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Nearshore Fish Species Richness and Species–Habitat Associations in the St. Clair–Detroit River System

Corbin D. Hilling [1,*,†], Jason L. Fischer [2], Jason Ross [3], Taaja R. Tucker [4], Robin L. DeBruyne [1], Christine M. Mayer [1] and Edward F. Roseman [4]

[1] Lake Erie Center, Department of Environmental Sciences, University of Toledo, Toledo, OH 43606, USA; robin.debruyne@utoledo.edu (R.L.D.); christine.mayer@utoledo.edu (C.M.M.)
[2] U.S. Fish and Wildlife Service, Alpena Fish and Wildlife Conservation Office, Detroit River Sub-Station, Trenton, MI 48183, USA; jason_fischer@fws.gov
[3] U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office, Ashland, WI 54806, USA; jason_ross@fws.gov
[4] U.S. Geological Survey, Great Lakes Science Center, Ann Arbor, MI 48105, USA; trtucker@usgs.gov (T.R.T.); eroseman@usgs.gov (E.F.R.)
* Correspondence: hillingc5@gmail.com; Tel.: +1-304-288-9336
† Present Address: U.S. Fish and Wildlife Service Maine Field Office, East Orland, ME 04431, USA.

Abstract: Shallow water riparian zones of large rivers provide important habitat for fishes, but anthropogenic influences have reduced the availability and quality of these habitats. In the St. Clair–Detroit River System, a Laurentian Great Lakes connecting channel, losses of riparian habitat contributed to impairment of fish populations and their habitats. We conducted a seine survey annually from 2013 to 2019 at ten sites in the St. Clair and Detroit rivers to assess riparian fish communities, and to identify habitat attributes associated with fish species richness and catches of common species. We captured a total of 38,451 fish representing 60 species, with emerald shiner *Notropis atherinoides* composing the largest portion of the catch. We used an information-theoretic approach to assess the associations between species richness and catches of 33 species with habitat variables (substrate, shoreline vegetation types, and aquatic macrophyte richness). Sand, cobble, and algal substrates and shoreline vegetation were important predictors of species richness based on a multimodel inference approach. However, habitat associations of individual species varied. This work identified manageable habitat variables associated with species richness, while identifying potential tradeoffs for individual species. Further, this work provides baselines for development and evaluation of fish community and shoreline habitat restoration goals.

Keywords: fish community; great lakes; large river; riparian; river restoration; shallow water habitat

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1. Introduction

Low-velocity, shallow water riparian zones in large rivers are productive habitats supporting primary and secondary production for many aquatic organisms [1–3]. Many fishes use vegetated riparian zones as spawning and sheltered nursery habitats [4–8]. Additionally, these low-velocity areas often retain zooplankton prey for larval and juvenile fishes, providing more efficient foraging opportunities for early life stages than in swifter main-channel habitats [2,9]. Riparian areas also provide societal and economic services that can interfere with natural ecological processes. Riverine modifications to support navigation and shoreline development have contributed to losses of many shallow water riparian areas in large rivers [10–12]. The St. Clair–Detroit River System (SCDRS) on the Canada–United States (U.S.) border is a unique system that shares a common history of habitat degradation with many large rivers worldwide. As a connecting channel of the Laurentian Great Lakes, the SCDRS has a relatively consistent discharge and lacks a floodplain [13,14]. However, like most of the world's large rivers, the SCDRS was altered to better accommodate transportation, trade, and development. Channels were re-routed and deepened in the early 1900s to facilitate navigation of deep-draft vessels, removing over 46 million m^3 of substrate and burying over 4050 ha of fish spawning habitat with dredged spoils [15]. Through this process, shallow water areas were converted to deep shipping channels and artificial islands. Industrial and residential development along the SCDRS further altered the riparian zone. Wetlands were in-filled and shallow sloping banks were converted to deep, vertical banks to allow boats direct access to loading docks and marinas [14,16]. Shorelines were hardened with an estimated 55% of U.S. mainland shoreline on the Detroit River converted to steel sheet piling or concrete breakwater by 1985 [17]. The cumulative result of these alterations was a loss of approximately 97% of riparian wetlands in the Detroit River [18]. Although the St. Clair River still features a river delta marsh, wetland losses in the delta from 1868–1873 to 1973 were estimated as 68% (Jaworski and Raphael 1976 as cited in [19]).

Declines and impairments of habitat and fish and wildlife populations were contributors leading to the St. Clair and Detroit rivers' designations as Great Lakes Areas of Concern (AOC) in 1987 [18,20]. In 1987, fish populations were not designated as impaired based on reports of a rich fish community (>60 species in Detroit River; [21]); however, recognition of the linkage of negative impacts of large-scale habitat degradation on fish and wildlife populations contributed to eventual listing as a beneficial use impairment (BUI, see [20] for definition) [22]. Consequently, although Francis et al. [19] noted 63 and 56 fish species in nearshore habitats of the Detroit River (sampled in 2004, 2006, and 2008) and the St. Clair River Delta (sampled in 2007), respectively, carrying capacity of the system has likely changed and fish communities differ from pre-colonial times [23]. Work in the Detroit River supported that uncommon and imperiled fishes (e.g., pugnose minnow *Opsopoeodus emiliae* and spotted sucker *Minytrema melanops*) were found in areas with wetland habitats, whereas upstream habitats featured few uncommon species and more non-native fishes [7]. In 1991, resource managers identified increasing or improving wetland habitats as a way to improve conditions in the Detroit River [23]. Previous research has shown that riparian and shoreline habitat enhancement projects benefit larval and juvenile fishes by supporting greater fish densities, feeding, and growth [24,25]. Additional information on fish community–habitat associations could help guide riparian and shoreline habitat enhancement projects to maximize benefits and assess potential non-target effects to at-risk or undesirable species.

Establishing an ecological baseline that identifies attributes and processes supporting functional riparian habitat is an important first step for rehabilitation efforts [26,27] and was the impetus for this study. Development and implementation of restoration projects guided by key habitat attributes and processes can lead to achievement and maintenance of desirable restoration outcomes, such as higher richness of small-bodied and juvenile fishes. Additionally, establishing a baseline facilitates development of tangible (achievable and measurable) objectives and provides a starting point to gauge the effectiveness of restoration projects [28]. Further, jurisdictional wildlife action plans have specified a need to understand habitat use of at-risk fishes [29]. Therefore, the objectives of this study were to assess shallow water riparian fish communities in the SCDRS and identify habitat attributes associated with fish species richness based on a shoreline seine survey conducted from 2013 to 2019. Further, we examined habitat associations of commonly collected species to inform targeted restoration projects to meet management goals for individual species of interest, as well as the entire fish community.

