Macrohabitat associations of fishes in shallow waters of the Detroit River

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Seasonal variation in large-scale habitat selection by fishes in shallow, Canadian waters of the Detroit River was examined. Fish communities were compared among three river segments (upstream, middle and downstream) consisting of areas of shallow water habitat separated by wide hydrologic barriers of deep, flowing water and between inshore and offshore areas. In spring, the most unique, diverse and abundant fish assemblages were found at inshore sites in the middle segment where the largest remaining wetland habitats are located. Fishes used inshore habitat to spawn and probably avoided offshore areas because macrophyte cover was not available in spring. In summer, juvenile gizzard shad *Dorosoma cepedianum* and white bass *Morone chrysops* were observed in high densities in the upstream segment, probably migrating downstream from Lake St Clair. There was little difference in the fish assemblage among macrohabitats in autumn. The upstream segment appeared to be the most degraded, because it contained no species that were not found in the other segments, had a paucity of uncommon species and had significantly more non-native species. This state was attributed to the infilling of coastal wetlands by urban land use and a resulting loss of habitat heterogeneity. The middle segment, with the only remaining wetland habitats, had the greatest occurrence of uncommon species and the only species at risk found in this study. Conservation and restoration efforts should be greatest for wetlands; however, shallow offshore areas provide important fish habitat in summer and autumn. © 2010 The Authors

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INTRODUCTION

The ecology of large rivers has received increased attention in the past decade; however, little research has been done on the habitat requirements of fishes in the Great Lakes connecting rivers (Leslie & Timmins, 1991; Caswell *et al*., 2004), which are recognized as unique ecosystems (Edwards *et al*., 1989). The inputs to these rivers are regulated by large upstream lakes, creating more stable water levels and current velocities than other large rivers (Edwards *et al*., 1989), influencing the

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habitats used by fishes. For example, the Detroit River is distinguished from other large rivers by expansive shallow flats that extend from the shoreline to a steep channel edge. This study focuses on large-scale habitat preferences of fishes in these shallow waters.

The banks of the Detroit River originally consisted of *c*. 1 km wide wetlands and the river contained several large rapids that were once a major spawning ground for Lake Erie whitefish *Coregonus clupeaformis* (Mitchill); however, most of these habitats have been eliminated through extensive bank hardening and channel dredging (Manny, 2003). Thus, although the Detroit River continues to provide a valuable variety of habitats for fishes in the Great Lakes, these habitats are significantly altered and depleted. Several non-native fish species persist in the river and some, such as round goby *Neogobius melanostomus* (Pallas) dominate (Dopazo *et al.*, 2008). As a result of habitat alteration and fish invasions in the Detroit River, the distribution and abundance of native fishes has changed dramatically. Up to 15 fish species are listed as at risk in Canada, although many of these may already be extirpated from the river (N. E. Mandrak, unpubl. data). An understanding of the macrohabitat preferences of fishes will help in efforts to manage and restore habitats in the Detroit River.

Studies of large river fish assemblages were often restricted to shoreline fishes (Madejczyk *et al.*, 1998; Jurajda, 1999), or compared shoreline assemblages with those found in the main channel (Wolter & Bischoff, 2001; Stewart *et al.*, 2002). Some studies of fish-habitat associations examined shallow, offshore waters (Gozlan *et al.*, 1998; Bischoff & Wolter, 2001); however, these studies tended to focus on microhabitat selection and there have been no large-scale comparisons of offshore and inshore (*i.e.* along the shoreline) shallow water fish assemblages. Inshore areas represent one type of macrohabitat, and may contain woody debris, be shaded and have undercut banks (Pusey & Arthington, 2003), thus having cover that is generally unavailable offshore.

Leslie & Timmins (1991) suggested that the deep, flowing waters of the navigation channel in the St Clair River may act as a hydrologic barrier, inhibiting movement of small fishes. Although little information is available on the movements of small fishes in large rivers, the dispersal of small fishes in streams can be limited by the deep waters of a downstream reservoir (Herbert & Gelwick, 2003; Falke & Gido, 2006; Matthews & Marsh-Matthews, 2007). The shallow Canadian waters of the Detroit River can be sectioned into three distinct segments (upstream, middle and downstream) separated by large expanses of deep, flowing water. These deep-water areas are expected to act as a barrier to small fish movement among shallow habitats. Additionally, the fish assemblage in each segment is influenced differentially by waters upstream (Lake St Clair), downstream (Lake Erie) and within (the tributaries of the Detroit River). Therefore, each segment of shallow water habitat represents a distinct macrohabitat that may support a characteristic fish assemblage.

Habitat use may vary with fish size and season (Copp & Jurajda, 1999; Davey *et al.*, 2005). Seasonal changes in habitat, such as the growth and senescence of macrophyte beds, may affect faunal composition (Armitage *et al.*, 1995). Pusey *et al.* (1993) suggested that adult fishes may move into stream reaches in response to macrophyte growth in the Mary River, Australia, and Reid & Mandrak (2009) showed that fish assemblages varied with season in Lake Erie beach habitats. Macrohabitat preference may change with season for individual species. Adult pike *Esox lucius* L. move to new habitats to spawn during spring (Vehanen *et al.*, 2006). Other

species show distinct ontogenic shifts in habitat use (Rosenberger & Angermeier, 2003; Koczaja *et al.*, 2005).

In this study, the seasonal fish assemblages of shallow-water macrohabitats in a large connecting river are compared and discussed. Richness and abundance are common metrics that summarize assemblage-level data. Differences in richness and abundance among sites within macrohabitats may be the result of differences in productivity or habitat quality; however, it is possible that two habitats with equal richness and abundance contain different assemblages. The objective of this study was to determine how assemblages differed among macrohabitats and across seasons in the Detroit River. The null hypotheses that fish species richness, abundance and assemblages do not differ between inshore and offshore areas, or among river segments in spring, summer and autumn, were tested. The interaction between distance from shore and river segments was also tested, because main effects may be confounded by such interactions.

MATERIALS AND METHODS

SITE DESCRIPTION

The Detroit River, 51 km long, connects Lake St Clair and Lake Erie, providing nearly 90% of the water input to the lake (Carter & Hites, 1992). It is the first recognized International Heritage River and Wildlife Refuge (Hartig, 2003). Excluding the upper Great Lakes drainage, the Detroit River drains >2000 km^2 through its tributaries (Detroit River Canadian Cleanup Committee, 1999). In addition to having the stable water levels and current velocities characteristic of a large connecting river, the Detroit River is distinguished from other large rivers by expansive shallow flats that extend from the shoreline to a steep channel edge. This study focuses on large-scale habitat preferences of fishes in these shallow waters.

