, whereas habitats with flowing waters and coarse substrates contained a fish assemblage dominated by pelagic species such as emerald shiner and gizzard shad. Intermediate habitats occurred as well; low macrophyte densities, coarser substrates, and moderate flow supported correspondingly mixed fish assemblages. The fishes found in lentic habitats may be associating with the physical habitat or selecting habitats with higher productivity, as described by the inshore retention concept (Schiemer et al. 2001). Although some of the sites with high macrophyte densities (thus with high autochthonous production) were found well offshore, many of these shallow weedy flats did not contain flowing water. There is little exchange of water between the shallow flats and the main channel because water levels do not change rapidly in large connecting channels. Productivity may be higher in such environments in large connecting channels than in similar habitats in large rivers, where changing water levels and current velocities may sweep more organic matter out than is deposited.

Macrophytes exhibit a strong seasonal pattern in the Detroit River, beginning to grow between April and June and senescing in November (Schloesser et al. 1985). Despite lower abundance in spring, macrophytes with complex morphology affected fish distributions in all seasons. This corroborates findings from studies examining large river environments with abundant macrophytes (Grenouillet et al. 2000; Petry et al. 2003). Young fishes associate with aquatic macrophytes, which provide protection from predation and better foraging opportunities (Rozas and Odum 1988). Although experimental studies have shown that fish prefer areas of intermediate macrophyte density because of increased foraging success (Crowder and Cooper 1982), the results from field studies have shown that higher fish abundances may occur in areas of either high (Killgore et al. 1989; Petry et al. 2003) or intermediate macrophyte density (Killgore et al. 1989; Grenouillet et al. 2000). The structural complexity of macrophytes may play a stronger role than macrophyte density in determining fish distributions. The quality of cover provided varies with macrophyte species, as does the abundance of associated prey items; therefore, different species provide unique microhabitats for fishes (Dionne and Folt 1991; Grenouillet et al. 2000). We found that many fishes were more strongly associated with complex macrophytes than simple ones, in contrast to Grenouillet et al. (2001), who found that fish assemblages did not differ with macrophyte type in a large river in France. Fishes associate strongly with cover in large rivers (Copp et al. 1994; Lehtinen et al. 1997); however, complex woody debris was virtually absent from our sites. Given that much of the riparian zone of the Detroit River is urbanized, armored, or comprises wetlands, such cover was unavailable. Compared with large rivers, fishes in the Detroit River may relate more strongly to complex macrophytes owing to the low availability of more permanent cover.

Several small fishes, such as round goby and young smallmouth bass, had negative associations with fine substrates, probably indicating a preference for cover provided by coarser substrates. Fishes were more strongly associated with depth than anticipated, given that we examined only shallow waters and not the full range of available depths. Although some small fishes may have used shallow depths as a refuge from predators (Schlosser 1987), it is likely that depth was

3a: Spring



3b: Summer

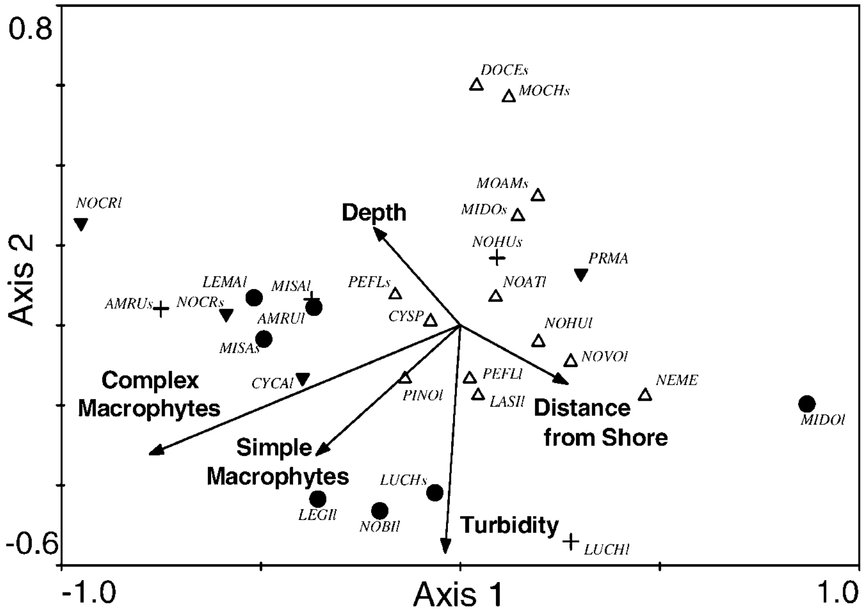


FIGURE 3.—Canonical correspondence analysis biplots of species size category–microhabitat correlations for spring, summer, and fall. Axes 1 and 2 are shown. Species codes are defined in Table 1. Codes followed by the letter "l" represent large species size categories, those followed by the letter "s" represent small species size categories, and those without a lowercase letter represent species that were not split into size categories. Symbols represent group membership defined by cluster analysis. The solid circles represent groups dominated by centrarchids, and the open triangles represent groups dominated by *Notropis* spp., small yellow perch, spotfin shiner, and round goby. The species composition of the other groups, represented by plus signs and filled triangles, varied by season.