2. Materials and Methods

2.1. Study Area

The SCDRS is a 148 km international waterway connecting Lake Huron and Lake Erie in the southern portion of the Michigan, USA–Ontario, Canada border (Figure 1). The system is composed of three distinct parts, the St. Clair River, Lake St. Clair, and the Detroit River, and is the only Laurentian Great Lakes connecting channel with unregulated flow [14,30]. Lake Huron is the primary water supply to the system and acts as a large reservoir, stabilizing flows and minimizing fluctuations in discharge. Consequently, the system maintains a relatively constant discharge of 5300 m^3/s [13] and consistent water velocities [31]. Water depths in both the St. Clair and Detroit rivers are variable, with depths reaching 27 m and shipping channel depths maintained at a 10 m minimum [15,32]. However, water levels have increased by approximately 1 m over the study period (Figure 2). The St. Clair River is generally narrower and faster than the Detroit River, maintaining a single channel before forming a large delta at the transition to Lake St. Clair. Lake St. Clair empties into the Detroit River, which forms multiple channels in the lower half of the river before flowing into Lake Erie. The shallow waters and large surface area of Lake St. Clair allow water entering the Detroit River to warm and cool more quickly in the spring and fall than in the St. Clair River, where water temperature is more similar to Lake Huron [14,33].

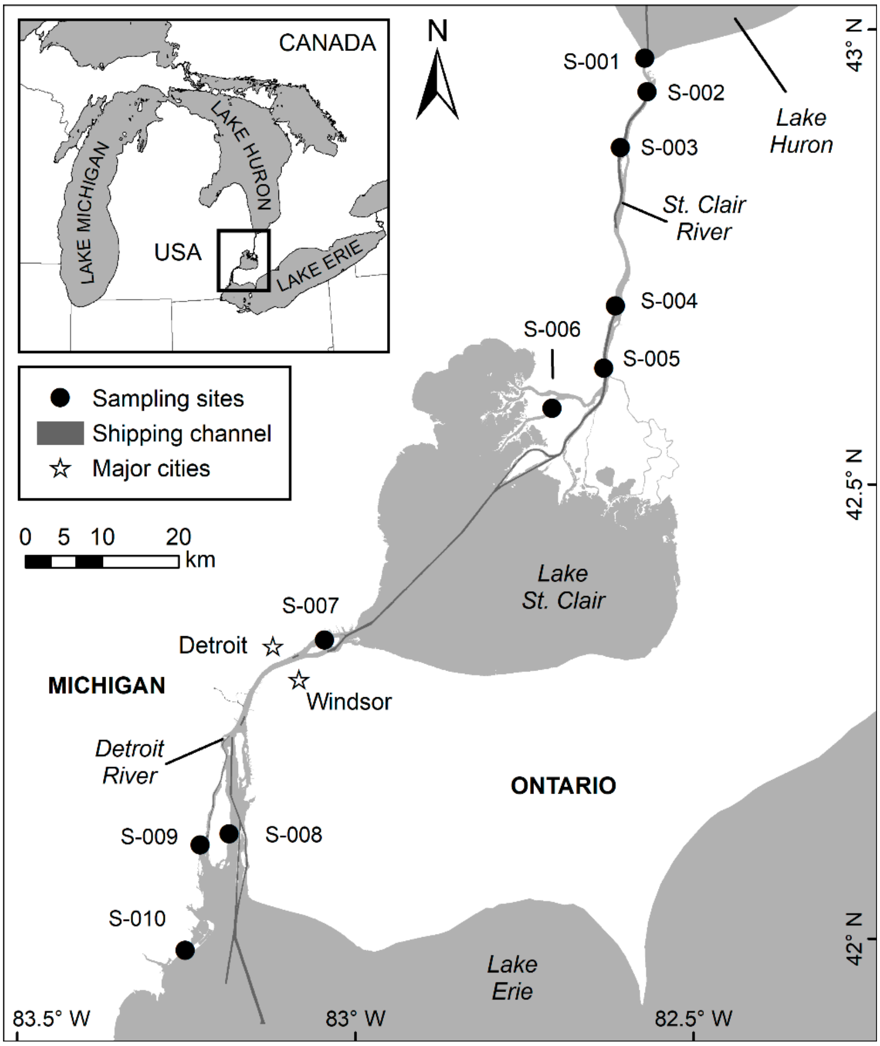

Figure 1. Map of the St. Clair–Detroit River System showing locations of sample sites for a shoreline seine survey in relation to metropolitan areas of Detroit, Michigan, USA and Windsor, Ontario, Canada.

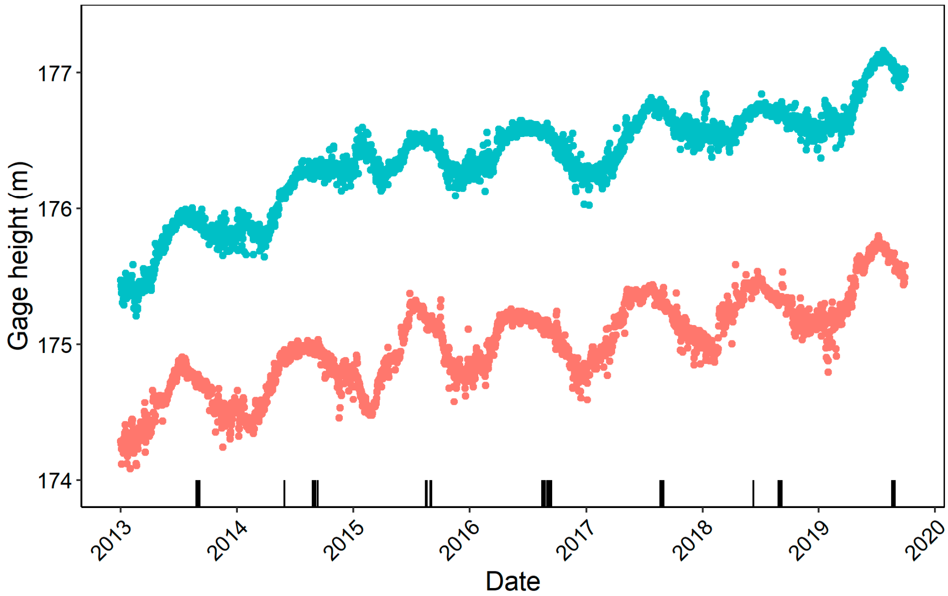

Figure 2. Water levels at the Detroit River (red circles; USGS—US Geological Survey stream gage 04165710, Fort Wayne, Michigan; https://waterdata.usgs.gov/ accessed on 6 June 2021) and St. Clair River (blue circles; USGS stream gage 04159130, Port Huron, Michigan). The rugs (black bars) denote timing of seine sampling events.