Two distinct upstream and downstream segments are commonly recognized in the Detroit River (Fig. 1) (Hatcher *et al.*, 1991; Manny & Kenaga, 1991; Bolsenga & Herdendorf, 1993). The upstream segment drops 0·3 m over 21 km and, with the exception of the Peche and Belle Isle region, is characterized by a single channel with steep banks, channel widths of 600 to 1000 m, depths to 15 m and a mean current velocity of 1·6 m s^{-1} (Haas *et al.*, 1985; Edwards *et al.*, 1989; Bolsenga & Herdendorf, 1993). Little River is the main Canadian tributary to the upstream segment of the Detroit River. The lower 30 km is 1500 to 6000 m wide, with braided channels (depths of <9 m, mean current velocity of 1·2 m s^{-1}) and broad shallow flats (depths of 1·5–2·5 m, low to no current) (Haas *et al.*, 1985; Edwards *et al.*, 1989; Bolsenga & Herdendorf, 1993). The upstream segment is the most heavily modified, with the downtown cores of Windsor, Ontario, and Detroit, Michigan, located along each shore.

The shallow Canadian waters in the lower 30 km were split into two segments (middle and downstream), because they were separated by deep waters with high current velocity (Fig. 1). The middle segment of the Detroit River is bounded by tributaries, Turkey Creek to the north and the River Canard to the south. The largest area of shallow water was found in the middle segment, which contained large shipping channels, braided channels, islands, expansive (many km^2) shallow offshore flats and both heavily modified and semi-natural shorelines. Wetlands in the middle segment represent the only expansive remaining section of semi-natural shoreline in the river. The downstream segment comprised Crystal Bay, the waters surrounding Bois Blanc Island and the area adjacent to Lake Erie.

SITE SELECTION

Sixty sites were selected from shallow (<2·5 m) Canadian waters of the Detroit River (Fig. 1). A polygon shapefile (14·4 km^2) outlining all shallow, permanent, Canadian waters
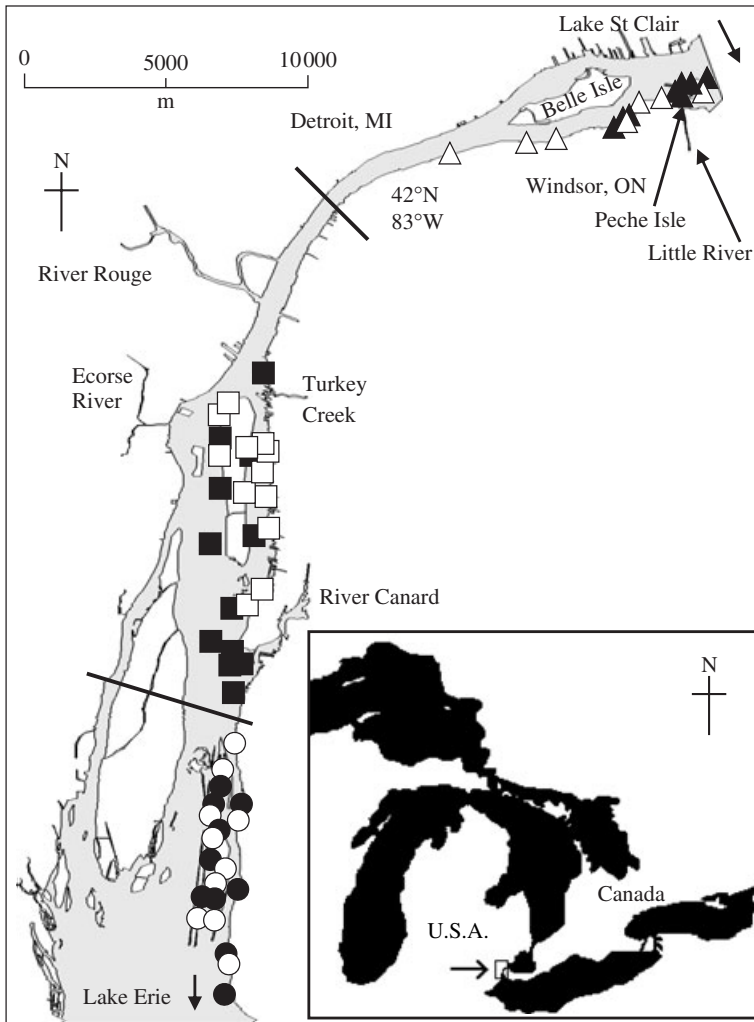
FIG. 1. Map showing the distribution of inshore and offshore sampling sites across three river segments in shallow Canadian waters of the Detroit River. Segments are separated by ——— (△, inshore-upstream; □, inshore-middle; ○, inshore-downstream; ▲, offshore-upstream; ■, offshore-middle; ●, offshore-downstream).

of the river, was created using ArcMap 8.3 (ESRI, Inc.; www.esri.com). The Universal Transverse Mercator co-ordinates of sites were plotted in the area outlined by the polygon using randomization macros in ArcMap, following a stratified random-sampling design described below. These co-ordinates represented the centroids of sites, which covered *c.* 18 m^2 (*i.e.* the area enclosed by the seine). Tributary confluence regions were removed from the potential sampling area prior to site selection to avoid sampling non-resident fishes. Marinas and other small inlets were also removed from the sampling area, given that small channel width and increased depth prevented the use of a seine. 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 and high current velocity) were replaced with other randomly selected sites.

A stratified random-sampling approach was used to ensure that a sufficient number of sites were placed at random in each macrohabitat. The amount of shallow water habitat differed markedly among segments (1·2 km² upstream, 9·1 km² middle, 4·1 km² downstream). Sites were selected in rough proportion to habitat availability, while still ensuring sufficient samples size in each segment. Of the 60 sites, 16 (eight inshore and eight offshore) were in the upstream segment, 24 (12 inshore and 12 offshore) were in the middle segment and 20 (10 inshore and 10 offshore) were in the downstream segment. Inshore sites were placed along the shoreline (*i.e.* the edge of the polygon), whereas offshore sites were placed at least 15 m (the length of the seine) from shore.