3c: Fall

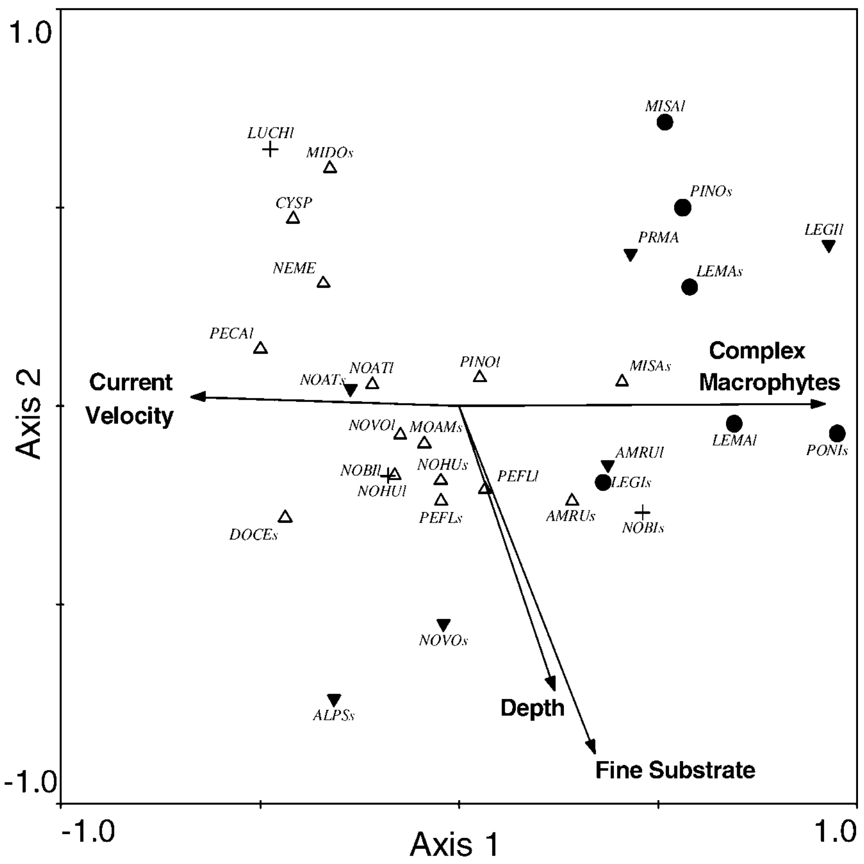


FIGURE 3.—Continued.

also important as a proximate variable for other variables, such as substrate size. In contrast with other studies of size-related habitat use (Grossman et al. 1987; Lamouroux et al. 1999; Fladung et al. 2003), large fishes did not prefer deeper habitats than did small conspecifics. This may be an artifact of sampling design and analysis rather than a true representation of life history patterns. The limited range of depths examined made detecting relationships difficult, and large fishes may prefer much deeper (i.e., channel) rather than marginally deeper habitats (Wolter and Bischoff 2001). Additionally, we separated the youngest age-class in a given season from older fishes; however, age-1 or age-2 juveniles of longer-lived species, such as bluegill, may have habitat requirements more similar to young of year than to adults (Werner and Hall 1988), confounding the habitat associations of large fishes.

Although small fishes generally associated more strongly (especially in the spring) with microhabitat variables than did large conspecifics in the Detroit River, results were mixed among seasons. Grossman et al. (1987) and Reichard et al. (2002) also found that younger fishes are more strongly associated with microhabitat variables than are adults in large rivers. We attribute the stronger microhabitat associations of small fishes to predator avoidance. Small species size categories and small species (those not separated into species size categories) were often linked to cover in the form of shallow water (spotfin shiner), coarse substrate (round goby, young smallmouth bass), or complex macrophytes (hornyhead chub, bluntnose minnow, most centrarchids). Additionally, fishes with similar feeding habits may reduce competition by selecting different habitats (Crowder et al. 1981). For example, bluntnose minnow and small hornyhead chub both feed on cladocerans and algae (Scott and Crossman 1979), but small hornyhead chub had a stronger

TABLE 4.—Seasonal rank of microhabitat variables in structuring fish assemblages, as determined by forward selection in CCA of species size categories common in all seasons. Significance was tested by 9,999 Monte Carlo permutations; $P < 0.05$*, $P < 0.01$**.

Microhabitat variable	Spring	Summer	Fall
Complex macrophytes	1**	1**	1**
Depth	2**	2**	3*
Turbidity	7	4*	5
Fine substrate	4*	12	2**
Slope	6*	6*	6
Current velocity	11	3*	4*
Coarse substrate	3*	8	10
Filamentous algae	5*	7	11
Simple macrophytes	8	11	7
Distance from shore	9	5*	12
Water temperature	10	9	8
Sand substrate	12	10	9

preference for sites with high complex macrophyte densities. The ontogenic shifts in habitat use observed in many species may also be partially explained by a reduction in intraspecific competition for food resources.

With a few exceptions, habitat preferences were similar among seasons for each species size category. The large bluegills probably preferred shallow areas with fine substrate for spawning grounds in the spring (Scott and Crossman 1979) and moved away from such areas later in the year. For individual species, habitat preferences appear to shift more strongly with size than with season, again indicating that cover is an important consideration for young fishes. At the community level, the set of microhabitat variables that are important in structuring the fish assemblage did vary with season; however, complex macrophytes remained the most important variable in all seasons, and depth ranked second or third. Examinations at both assemblage and species size category levels revealed corroborating results; the primary factors affecting fish distributions remain constant from May to September. However, in early spring, late fall or winter, greater shifts in habitat use may occur than were observed among the warmer months sampled in this study.

Conclusions

Complex macrophytes was the most important factor for describing fish distributions; however, fishes use an array of microhabitats in the Detroit River, and habitat heterogeneity is essential in promoting a diverse fish assemblage. Complex macrophytes were important because many fishes (e.g., centrarchids) preferred them, while others (e.g., emerald shiner, gizzard shad) avoided them. Similarly, opposing preferences existed for depth, current velocity, and substrate. Thus, maintaining habitat heterogeneity should be a priority for managers, developers, and conservationists planning restoration or development projects along the river.

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