2.2. Data Collection

Scientists from U.S. Geological Survey (USGS) Great Lakes Science Center (Ann Arbor, MI, USA) sampled ten sites with seines along the SCDRS Michigan shoreline (Figure 1) from 2013 to 2019, although two of the sites were not sampled in 2013: S-009 (Detroit River) and S-002 (St. Clair River). Sampling was conducted in August or September (15 August–13 September) of each year using a 9.14 × 1.83 m bag seine with 1.6 mm delta nylon mesh. Scientists pulled the seine against the current for 15.25 m when the ends were brought together and all fish were gathered in the bag end. Scientists identified most fish on site and released them downstream of the sampling site, whereas some fishes were retained as reference specimens. Individuals not identified in the field were fixed in a 10% formalin solution and identified in a laboratory setting. Generally, scientists sampled up to five hauls at each site, although limited availability of wadable water without obstructions prevented five hauls of 15.25 m at some sites within a given year (Table 1). Eight seine hauls were completed at S-001 (St. Clair River) in 2019. Due to high water levels, scientists were unable to sample at the S-006 site in the St. Clair River Delta in 2019.

To understand fish community associations with habitat variables and inform potential habitat enhancement projects, we focused analyses on habitat variables that could be manipulated to achieve management objectives. Habitat metrics were documented at all sites and included the presence/absence of in-river substrates, dominant shoreline substrate type, dominant shoreline vegetation type, and aquatic macrophyte species richness and percent cover. Inorganic substrates were classified based on the Wentworth scale [34] with organic substrates (e.g., detritus) and algae also included. Shoreline vegetation was classified as grassy, woody, or absent, based on the dominant vegetation type. In some instances, shoreline vegetation was "mixed", with areas lacking shoreline vegetation and restored areas comprised of grassy vegetation. Scientists visually estimated the percent cover of aquatic macrophytes for the entire area seined, then raked aquatic macrophytes along transects through the seined area to uproot and collect plants. All unique macrophyte species collected were identified in the laboratory based on descriptions by Crow et al. [35,36].

Table 1. Number of individual fish collected and the number of seine hauls conducted at shoreline seine survey sites (parentheses) in the St. Clair (S-001–006) and Detroit rivers (S-007–010) from 2013 to 2019. Sites are arranged from upstream to downstream (top to bottom). "-" indicates no samples were collected for a given site and year.

Site	2013	2014	2015	2016	2017	2018	2019	Total
S-001	156 (4)	736 (5)	507 (5)	10 (4)	148 (5)	1 (4)	142 (8)	1700 (35)
S-002	-	381 (1)	26 (2)	25 (1)	215 (3)	1 (2)	18 (2)	666 (11)
S-003	893(4)	2438 (5)	218 (5)	385 (4)	8939 (4)	188 (4)	340 (4)	13,401 (30)
S-004	192 (4)	203 (4)	104 (5)	148 (4)	723 (4)	57 (4)	3199 (4)	4626 (29)
S-005	74 (4)	120 (4)	311 (5)	219 (4)	636 (4)	21 (4)	167 (4)	1548 (29)
S-006	1835 (4)	1013 (5)	689 (3)	220(5)	1338 (3)	506 (4)	-	5601 (24)
S-007	386 (4)	59 (5)	282 (5)	17 (5)	10 (4)	87 (4)	167 (5)	1008 (32)
S-008	652 (3)	343 (2)	170 (3)	407 (3)	110 (3)	241 (3)	159 (3)	2082 (20)
S-009	-	1007 (5)	947 (5)	242 (5)	260 (4)	295 (4)	718 (5)	3469 (28)
S-010	798 (4)	729 (5)	814(4)	861 (5)	513 (4)	337 (4)	298 (5)	4350 (31)
Total	4986 (30)	7029 (38)	4068 (42)	2534 (40)	12,892 (38)	1734 (37)	5208 (44)	38,451 (269)

2.3. Data Analysis

We evaluated prospective habitat variables to ensure assumptions of linear modeling were met. Collinearity of predictor variables was explored in preliminary analysis via variance inflation factors (VIF) and Pearson's correlation coefficient (r). A global species richness model was developed based on all available predictor variables and variables with VIF > 5 were examined more closely [37]. We also examined r for pairs of numeric predictor variables and removed variables when $|r| > 0.7$ [38]. Shore substrate type was omitted from further analysis due to correlations with in-river substrate types based on VIF values in preliminary models. Percent aquatic macrophyte cover was also considered in exploratory analysis; however, it was strongly correlated ($r = 0.85$) with macrophyte richness, which was less subjective to estimate and was therefore kept in the final analysis. To account for a potential non-linear relationship between fish species richness and aquatic macrophyte species richness, aquatic macrophyte species richness was treated as a categorical variable. Aquatic macrophyte richness was classified as none, low (1–5 species), or high (>5 species), which roughly corresponded to the first, second, and third quartiles of aquatic macrophyte species richness. This categorization also followed percent vegetative cover, where sites with 1–5 aquatic macrophyte species tended to have <50% coverage by aquatic macrophytes and sites with >5 species of aquatic macrophytes tended to have >50% coverage. Consequently, the habitat predictor variables examined further were six in-river substrate types (silt, sand, gravel, cobble, organic, and algae), aquatic macrophyte richness, and shoreline vegetation type.

We examined fish community associations with manageable habitat variables based on an information theoretic, multimodel inference framework. Because hypothesis testing and p-values only compare an alternative hypothesis to a trivial null hypothesis of no relationship [39], we took a model comparison approach to test numerous candidate hypotheses for habitat associations with fish species richness and individual species catches. Generalized linear mixed models (GLMMs) were used to evaluate the relationships of fish species richness and species-specific seine haul catches with manageable habitat variables. Generalized linear mixed models offered two advantages. First, they allowed species richness and individual species catches to be modelled using non-Gaussian distributions, which are more appropriate for count data and better approximated observed distributions. Second, they allowed for a hierarchical model structure and use of a common prior for group variables that allowed for shrinkage of individual estimates towards the group mean, which is a more appropriate approach for assessing imbalanced and repeated measurements [40,41]. Given that not all sampling sites received the same number of seine hauls per year and some sites were not sampled in all years (Table 1), site and year were included as random effects on the model intercept for all candidate models. An offset standardizing species richness to effort was included in the model given that not all seine hauls areas differed due to availability of seinable habitat.

To model species richness and associations with habitat variables, we developed 256 candidate GLMMs with random effects of site and year and all combinations of the six predictor variables presented above as fixed effects (i.e., the 'all subset approach') [42]. This included a model with random effects of site and year and no fixed effects. Previous works have cautioned against the use of an all subset approach in favor of more thoughtful analyses based on a handful of hypotheses (e.g., [43]), but its use has been supported in an exploratory context to aid development of more refined hypotheses and provide guidance for future studies [42]. Given that data analyzed in the present study were from an annual monitoring survey rather than a designed experiment, we determined using an exploratory approach may be most appropriate to avoid subjective decisions on which predictors to exclude. We assumed species richness followed a Poisson distribution and used a log-link function for GLMMs. Generalized linear mixed models were fitted in program R 3.6.3 [44] using the 'glmmTMB' function in the 'glmmTMB' package version 1.0.2.1, which fits GLMMs based on maximum likelihood estimation via Template Model Builder (TMB; [45]).