FISH SAMPLING

Fishes were sampled in May (spring), July (summer) and September (autumn) of 2004 by boat seining, because this technique is effective for capturing high fish species richness (Lapointe *et al.,* 2006). A 15 m long, 2·5 m high seine with a 2·5 m bag and 0·64 cm ace mesh was used. The net was anchored to the substratum at offshore sites, whereas at inshore sites it was tied to shore. One sample was taken per season, resulting in three samples per site across seasons. Five replicate hauls were taken for each sample, using the same anchoring location. 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 L_T) for each sample (Table I). Fishes were released alive, except for vouchers that were anaesthetized with clove oil and fixed with 10% formalin. Fish assemblages can be defined at many scales. In this study, the assemblage of a given sample site was represented by the fishes captured there, whereas data were combined from many sites to represent the fish assemblage of a macrohabitat.

MICROHABITAT MEASUREMENTS

Environmental variables were measured at each site to determine whether microhabitats were similar among macrohabitats. The most commonly measured variables, based on a review of 20 recent papers on fish-microhabitat associations in large rivers, were (in descending order of use): depth, current speed, macrophytes, substratum, temperature, turbidity, cover (*e.g.* woody debris or man-made structures) and distance from shore (Lapointe, 2005). Of these, all but cover were measured, given that coarse woody debris and other forms of cover were rarely found in the Detroit River. Water temperature, turbidity and current speed were measured at the centroid of each sample site, whereas maximum depth, per cent cover of macrophytes, slope and substratum were estimated for the 18 m² enclosed by the seine. Depth and substratum were measured once at each site because these were not expected to change during the study period. All other variables were measured once per season at each site. Turbidity was measured using a Secchi disc (only where it could not be seen on the substratum) and a turbidity tube. Turbidity tube measurements could be taken in shallower waters, but Secchi discs could be used in deeper, clearer waters where a maximum reading would be obtained from a turbidity tube. Current speed (Z21 Ott current meter; www.ott-hydrometry.de) was measured at 0·2 and 0·8% of the water column at sites with a mean depth of <1 m. At depths of ≥1 m, current speed was measured 1 m below the surface. Depth was measured to the nearest 0·05 m using markings on the seine brail. The per cent cover of each taxonomic group of macrophytes and filamentous algae was estimated visually. Per cent composition of substratum 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 substrata. Substratum type estimates were supplemented by manual prodding of the channel bottom using the seine brail and by examination of sediments attached to the anchor, to insure that all substratum sizes in the sampling area were identified. Substratum classes were defined according to the Wentworth scale as coarse (>2 mm), sand (2–0·075 mm) and fine (<0·075 mm).

TABLE I. Total abundance by season of species captured by seining in the Detroit River, May to September, 2004. Scientific and common names according to Nelson *et al.* (2004)

Scientific name	Common name	Spring	Summer	Autumn
Alosa pseudoharengus (Wilson)	Alewife*	1		130
Ambloplites rupestris (Rafinesque)	Rock bass	51	29	294
Ameiurus melas (Rafinesque)	Black bullhead	1		
Ameiurus nebulosus (Lesueur)	Brown bullhead			1
Aplodinotus grunniens Rafinesque	Freshwater drum	2	2	1
Catostomus commersonii (Lacépède)	White sucker	1	1	
Carassius auratus (L.)	Goldfish*	7	2	
Cyprinella spiloptera (Cope)	Spotfin shiner	32	104	140
Cyprinus carpio L.	Common carp*	6	3	
Dorosoma cepedianum (Lesueur)	Gizzard shad	2	2002	659
Esox lucius L.	Pike	3	1	1
Esox masquinongy Mitchill	Muskellunge	1	1	
Etheostoma nigrum Rafinesque	Johnny darter	25		3
Fundulus diaphanous (Lesueur)	Banded killifish	2	9	4
Gasterosteus aculeatus L.	Three-spined stickleback*	1	1	
Labidesthes sicculus (Cope)	Brook silverside	53	163	3
Lepisosteus osseus (L.)	Longnose gar			1
Lepomis gibbosus (L.)	Pumpkinseed	114	47	40
Lepomis macrochirus Rafinesque	Bluegill	87	151	249
Lepomis megalotis (Rafinesque)	Longear sunfish	56	3	5
Luxilus chrysocephalus Rafinesque	Striped shiner	195	52	55
Micropterus dolomieu Lacepède	Smallmouth bass	6	33	34
Micropterus salmoides (Lacepède)	Largemouth bass	16	179	202
Minytrema melanops (Rafinesque)	Spotted sucker			1
Morone americana (Gmelin)	White perch*	18	139	247
Morone chrysops (Rafinesque)	White bass	2	466	
Moxostoma anisurum (Rafinesque)	Silver redhorse	1	1	
Moxostoma erythrurum (Rafinesque)	Golden redhorse			1
Moxostoma macrolepidotum (Lesueur)	Shorthead redhorse	2	1	
Neogobius melanostomus (Pallas)	Round goby*	283	313	302
Nocomis biguttatus (Kirtland)	Hornyhead chub	23	15	54
Notemigonus crysoleucas (Mitchill)	Golden shiner	10	55	22
Notropis atherinoides Rafinesque	Emerald shiner	15470	1489	417
Notropis hudsonius (Clinton)	Spottail shiner	841	400	930
Notropis stramineus (Cope)	Sand shiner	6	2	17
Notropis volucellus (Cope)	Mimic shiner	688	290	194
Opsopoeodus emiliae Hay	Pugnose minnow			1
Osmerus mordax (Mitchill)	Rainbow smelt*	132	2	
Perca flavescens (Mitchill)	Yellow perch	932	479	370
Percina caprodes (Rafinesque)	Logperch	6	7	56
Percopsis omiscomaycus (Walbaum)	Trout-perch	12		
Pimephales notatus (Rafinesque)	Bluntnose minnow	557	199	155
Pimephales promelas Rafinesque	Fathead minnow	4		
Pomoxis nigromaculatus (Lesueur)	Black crappie	1	4	10
Proterorhinus marmoratus (Pallas)	Tubenose goby*	4	5	13
Sander vitreus (Mitchill)	Walleye	1		

*, non-native species.

FISH DATA PREPARATION

Length-frequency distributions and reported length at age (Scott & Crossman, 1979) were used to differentiate the youngest age class from older (large) fishes for each species for each season. Reported L_T at age were used to interpret L_T-frequency distributions and when there were insufficient L_T data to differentiate among age classes. Only the youngest size class could be identified as distinct with confidence in L_T-frequency distributions. No young-of-year (YOY) were present in spring (or had not yet recruited to the gear for early-spawning species); thus, year-1 individuals were separated from older fish. By summer, year-1 individuals had grown to variable L_T and their abundance was dwarfed by the abundance of YOY. This made distinguishing year-1 individuals from older fishes very difficult in the summer and autumn; thus, only YOY were separated from older fish in these seasons. The 'small' fishes caught in the spring represent the previous year class (*i.e.* year-1 individuals), the 'small' fishes caught in the summer represent the current year class (*i.e.* YOY) shortly after hatch and the 'small' fishes caught in the autumn represents the current year class (*i.e.* YOY) after several months of growth. Different L_T were used to split small and large fish of a species for each season, because small fish grew considerably throughout the year. For example, YOY white perch *Morone americana* (Gmelin) did not surpass 70 mm (*i.e.* the L_T used to split species-size categories) in summer, but had grown to as much as 100 mm by autumn, with the mean size increasing by 15 mm from summer (mean 43 mm) to autumn (mean 58 mm) (Table II). Small and large fishes of the same species were considered separate variables in all analyses and will, henceforth, be referred to as species size categories. Three species [spotfin shiner *Cyprinella spiloptera* (Cope), *N. melanostomus* and tubenose goby *Proterorhinus marmoratus* (Pallas)] had L_T-frequency distributions that did not show multiple size classes; therefore, small and large individuals of these three species were grouped into a single variable.

Total abundance was calculated from the first five seine hauls of each sample. The number of fish species in each sample (fish species richness) was determined from the first five seine hauls, plus any additional seine hauls for that sample. For analyses of fish assemblages, species size categories found in <5% of the samples in a season were considered uncommon and excluded from analysis (Gauch, 1982). Presence or absence of species for a site was used, rather than the total abundance because seining differs in efficiency with substratum and species (*e.g.* benthic species are more difficult to capture by seining) (Pierce *et al.*, 1990; Bayley & Herendeen, 2000). Sample outliers were identified by first calculating the Sorenson distance between samples for the species size categories by samples matrix. This distance measure is generally appropriate for ecological data (McCune & Grace, 2002). Outlier samples were then removed if their distance exceeded 2·5 deviations from the mean distance.

UNIVARIATE ANALYSES

Differences in fish species richness and abundance between inshore and offshore sites, and among river segments were tested. Differences in fish species richness and total abundance were examined separately for each season. Normality was tested using Shapiro−Wilk tests, and non-normal data were $\log_{10}(x + 1)$ (richness) or square-root transformed (abundance) prior to testing for differences. Two-way factorial ANOVA was used to determine whether any interaction existed between segments and inshore and offshore sites in the distribution of richness or total abundance. Main effects were tested when the interaction term (*i.e.* segment ×inshore and offshore) was not significant. Tukey's honest significant difference test was applied *post hoc* to determine differences within groups. All univariate analyses were performed using Statistica 6.1 (StatSoft, Inc.; www.statsoft.com/).

Holm's sequentially rejective Bonferroni test was used to maintain $\alpha = 0.05$ (Holm, 1979). Significant *P*-values were corrected by adjusting to P_i', using $P_i' = (k - i + 1)P_i$, where k represents the total number of non-independent tests (by season) and *P*-values have been ranked (i) from largest to smallest. Significance was accepted at $\alpha' = \alpha(k - i + 1)^{-1}$, where i is the ranked *P*-value of the factor being tested. Given that unique data were collected for each season, Holm's procedure was applied to the combined univariate (ANOVA) and multivariate (DISTLM) results for each season to maintain $\alpha = 0.05$ for multiple comparisons. Holm's procedure was also applied to pair-wise *post hoc* tests of multivariate data.

TABLE II. Common species size categories by season, with mean ± s.e. total lengths (L_T) of small and large categories. The L_T used to split species into size categories for each season is listed under S(≤). All fishes smaller than or equal to this value were considered small. Species that were not split into size categories are marked by a c and the mean ± s.e. of all individuals of these species is listed under the large category for each season

Scientific name	Spring			Summer			Autumn		
	Small L_T (mm)	S(≤) (mm)	Large L_T (mm)	Small L_T (mm)	S(≤) (mm)	Large L_T (mm)	Small L_T (mm)	S(≤) (mm)	Large L_T (mm)
Alosa pseudoharengus	44 ± 1	50	100 ± 7	31 ± 2	45	98 ± 10	64 ± 1	90	
Ambloplites rupestris		50	105 ± 5				41 ± 0	65	133 ± 13
Catostomus commersonii									
Cyprinella spiloptera		c	76 ± 2		c	68 ± 1		c	74 ± 1
Cyprinus carpio		150	507 ± 21		150	519 ± 32			
Dorosoma cepedianum				41 ± 0	100		59 ± 0	100	
Etheostoma nigrum	48 ± 1	40	53 ± 1		55	80 ± 1			
Labidesthes sicculus		55	73 ± 2		55				
Lepomis gibbosus		70	119 ± 3		30	88 ± 4	44 ± 1	70	109 ± 5
Lepomis macrochirus		65	114 ± 5		35	96 ± 3	39 ± 1	55	101 ± 4
Luxilus chrysocephalus	60 ± 1	75	118 ± 3	74 ± 1	80	97 ± 2		65	103 ± 2
Micropterus dolomieu		90	161 ± 31	46 ± 1	75	162 ± 18	76 ± 2	95	
Micropterus salmoides		100	209 ± 20	49 ± 1	80	213 ± 37	69 ± 1	100	218 ± 31
Morone americana	76 ± 3	100	164 ± 4	43 ± 1	70		58 ± 1	100	
Morone chrysops				50 ± 1	80				
Neogobius melanostomus		c	53 ± 1		c	65 ± 1		c	61 ± 1
Nocomis biguttatus	57 ± 2	75	117 ± 6		60	97 ± 7	52 ± 1	65	103 ± 4
Notemigonus crysoleucas				54 ± 1	75	102 ± 9			
Notropis atherinoides	44 ± 2	50	70 ± 0		50	71 ± 0	44 ± 1	50	76 ± 1
Notropis hudsonius		40	67 ± 1	44 ± 1	60	80 ± 1	59 ± 0	70	85 ± 1