We compared candidate models using Akaike's information criterion (AIC) with a small sample size bias correction (AICc). The use of AIC (and its variants) presents challenges in the context of mixed effects models due to difficulties in estimation of residual degrees of freedom and boundary effects [46]. However, all models in this analysis had the same random effects specification, indicating the number of random effects groupings was consistent across models. We assessed the relative support of candidate models via calculation of the difference in AICc between candidate models and the best model (ΔAICc), where the best model was the model with the lowest AICc. Relative support was judged based on conventions presented by Burnham and Anderson [47], where models with ΔAICc ≤ 2 had substantial relative support, models with ΔAICc between 4 and 7 had considerably less support, and models with ΔAICc > 10 were unsupported. Akaike weights (w_i), which represent the relative likelihood, were calculated for each model i from ΔAICc values as in Equation (1).

$$w_i = \frac{\exp(-0.5 \cdot \Delta \text{AICc}_i)}{\sum_i^I \Delta \text{AICc}_i} \tag{1}$$

Values of w_i were incorporated into calculation of model-averaged parameter estimates and uncertainty. Model-averaged parameter estimates ($\hat{\hat{\theta}}$) were calculated as $\hat{\hat{\theta}} = \sum_i^I w_i \cdot \hat{\theta}_i$, where $\hat{\theta}_i$ is the estimate of parameter θ for model i. We also calculated unconditional standard errors for fixed effects. Unconditional standard errors differ from conventional "conditional" measures of uncertainty in that they include uncertainty from model selection. Unconditional standard errors ($se(\hat{\hat{\theta}})$) were calculated as in Equation (2),

$$se\left(\hat{\hat{\theta}}\right) = \sqrt{\sum_i^I w_i [v\hat{a}r(\hat{\theta}_i | g_i) + (\hat{\theta}_i - \hat{\hat{\theta}})^2]} \tag{2}$$

where $v\hat{a}r(\hat{\theta}|g_i)$ is the estimated variance of parameter θ for model i [48]. We calculated 95% confidence intervals surrounding $\hat{\hat{\theta}}$ as $\hat{\hat{\theta}} \pm 1.96 \cdot se\left(\hat{\hat{\theta}}\right)$ [48]. Parameters were assessed for significant influence on species richness via examination of the presence or absence of confidence interval overlap with zero.

Given the existence of species-specific management interests, especially for non-native, at-risk, and economically important species, we also examined habitat associations of individual species. We used the same analytical framework as presented above for species richness with some differences. The response variable was specified as catches for individual seine hauls and the model fitting and selection procedure was conducted independently for each species. As is typical for community data, some species were rarely encountered and required consideration of tradeoffs associated with modeling scarce data and understanding uncommon species' habitat associations. We omitted species that were present in <2.5% of seine hauls, following work of Larkin et al. [49] which examined aquatic plant communities via multivariate statistics. Like GLMMs for species richness, species-specific GLMMs included random effects of sampling site and year and an offset for sampling effort but assumed response variables followed a negative binomial distribution due to overdispersion concerns identified in preliminary data exploration for many species.

We also assessed species–habitat interactions based on canonical correspondence analysis (CCA), which permitted visualization of habitat associations in multivariate space. Given that CCA does not account for repeated measures at sites within or across years, CCA was primarily used as an ordination technique to visualize results relevant to species-specific GLMMs. We tested for significance of the CCA model, which included all predictor variables from GLMMs, using a permutation test with 999 permutations and evaluated significance at $\alpha = 0.05$ [50]. This analysis was completed via the 'vegan' R package version 2.5-2 [51].

3. Results

Over the seven-year study period, 38,451 fish representing 60 species were collected in 269 seine hauls, with a mean observed species richness of 5 (SD = 4) species per seine haul. Identification to species was achieved for 30,873 individuals, whereas 7578 individuals were identified to higher taxonomic levels (e.g., family or genus) or were impractical to identify (e.g., due to size). Fourteen seine hauls from three different sites (S-001, S-002, and S-004) had catches of zero fish. The maximum observed species richness for individual seine hauls was 17 from the S-006 site in 2017. Emerald shiner *Notropis atherinoides* composed the largest proportion of the catch; 11,668 individuals (38% of individuals identified to species) were collected during the study period and the species was observed at every site except S-006 in the St. Clair River Delta (Supplementary Materials Table S1). The next most abundant species were bluntnose minnow *Pimephales notatus* (n = 4193; 14% of individuals identified to species), brook silverside *Labidesthes sicculus* (n = 2105; 7%), round goby *Neogobius melanostomus* (n = 1916; 6%), and spottail shiner *Notropis hudsonius* (n = 1799; 6%).

The species composition of samples featured a mix of species of management interest including at-risk, economically important, and non-native species. At-risk species collected during seine surveys (based on state, provincial, or federal designations covering the SCDRS) included grass pickerel *Esox americanus*, lake chubsucker *Erimyzon sucetta*, northern sunfish *Lepomis peltastes*, pugnose minnow, pugnose shiner *Notropis anogenus*, and spotted sucker, comprising 3% of fish collected (n = 851). The most commonly collected at-risk species was pugnose shiner (n = 614), all of which were collected at site S-006. Five of the six at-risk species collected were sampled exclusively at one site, with four of those collected at site S-006 in the St. Clair River delta (lake chubsucker, grass pickerel, pugnose minnow, and pugnose shiner). Several species of recreational or commercial interest were collected such as largemouth bass *Micropterus salmoides*, *Lepomis* spp., muskellunge *Esox masquinongy*, northern pike *Esox niger*, smallmouth bass *Micropterus dolomieu*, and yellow perch *Perca flavescens*, with yellow perch being the most common (n = 1313). A total of nine non-native species were collected, including alewife *Alosa pseudoharengus*, brown trout *Salmo trutta*, common carp *Cyprinus carpio*, ghost shiner *Notropis buchanani*, goldfish *Carassius auratus*, rainbow smelt *Osmerus mordax*, round goby, tubenose goby *Proterorhinus marmoratus*, and white perch *Morone americana*. Non-native fishes made up 9% of the total sample identifiable to species (2795 individuals) and were dominated by round goby and tubenose goby.

Fifteen species were unique to individual sampling sites. The S-009 site on the Detroit River had the most unique species (n = 4), whereas seven other sites had at least one unique species (Table S1). A total of 16 species was unique to the Detroit River, whereas 9 species were exclusively collected in the St. Clair River. Only three species (round goby, spottail shiner, and yellow perch) were collected at all sites. Centrarchidae species were more common in the Detroit River: 94% of centrarchids collected during the study were from Detroit River sites, 88% of which came from S-009 and S-010. Fishes from the family Catostomidae were found at relatively few sites and most species were uncommonly collected (Table S1). Additional details on the species composition of samples can be obtained and summarized using the supplemental datafile produced by Fischer et al. [52].

In-river substrate types differed across sites and through the time series. As many as four substrate types were documented at a site in a given year (Table 2). Upstream sites within both rivers were generally characterized by sand and gravel substrates, whereas the downstream site(s) were more likely to feature silt, organic matter, or algal substrates (Table 2). Cobble and algal substrates were only documented in the St. Clair River, whereas all other substrate types were documented at sites in both rivers. Aquatic macrophytes were present at all sites at some point in the time series, except the most upstream site in the St. Clair River, S-001 (Table 3). Macrophyte richness was greatest at the S-006 and S-009 sites in 2017, where 10 species were collected within the time series (Table 3).

Table 2. Substrate types present by year at sampling sites for a shoreline seine survey on the St. Clair and Detroit rivers. Si = Silt, Sa = Sand, Gr = Gravel, Co = Cobble, Or = Organic, and Al = Algae. "-" indicates no data. Sites are arranged from upstream to downstream (top to bottom).

Site	2013	2014	2015	2016	2017	2018	2019
S-001	Gr	Gr	Gr	Gr	Sa, Gr	Sa, Gr	Sa, Gr
S-002	-	Gr	Gr	Gr	Sa, Gr	Sa, Gr	Sa, Gr
S-003	Gr	Gr	Gr	Gr	Sa, Co	Sa, Gr	Sa, Gr, Co
S-004	Sa	Sa	Sa	Sa	Sa, Co	Sa	Sa, Gr, Co
S-005	Sa	Sa	Sa	Sa	Sa, Co	Sa, Gr	Sa, Gr
S-006	Or	Or	Or	Or	Si, Sa, Or, Al	Si, Sa	-
S-007	Sa	Sa	Sa	Sa	Sa, Gr	Sa	Sa
S-008	Gr	Gr	Gr	Gr	Si, Sa	Sa	Sa
S-009	-	Or	Or	Or	Si, Or	Si, Sa	Si, Sa
S-010	Or	Or	Or	Or	Sa	Si, Sa	Si, Sa

Table 3. Shoreline vegetation type (Type) and yearly aquatic macrophyte richness at sampling sites for a shoreline seine survey on the St. Clair and Detroit rivers. "-" indicates no data. Sites are arranged from upstream to downstream (top to bottom).

Site	Type	2013	2014	2015	2016	2017	2018	2019
S-001	None	0	0	0	0	0	0	0
S-002	Mixed	-	0	0	1	0	0	0
S-003	None	3	4	0	3	4	5	2
S-004	None	0	0	0	1	3	2	2
S-005	Grassy	0	0	0	2	4	3	0
S-006	Grassy	6	7	5	8	10	6	-
S-007	Grassy	1	6	0	2	2	1	2
S-008	Woody	5	7	0	7	5	9	7
S-009	Woody	-	8	4	10	8	9	5
S-010	Grassy	0	0	0	8	4	0	5

Of the 256 candidate models describing fish species richness, no model was clearly superior based on AICc but 4 models had ΔAICc values less than 2 and were interpreted as substantially supported (Table 4). All four models featured sand, cobble, algae, and shoreline vegetation type as predictor variables. Further, all candidate models with ΔAICc < 4 featured sand, cobble, algae, and shoreline vegetation as a predictor variable. None of the most-supported models (ΔAICc < 4) featured aquatic macrophyte richness as a predictor variable, but all substrate types were represented in at least one of the most-supported candidate models.

Table 4. Model selection table for the most-supported models (Δ_{AICc} < 4) based on 256 candidate generalized linear mixed models to understand fish species richness-habitat associations in the St. Clair and Detroit rivers based on a shoreline seine survey from 10 sites sampled 2013–2019. "Model" indicates the fixed effects specified for individual models (SV = shoreline vegetation type), "AICc" is the Akaike information criterion with a small sample size correction, "Δ_{AICc}" is the difference in AICc for a given model and the best model, w_i is the weight of support for model *i* and "Cum. Weight" is the cumulative weight of candidate models. All models included random effects of site and year.

Model	AICc	Δ_{AICc}	w_i	Cum. Weight
Sand+Cobble+Organic+Algae+SV	1202.29	0.00	0.29	0.29
Sand+Gravel+Cobble+Organic+Algae+SV	1204.10	1.81	0.12	0.41
Silt+Sand+Cobble+Organic+Algae+SV	1204.19	1.90	0.11	0.52
Sand+Cobble+Algae+SV	1204.23	1.94	0.11	0.63
Silt+Sand+Gravel+Gravel+Cobble+Organic+Algae+SV	1205.90	3.61	0.05	0.68
Silt+Sand+Cobble+Algae+SV	1206.09	3.80	0.04	0.72
Sand+ Gravel+Cobble+Algae+SV	1206.20	3.91	0.04	0.76

Model-averaged slope parameter estimates were similar to model selection outcomes, as most predictor variables common to all most-supported models were deemed significant based on lacking overlap of 95% confidence intervals with zero (Figure 3). Cobble, algae, grassy shoreline vegetation, and woody shoreline vegetation were interpreted as significant. Although sand was present as a predictor variable in all most-supported models, it was not interpreted as a significant predictor variable to explain species richness based (95% CI: −0.70, 0.07). Cobble was not associated with greater richness based on observed data (Figure 4) but had a positive influence on richness based on model-averaged slope estimates from mixed effects models (Figure 3). Algal substrates were associated with greater species richness based on the positive value of the model-averaged parameter estimate. Woody shoreline vegetation was the vegetation type associated with greatest fish species richness (Figures 3 and 4). However, grassy shoreline vegetation was typically associated with greater fish richness than no or mixed shoreline vegetation (Figure 4). Fitted values from model averaging suggested greatest richness at the S-006, S-008, S-009, and S-010 sites (Figure 5).

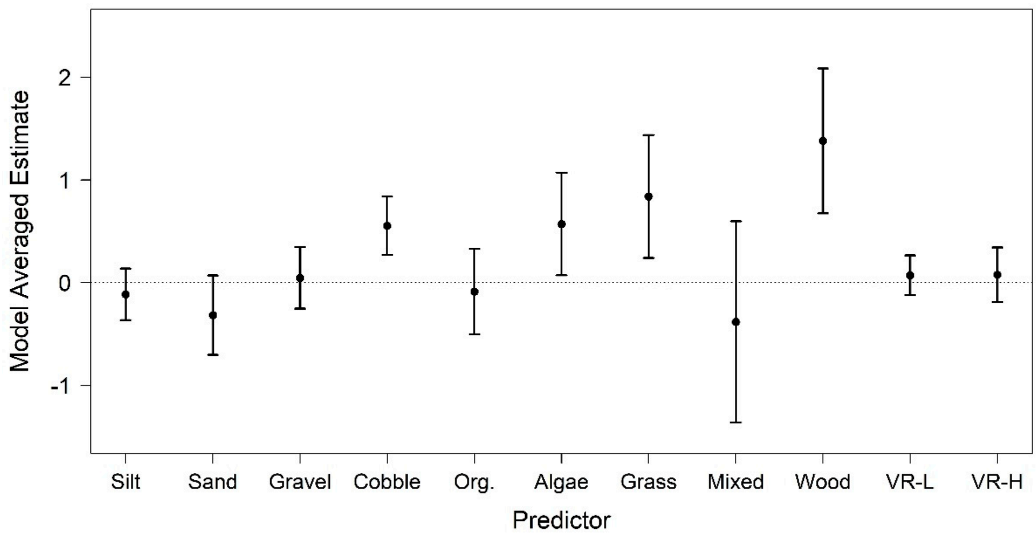

Figure 3. Model-averaged slope parameter estimates for predictor variables from 256 candidate generalized linear mixed models. 'Grass', 'Mixed', and 'Wood' refer to shoreline vegetation types, whereas 'VR-L' and 'VR-H' refer to low and high aquatic macrophyte richness, respectively. Error bars represent 95% confidence intervals calculated based on unconditional standard errors.