Table II. Continued

Scientific name	Spring			Summer			Autumn		
	Small L_T (mm)	S($\leq$) (mm)	Large L_T (mm)	Small L_T (mm)	S($\leq$) (mm)	Large L_T (mm)	Small L_T (mm)	S($\leq$) (mm)	Large L_T (mm)
Notropis stramineus		50	64 ± 3						
Notropis volucellus		45	60 ± 0		35	54 ± 0	38 ± 1	45	58 ± 0
Osmerus mordax		50	82 ± 1						
Perca flavescens	77 ± 1	120	195 ± 8	53 ± 1	70	108 ± 2	70 ± 1	90	125 ± 2
Percina caprodes								50	68 ± 1
Percopsis omiscomaycus		70	85 ± 5						
Pimephales notatus		40	67 ± 1		40	63 ± 1	45 ± 1	55	69 ± 1
Pimephales promelas		55	70 ± 9						
Pomoxis nigromaculatus							68 ± 4	100	
Proterorhinus marmoratus		c	49 ± 1		c	37 ± 5		c	40 ± 4

MULTIVARIATE ANALYSES

Multivariate analyses were used to test for differences in fish assemblages between inshore and offshore sites, and among river segments, because univariate tests provided an incomplete assessment. Non-parametric two-way factorial MANOVA (by permutation) was used to determine whether any interaction existed between segments and inshore and offshore sites for the fish assemblage, because of non-normally distributed multiple response variables. Tests were performed separately for each season, using DISTLM v.5, which is appropriate for unbalanced designs (Anderson, 2004). Sorenson distance was selected to calculate the distance matrix and 9999 permutations were used. Main effects were tested when the interaction term was not significant.

Although MANOVA can reveal significant differences among assemblages, it cannot be used to describe how these assemblages differ. The nature of the differences in assemblages was then explored using indicator species analysis (ISA) and non-metric multidimensional scaling (NMS). NMS was used to examine whether samples from each habitat clustered together in multivariate space, which would suggest that each habitat contained a distinct assemblage. This ordination technique was selected because it is suited for non-normally distributed data and avoids the assumption of linear relationships among variables (McCune & Grace, 2002). Sorenson distance was used in NMS analyses. ISA calculates an indicator value (I_v) for each species from the relative frequency of each species in each group and tests for significance. A perfect indicator species ($I_v = 100$) would be found at every sample in a group and at no samples in any other group (McCune & Grace, 2002). Species are indicators for the group in which they have the highest I_v and the significance (at $\alpha = 0.05$) of the I_v is determined by Monte-Carlo permutation (9999). ISA and NMS tests were performed using PC-ORD 4.14 (McCune & Mefford, 1999).

COMPARING MICROHABITATS AMONG MACROHABITATS

Turbidity tube values were used to represent turbidity. Where possible, missing or maximum turbidity tube values (y, cm) were calculated from Secchi disc values (x, cm), using simple linear regression between all corresponding Secchi disc and turbidity tube measurements: $y = 19.8 + 0.48x$ ($r^2 = 0.63$, $P < 0.001$). Macrophytes were grouped by species according to whether their morphological structure was simple or complex, because 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 per cent cover of filamentous algae. Bottom slope (Z_B) was calculated for offshore sites as: $Z_B = (D_{max} - D_{min})15^{-1}$, where D_{max} is the maximum depth, D_{min} is the minimum depth and 15 represents the maximum diameter of the site in meters (*i.e.* the length of the seine). For inshore sites, slope (Z_I) was calculated as $Z_I = (D_{max} - D_0)d^{-1}$, 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 from shore). Proportional variables (macrophyte and substratum classes and slope) were arcsin square-root transformed, whereas all other variables were $\log_{10}(x + 1)$ transformed to improve normality (McCune & Grace, 2002). To determine how microhabitats differed among segments, or between inshore and offshore sites, principal components analysis (PCA), based on a correlation matrix, was used to ordinate microhabitat variables for all seasons combined.

RESULTS

A total of 30 943 fishes (16 families, 46 species) was captured in 1141 seine hauls (Table I). There were 19 657 fishes (15 families, 41 species) captured in spring, 6654 fishes (13 families, 35 species) captured in summer and 4632 fishes (13 families and 33 species) captured in autumn, 2004. There were 31, 28 and 30 common (>5% of samples) species size categories in the spring, summer and autumn, respectively (Table II).

Of the 46 species, 16 were too uncommon to include in multivariate analyses; however, their distribution of occurrence provides insight into the importance of each microhabitat to the complete fish assemblage. Two of the 16 uncommon species were non-native, goldfish *Carassius auratus* (L.) and three-spined stickleback *Gasterosteus aculeatus* L., and were excluded from the following comparisons. Of the 37 occurrences of uncommon native species in 180 samples, 11% were in the upstream segment (27% of samples), 57% in the middle segment (40% of samples) and 35% in the downstream segment (33% of samples). Comparing inshore and offshore habitats, 59% of the occurrences of uncommon native species were inshore, whereas 41% were offshore. Inshore sites in the middle segment (20% of samples) had the highest frequency (43%) of occurrence of uncommon native species, whereas no uncommon native species were found in offshore sites in the upstream segment (13% of samples).

Emerald shiner *Notropis atherinoides* Rafinesque comprised 78% of the catch in the spring and were removed from the calculation of total abundance for spring samples. Although *N. atherinoides* represented an important part of the fish assemblage, analyses with these data would have only reflected patterns of *N. atherinoides* distribution, not of differences in the rest of the fish assemblage. In spring, there was a significant interaction between distance from shore and river segment for fish species richness, abundance and assemblages (Table III). In general, the inshore areas of the middle and downstream segments had higher richness and unique assemblages from other areas of the river. Abundance was higher in these areas than in the offshore area of the middle segment. Results from ISA and NMS analyses were similar. Inshore areas in the middle segment had the most unique assemblage, which was dominated by centrarchid species (Table IV and Fig. 2). Large and small striped shiner *Luxilus chrysocephalus* Rafinesque, as well as fathead minnow *Pimephales promelas* Rafinesque, were particularly common at inshore sites in the downstream segment (Table IV and Fig. 2), whereas large Johnny darter *Etheostoma nigrum* Rafinesque had the highest indicator value for inshore sites in the middle segment (Table IV).