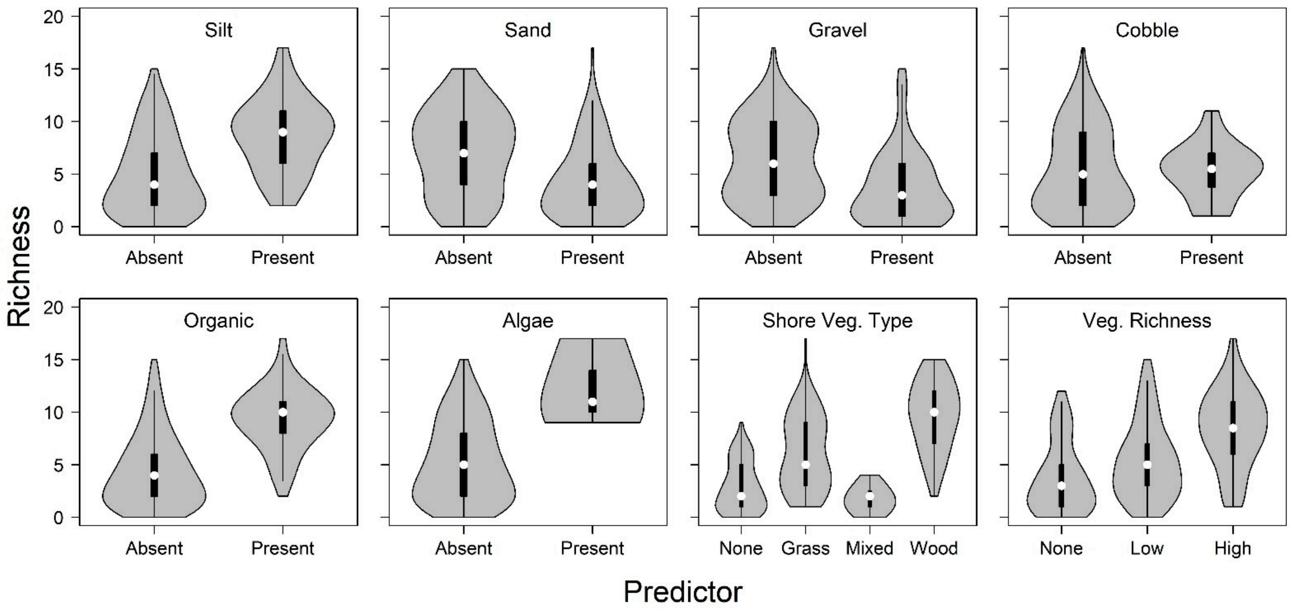

Figure 4. Observed fish species richness from seine hauls in association with habitat variables from the St. Clair and Detroit rivers aggregated across sampling sites and years.

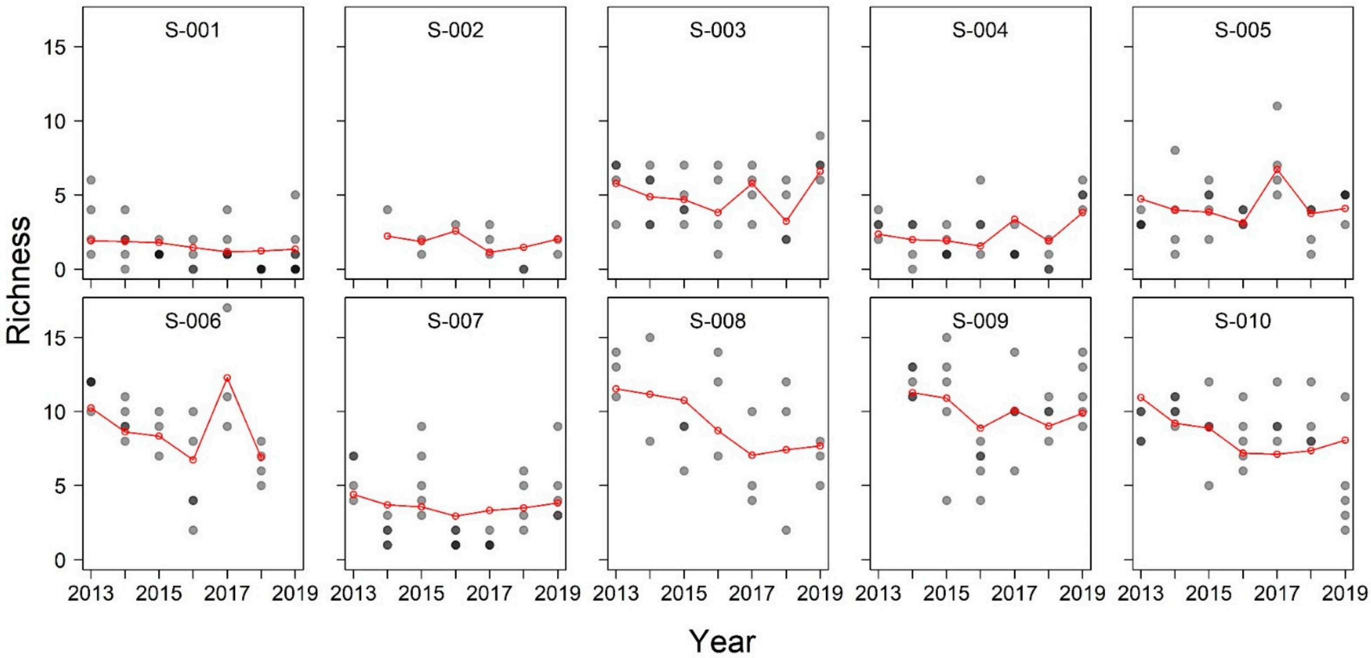

Figure 5. Observed (filled circles) and fitted fish species richness (open circles with lines) for sites over time in the St. Clair and Detroit rivers based on model averaging of 256 candidate generalized linear models. Darkness of circles reflects existence (or not) of overlapping observations. See Figure 1 for locations of sites.

After excluding uncommon species, 256 species-specific candidate GLMMs were fitted for 33 species for a total of 8448 model estimation runs. Given that we strived to include as many species as possible in individual species analyses, some models were not well fitted, and convergence issues arose. A total of 1394 models were unable to converge using default settings for GLMMs in the glmmTMB package. The average number of model convergence failures per species was 42 (SD = 37), with a range of 0–140. Nine species achieved convergence for all candidate models, including bluntnose minnow, brook silverside, largemouth bass, mimic shiner *Notropis volucellus*, round goby, spotfin shiner *Cyprinella spiloptera*, spottail shiner, tubenose goby, and yellow perch. Green sunfish *Lepomis cyanellus* had the most model convergence failures (n = 140).

The best model explaining habitat and catch rate associations varied by species (Table S2). For three species (goldfish, northern hogsucker *Hypentelium nigricans*, northern sunfish), models with random effects of site and year and no fixed effects were supported as the AICc best supported model. The global model (i.e., all predictor variables included) was not supported as the best model describing habitat associations for any species, but best models included as many as seven predictor variables (hornyhead chub *Nocomis buguttatus*). For 18 examined species, all model-averaged slope parameters were non-significant (Table S2). In these and many other cases, unconditional standard errors were large, sometimes 4+ orders of magnitude greater than the model-averaged parameter estimates (Table S2). All statistically significant slope parameters were featured in the "best" models selected by AICc.

The CCA model including all predictor variables was significant (F = 9.45, df = 11, 240, p = 0.001) and explained 30% of the variability in species catches. The first CCA axis could be interpreted as an axis of course substrates (e.g., sand, gravel, and cobble) and low aquatic vegetation richness versus very fine substrate particles (e.g., silt) and high organic matter (i.e., vegetated shores, high aquatic macrophyte richness, and organic substrates; Figure 6). The second CCA axis was largely characterized by segregation of woody shoreline vegetation versus silt and algal substrates (Figure 6). Most fish species were congregated in the bottom-right quadrant (characterized by woody shorelines and high organic matter), but some species were more strongly associated with CCA axes (Figure 6). Emerald shiner catches were most associated with the first CCA axis (course substrates and low aquatic vegetation richness), whereas most species were more associated with fine substrates and high organic matter (Figure 6). In terms of the second CCA axis, blackchin shiner *Notropis heterodon*, pugnose minnow, and pugnose shiner were associated with algal substrates, whereas species such as goldfish, northern sunfish, rock bass *Ambloplites rupestris*, spotted sucker, striped shiner *Luxilus chrysocephalus*, and white sucker *Catostomus commersonii* were more associated with woody shorelines (Figure 6).

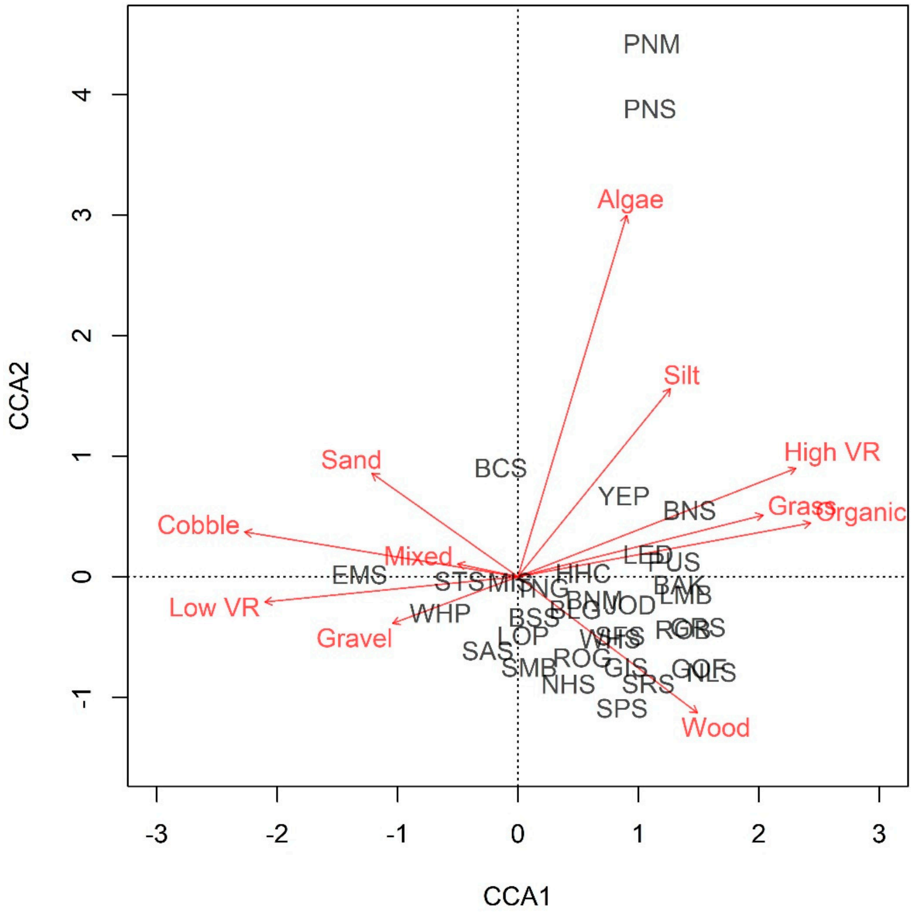

Figure 6. The first two axes from a canonical correspondence analysis examining fish species–habitat associations. Labels for arrows indicate in-river substrate types, aquatic macrophyte richness ('Low VR' = low macrophyte richness and 'High VR' = high macrophyte richness), or shoreline vegetation types ('Grass', 'Mixed', and 'Wood'). Three-letter codes indicate species: BAK = banded killifish, BCS = blackchin shiner, BLG = bluegill, BNM = bluntnose minnow, BNS = blacknose shiner, BSS = brook silverside, EMS = emerald shiner, GIS = gizzard shad, GOF = goldfish, GRS = green sunfish, HHC = hornyhead chub, JOD = Johnny darter, LED = least darter, LMB = largemouth bass, LOP = logperch, MIS = mimic shiner, NHS = Northern hogsucker, NLS = northern sunfish, PNM = pugnose minnow, PNS = pugnose shiner, PUS = pumpkinseed, ROB = rock bass, ROG = round goby, SAS = sand shiner, SFS = spotfin shiner, SMB = smallmouth bass, SPS = spotted sucker, SRS = striped shiner, STS = spottail shiner, TNG = tubenose goby, WHP = white perch, WHS = white sucker, and YEP = yellow perch. Scientific names for species are provided in Table S1.

4. Discussion

This study provides important information on fish community–habitat associations in shoreline zones of the St. Clair and Detroit rivers. Shoreline habitats have been degraded over time in the SCDRS, but this study supports that a diverse shoreline fish community exists. This work improves our understanding of habitat associations with fish species richness, as well as several at-risk, invasive, and economically important fishes. Species richness was associated with substrate types (e.g., sand, cobble, algae) and shoreline vegetation, providing possible opportunities for habitat enrichment to enhance fish communities and improve ecosystem function via flow and sediment management and restoring wetland connectivity. Further, this work permits identification of tradeoffs in habitat enhancement projects in relation to individual species. For instance, restoration practitioners can identify which species are likely to colonize or increase in abundance in response to habitat improvements and which may be less likely to be present for a given restoration prescription.