In summer, there were no significant differences in fish species richness, abundance or assemblages between inshore and offshore areas or among river segments (Table III). There was a marginally significant difference in fish assemblages between inshore and offshore sites (Table III), but little difference was revealed by NMS analysis, and there were only two indicator species, *C. spiloptera* (inshore) and large mimic shiner *Notropis volucellus* (Cope) (offshore) (Table IV). There was a marginally significant difference in fish abundance and assemblages among river segments, which was supported by similarities among ISA and NMS results (Table IV). Upstream sites were dominated by abundant small gizzard shad *Dorosoma cepedianum* (Lesueur) and white bass *Morone chrysops* (Rafinesque), which had the highest in I_v in summer (Table IV).

In autumn, there were no significant differences in fish species richness, abundance or assemblages between inshore and offshore areas or among river segments, and there was only a marginally significant difference in fish assemblages among segments (Table III). NMS and ISA results did not corroborate any differences in assemblages among segments, suggesting a small or spurious effect. This suggests that, with respect to river segment and distance from shore, fishes were most homogeneously distributed in the river in autumn. Large yellow perch *Perca flavescens*

TABLE III. Results from factorial analysis of fish species richness, abundance and assemblages, in spring, summer and autumn, 2004. When the interaction term was significant, main effects were not tested and are labelled NA. *P*-values are presented before and after Holm's correction was applied

Season	Biotic measure	Factor	*P*-value	Corrected *P*
Spring	Richness	Interaction	0·004	0·012
		Shore	NA	
		Segment	NA	
	Abundance	Interaction	0·015	0·030
		Shore	NA	
		Segment	NA	
	Assemblage	Interaction	0·012	0·012
		Shore	NA	
		Segment	NA	
Summer	Richness	Interaction	0·185	0·924
		Shore	0·238	0·950
		Segment	0·520	0·520
	Abundance	Interaction	0·442	1·000
		Shore	0·468	0·935
		Segment	0·016	0·109
	Assemblage	Interaction	0·058	0·350
		Shore	0·008	0·070
		Segment	0·012	0·092
Autumn	Richness	Interaction	0·732	1·000
		Shore	0·654	1·000
		Segment	0·481	1·000
	Abundance	Interaction	0·505	1·000
		Shore	0·827	0·827
		Segment	0·137	1·000
	Assemblage	Interaction	0·311	1·000
		Shore	0·145	1·000
		Segment	0·007	0·059

(Mitchill), however, were most common offshore (Table IV). *Neogobius melanostomus* and large *N. atherinoides* were common in the upstream segment and had the highest indicator value in autumn (Table IV).

The final stress of the two-dimensional NMS solution was high in all seasons (spring stress = 21·3, summer stress = 22·3 and autumn stress = 21·0). Stress is a measure of departure from monotonicity and can be used to evaluate the number of axes to interpret. Final stress >20 is considered high and the results from such analyses can be difficult to interpret; however, these results barely exceeded this limit in each season. Although high final stress suggests that substantial stress would have been explained by additional axes, only the first two axes were interpreted because only the strongest patterns in the fish assemblage data were of interest.

The number of significant indicator species decreased over the sampling period (spring = 13, summer = 10 and autumn = 7; Table IV), suggesting that fishes became more homogeneously distributed as the seasons progressed. Only

TABLE IV. Indicator species analysis results from May (spring), July (summer) and September (autumn), 2004 comparisons of inshore *v.* offshore sites and river segments (O, offshore; I, inshore; U, upstream; M, middle; D, downstream). Only significant (denoted by *P**) indicator species or species size categories are reported, with s representing small species size categories, l representing large species size categories and c representing species that were not split into size categories. Indicator values (I_v) represent the per cent of a perfect indication for a given macrohabitat

Groups Compared	Species	Size	Group	I_v	P*
Spring					
Interaction	*Neogobius melanostomus*	c	I-U	30·8	0·010
	Etheostoma nigrum	l	I-M	44·4	<0·001
	Micropterus salmoides	l	I-M	33·3	0·006
	Pimephales promelas	l	I-M	33·3	0·008
	Pimephales notatus	l	I-M	30·3	0·011
	Cyprinella spiloptera	c	I-M	28·4	0·019
	Perca flavescens	s	I-M	26·7	0·019
	Lepomis gibbosus	l	I-M	26·6	0·024
	Lepomis gibbosus	s	I-M	25·0	0·025
	Lepomis macrochirus	l	I-M	25·0	0·026
	Luxilus chrysocephalus	l	I-D	37·5	0·003
	Luxilus chrysocephalus	s	I-D	33·3	0·006
	Nocomis biguttatus	s	O-D	28·9	0·019
Summer					
Distance from shore	*Cyprinella spiloptera*	c	I	50·0	<0·001
	Notropis volucellus	l	O	39·4	0·032
Segment	*Morone chrysops*	s	U	57·0	<0·001
	Dorosoma cepedianum	s	U	46·9	<0·001
	Micropterus dolomieu	s	U	30·0	0·008
	Pimephales notatus	l	M	35·1	0·019
	Ambloplites rupestris	l	D	31·6	0·003
	Micropterus salmoides	s	D	28·4	0·047
	Luxilus chrysocephalus	s	D	27·3	0·010
	Lepomis macrochirus	l	D	25·6	0·037
Autumn					
Distance from shore	*Perca flavescens*	l	O	46·7	0·017
segment	*Neogobius melanostomus*	c	U	48·1	<0·001
	Notropis atherinoides	l	U	42·3	0·006
	Morone americana	s	U	35·0	0·023
	Perca flavescens	s	U	29·7	0·022
	Pomoxis nigromaculatus	s	M	17·4	0·035
	Luxilus chrysocephalus	l	D	24·0	0·014

L. chrysocephalus was a significant indicator for a macrohabitat (the downstream segment) in all three seasons.

PCA results revealed a distinct difference in microhabitats between inshore and offshore sites, whereas similar microhabitats appeared to exist among segments (Fig. 3). Only the first two axes are presented, as these explain the greatest amount of variation (axis 1, 24·9%; axis 2, 16·5%) in the microhabitat data, although the small
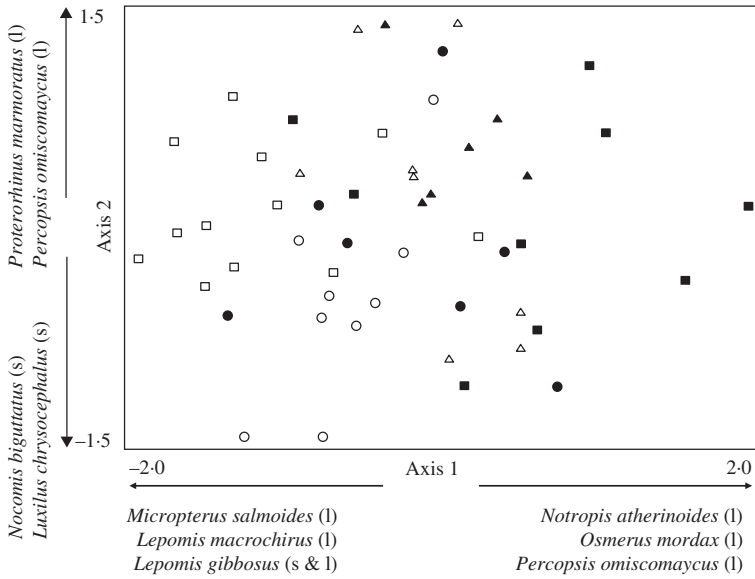
FIG. 2. Scatterplot of sample scores across spring fish assemblage non-metric multidimensional scaling axes 1 and 2. Species-size categories (*s*, small; l, large) with the most positive and negative scores on axes 1 and 2 are shown. Site locations with respect to the interaction term: inshore-upstream (△) inshore-middle (□), inshore-downstream (○), offshore-upstream (▲), offshore-middle (■) and offshore-downstream (●).
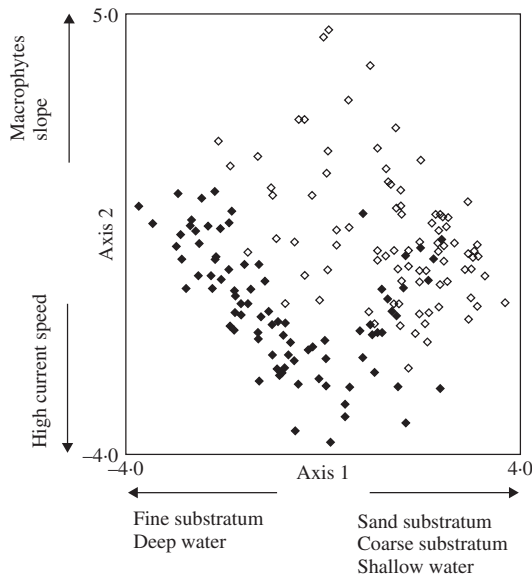
FIG. 3. Scatterplot of sample scores across microhabitat principal components analysis (PCA) axes 1 (eigenvalue = 2·74) and 2 (eigenvalue = 1·82). Microhabitat variables with the most positive and negative loadings on axes 1 and 2 are shown. Inshore (◇) and offshore (◆) group membership is overlaid.

amount of variation explained suggests weak linear relationships among microhabitat variables. Axis 1 represented an increasing gradient from deeper sites with fine substrata to shallow sites with sand and coarse substrata. Current speed loaded negatively on axis 2, whereas slope and macrophytes loaded positively. Thus, offshore sites were deeper and had finer substrata and higher current speeds than inshore sites, which had more macrophytes and greater slopes.

DISCUSSION

In shallow Canadian waters of the Detroit River, the strongest fish-macrohabitat relationships were observed in spring. Compared with other macrohabitats, inshore sites in the downstream segment and particularly in the middle segment had higher fish species richness and abundance and were inhabited by a unique fish assemblage. Higher fish species richness may be related to higher fish abundance, given that species richness tends to increase with the number of individuals observed (Gotelli & Colwell, 2001). Much of the fish spawning in the Detroit River occurs in the lower half of the river (Goodyear *et al.*, 1982), and high species diversity is often found during spring when many species are easily caught while spawning along river banks (De Leeuw *et al.*, 2007). In particular, spawning *N. atherinoides* dominated inshore sites in the middle segment during spring, where thousands of individuals were sometimes caught in a single seine haul. The inshore fish assemblage in the middle and downstream segments was characterized by centrarchid and cyprinid species that are known to spawn in shallow waters and along the shore (Scott & Crossman, 1979). Large *E. nigrum* was the most significant indicator species for this segment, and this species is known to spawn during May in Canada (Scott & Crossman, 1979). Several male *E. nigrum* with spawning colouration were observed at inshore-middle segment sites during spring.

In addition to spawning fishes, small fishes may have been selecting inshore habitats for cover during spring. Woody debris is rare along the shoreline of the Detroit River and is virtually absent in offshore areas. Thus, inshore sites offered cover in the form of coarser substrata, shallow water and occasional woody debris, which small fishes use to avoid predation (Schlosser, 1987; He & Kitchell, 1990; Troutman *et al.*, 2007). Such cover would have been particularly important in spring, when macrophytes were sparse in offshore habitats. Macrophytes provide protection from predation (Werner *et al.*, 1983) and were found to be the most important microhabitat variable influencing fish assemblages in the Detroit River (Lapointe *et al.*, 2007). Schloesser *et al.* (1985) stated that macrophyte growth begins between April and June, and lower macrophyte densities were observed in spring in this study. In later seasons, when offshore macrophyte beds were firmly established, there was little difference between inshore and offshore sites.

Although inshore and offshore sites contained similar richness and abundance in summer and autumn, certain species showed distinct preferences. Smaller fishes are commonly thought to be associated with the shoreline, whereas larger fishes are found offshore in large rivers (Wolter & Bischoff, 2001; Stewart *et al.*, 2002). Offshore, however, usually refers to deep channel habitats inhabited by large-bodied fishes. In this study, the difference in depth between inshore and offshore sites was relatively small, and few large-bodied fishes were sampled effectively by seining.

The trend of finding larger fishes offshore was only observed during autumn in *P. flavescens*. In general, adult *P. flavescens* are found in deeper open water than juveniles, which are found closer to shore (Scott & Crossman, 1979). *Cyprinella spiloptera* deposit eggs in crevices in woody debris and, as a fractional spawner, have a protracted spawning season (Jenkins & Burkhead, 1993). This species was found inshore during summer, probably because it was attracted to spawning structures found there. Conversely, *N. volucellus* were found offshore during summer. This pattern conflicts with most published literature, which suggests that *N. volucellus* are found inshore during the day and move offshore at night (Scott & Crossman, 1979; Jenkins & Burkhead, 1993), although Hanych *et al*. (1983) observed the opposite pattern. Small riverine fishes are known to move inshore at night (Copp & Jurajda, 1999; Wolter & Freyhof, 2004), so nocturnal sampling in the Detroit River may reveal different patterns between inshore and offshore shallow water habitats.

The most unique fish assemblages were observed in the middle segment, particularly at inshore sites during spring. Haas *et al*. (1985) reported higher catch per unit effort (CPUE) of fishes in the middle segment of the Detroit River, and higher fish species richness in the middle and downstream segments; however, they only sampled one site in each segment. Multivariate analyses did not reveal a significant difference between inshore sites in the middle and downstream segments; however, this may be, in part, due to the omission of uncommon species from analyses. Uncommon native species were most often found at inshore sites in the middle segment; the only species at risk captured in this study [pugnose minnow *Opsopoeodus emiliae* Hay and spotted sucker *Minytrema melanops* (Rafinesque)] were found at an inshore wetland site here. Bull & Craves (2003) indicated that *O. emiliae*, a species at risk in Canada, was found in the Gibraltar Bay wetland in the American waters of the Detroit River, and stressed the importance of the remaining coastal marshes for fishes. Great Lakes coastal wetland habitats are preferred by fishes, which use them to spawn and as nursery habitats (Wei *et al*., 2004). The importance of wetland areas for spawning fishes may have contributed to the increased richness and abundance, and unique assemblage found at middle inshore sites in the spring.

Dispersal within segments may be more common than dispersal among segments. The home range of fishes is smaller in rivers than in lakes, with bluegill *Lepomis macrochirus* Rafinesque and longear sunfish *Lepomis megalotis* (Rafinesque) having a home range of <200 m^2 in rivers (Minns, 1995). Crook (2004), however, showed that individual common carp *Cyprinus carpio* L. and golden perch *Macquaria ambigua* (Richardson) occasionally migrate well outside of their home range in a large lowland river in Australia. Such migrations could account for the connectivity of distant populations. Therefore, the hydrologic barriers imposed by the deep waters of the navigation channels should be viewed as semi-permeable barriers discouraging, rather than preventing, exchanges between the assemblages of each segment. These barriers appear to affect small fishes most strongly, as few large-bodied species were significant indicators for a particular segment. Hydrologic barriers also appear to affect longitudinal dispersal of small fishes in the Detroit River since species, such as orangethroat darter *Etheostoma spectabile* (Agassiz), are only found in American waters across the channel (Bailey *et al*., 2004). Genetic analyses of populations in different segments of the Detroit River could provide further evidence of a hydrologic barrier to dispersal.

The lack of species unique to the upstream segment could be related to the heavy influence of urban areas (Detroit, MI, and Windsor, Ontario) in this segment, and the difficulty of upstream dispersal for small fishes. The upstream segment did not contain any wetland habitat and had the most urban land use along the shoreline. It also had the lowest number of occurrences of uncommon native species and was the only segment with non-native species (*N. melanostomus* and *M. americana*) as significant indicators, suggesting that modified habitats in the upstream segment have led to an altered fish assemblage. The most detrimental habitat modification in this segment was probably the infilling of all coastal wetlands, resulting in reduced habitat heterogeneity compared with downstream segments. Passive dispersal of larval fishes probably occurs from the upstream to the downstream segments, but upstream dispersal would be more difficult for small fishes, given the large stretch of deep, flowing water that separates the upstream segment. For example, *L. chrysocephalus* was a significant indicator for the downstream segment in each season. This species spawns over gravel (Jenkins & Burkhead, 1993), and expansive gravel substrata were most common in the downstream segment. Upstream dispersal for this small fish from its ideal spawning grounds in the downstream segment was probably difficult and could explain its rarity in the middle and upstream segments.

Another marked difference in species among segments occurred during summer. Small *D. cepedianum* and *Morone chrysops* (Rafinesque) were common upstream in summer and were probably using the Detroit River as either a nursery or a migration route from Lake St Clair to Lake Erie. Goodyear *et al*. (1982) reported that *M. chrysops* spawn primarily in the downstream segment, whereas *D. cepedianum* spawn upstream or in Lake St Clair. Hatcher *et al*. (1991) reported that large larval *D. cepedianum* entered the upper segment from Lake St Clair in summer. Juveniles of both species began to appear at a few sites in the middle segment in late July. Further downstream migrations may have continued through August, when fishes were not sampled.

The combination of univariate and multiple multivariate analyses of separate size classes provided important insights into fish-macrohabitat associations that would have been obscured by simpler analyses. For example, analyses of fish species richness, abundance and assemblages showed no difference among macrohabitats in the summer and autumn, whereas ISA revealed several species that differed significantly among macrohabitats then. Some of these patterns were observed in the field, such as the profusion of small *D. cepedianum* and *M. chrysops* in the upstream segment in summer, and are believed to be biologically significant. Combining several multivariate techniques provided important insights into the nature of the differences among macrohabitat fish assemblages. When significant differences in assemblages were identified using DISLTM, these differences were characterized by ISA and NMS analyses, which provided similar results. During summer and autumn, differences among assemblages were more subtle; correspondingly, fewer indicator species were identified and the patterns revealed by ISA and NMS were less similar. These analyses involved a considerable amount of data exploration; thus, these interpretations should be viewed as hypothetical rather than conclusive. Certain patterns, such as the difference between fish assemblages of coastal wetlands and upstream areas with developed shorelines, were clearly observable both in the field and through data analyses. Such interpretations are more likely to be biologically significant than

those drawn from individual species found to be significant indicators for a given macrohabitat.

Large-scale habitat selection was observed in the Detroit River, primarily in spring when fishes preferred inshore areas in the lower portion of the river. This may be explained by the lack of vegetation cover found offshore at this time of year and the spawning habits of most species. In summer and autumn, shallow offshore areas provided important fish habitat. Such habitats should receive consideration in fisheries and fish habitat research programmes and management decisions. Heavy anthropogenic modification of the Detroit River has eliminated most of the wetland habitat that once lined both shores. The macrohabitat with the most remaining wetland habitat (the middle segment) had the highest richness, abundance and the most unique fish assemblage during the spring spawning season. Additionally, uncommon species were most frequently found in this macrohabitat, and species at risk were only found here. Future management programmes should focus on the protection and restoration of this habitat, which is important to sport fishes (*e.g.* centrarchids), small fishes and species at risk alike.

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