Finally, this work informs future monitoring programs by aiding scientists and managers to target habitats associated with species of management importance and understand biases in abundance indices based on characteristics of selected sampling sites.

This study provides a description of the nearshore fish community of the SCDRS and supports the presence of habitat diversity and importance of riparian and wetland habitats for maintenance of native fish assemblages. The St. Clair River generally featured species characteristic of a coolwater fish assemblage in a fast, flowing river. However, the St. Clair River Delta site (S-006) is characterized by slower flow velocities and marsh habitat. The fish community in the St. Clair River Delta was more characteristic of a warmwater fish community and appears to provide important habitat by supporting several at-risk fishes not collected elsewhere in the study. In the St. Clair River, species such as emerald shiner, sand shiner *Notropis stramineus*, and spottail shiner were predominant, with species such as banded killifish *Fundulus diaphanus*, largemouth bass, pugnose minnow, and pugnose shiner collected in the St. Clair Delta. The Detroit River also featured a warmwater fish community but was most characteristic of a warmwater community toward the mouth where habitats were more vegetated. Riverine fishes (e.g., northern hogsucker, smallmouth bass) were more common in upstream Detroit River sites than those closer to the mouth of the river.

Model selection criteria supported sand, cobble, and algae substrate as important predictors of fish species richness in the St. Clair and Detroit rivers. Model-averaged parameter estimates indicated a positive effect of the presence of algae and cobble on species richness. Although algal substrates were generally associated with greater richness, there was a lack of evidence of a positive influence of cobble in plots of site and year-aggregated observations of richness. However, median richness estimates were higher when cobble was present at sites where cobble was observed within the time series. Cobble may have represented a proxy for substrate heterogeneity as cobble was never observed as the only substrate type present. Sarkar and Bain [53] suggested maintenance of a range of habitat types given that habitat requirements of species occupying erosional and depositional habitats differed. Sites dominated by sand substrates (e.g., S-001) tended to have low species richness, possibly reflective of low habitat complexity [54,55]. High flow velocities in the upper reaches of the St. Clair River may also reduce habitat suitability for some fishes as Lapointe et al. [6] found many small and juvenile fishes were associated with fine sediments in the Detroit River.

In our study, grassy and woody shorelines were associated with greater fish species richness. The benefits of wooded riparian zones to fishes have been well described (e.g., [56,57]), but have received greater research attention in smaller systems than those examined here. Woody riparian vegetation contributes leaf litter, which supports productivity of invertebrates [58] and woody inputs enhance structural complexity, providing cover for fishes [59]. Further, woody vegetation provides benefits of stabilizing banks, thereby reducing sedimentation [60–62]. Grassy shoreline vegetation provides many of the same benefits as woody shoreline vegetation and can support greater abundances and species richness than more complex riparian plant assemblages [63]. Improving habitat complexity and diversity of shoreline areas of the St. Clair and Detroit rivers may benefit the diverse fish community present [64].

Aquatic macrophyte richness was not included as a fixed effect in any of the most-supported models (i.e., models with ΔAICc < 4) and was not supported as an important factor explaining species richness in this study. However, sites with the greatest fitted fish species richness typically had greater aquatic macrophyte richness. Consequently, a lack of support for increased species richness with greater aquatic macrophyte richness (and correlated percent macrophyte coverage) was unexpected. Most of the fish collected in this study were small (mean length = 48 mm, SD = 24 mm) and juvenile fishes for which previous research has supported the value of aquatic macrophytes [4,6–8]. Other studies in the Detroit River have shown juvenile fishes to be more strongly associated with microhabitat than their larger conspecifics and juvenile fishes were more abundant in areas with aquatic macrophytes [6]. Aquatic macrophytes can reduce predation risk and prey fish tend to concentrate in vegetated areas when predators are present [65]. Predation pressure may be a strong driver in habitat selection for small and juvenile fishes and prey availability may also be higher in vegetated areas. Grenouillet et al. [8,9] documented higher abundances of juvenile fishes in vegetated areas, which they attributed to higher availability of zooplankton prey and shelter from predators. Zooplankton have a limited ability to swim against the current and are more likely to be retained in slow-moving, vegetated portions of rivers [2]. Furthermore, vegetated areas of river systems may provide better feeding opportunities and yield higher growth rates for some fishes [66,67]. Consequently, further study may be needed to more explicitly evaluate relationships between fish communities and aquatic vegetation in the SCDRS to inform shoreline and wetland restoration projects.

While our models highlight structural components of sites with high species richness, it is also important to consider the processes that maintain those components to improve success and longevity of restoration [26,68]. Given that strong currents and turbulence are unfavorable for primary producers, aquatic macrophytes are more likely to establish in areas of low water velocity [1,69]. Additionally, deposition of particulate matter provides minerals and nutrients, in part, leading to the high primary and secondary productivity of large floodplain rivers [1,70] and supporting macroinvertebrate detritivores consumed by fish [71]. Since organic substrates are easily displaced by flowing water, they are most likely to accumulate in low-velocity areas. These are the same areas highlighted by the "inshore retention concept" as being crucial for larval fish development and retention of zooplankton food sources [2]. Areas that retain organic matter are therefore likely to have lower advection and higher colonization of larval fish. In the SCDRS, Pritt et al. [72] found larval fish assemblages in the upper river reaches to be a nested subset of lower river communities. Hydrologic processes within the St. Clair River delta and portions of the Detroit River may more be conducive to retention of larval fish that may later recruit to juvenile stages. However, riparian wetlands and shallow beds of aquatic macrophytes have been restricted to the lower portions of each river [18,73] and these vegetated areas may provide spawning habitat to a different suite of species [74]. Thus, high fish species richness at these locations may arise from both pattern (e.g., physical habitat) and process (e.g., larval retention).

The use of an information theoretic approach and multimodel inference allowed us to make inferences related to fish–habitat associations, while accounting for model selection uncertainty [43,75]. In most cases, several models were supported by the data and assuming one model was the correct model would have resulted in information loss, although not all models achieved convergence. Model fitting issues appeared to arise due to several factors. Low occurrence in samples was likely a contributing factor to model fitting issues as some species were rarely observed (e.g., spotted sucker or green sunfish) or were collected at single sites. Goldfish were only collected at the S-009 site with most fish collected in 2014. Another issue may have been related to segregation of species among habitat types. Some species have relatively specific habitat use tendencies and were collected exclusively in samples from one category of the included predictor variables or presumably avoided some habitat types which may have contributed to large uncertainty estimates. Further, some generalist species were collected across levels of predictor variables but were collected relatively infrequently among the total number of seine hauls yielding large estimates of uncertainty. Although model fitting issues arose for some specified models, the use of a multimodel approach allowed us to model habitat associations for species despite data limitations and gain some insights on catch rates and associations with habitat variables.

Although this work provides insights on fish–habitat associations, the results of this study should not be interpreted as definitive depictions of habitat use by examined species. Factors such as gear efficiency and fish behavior may influence observed results. For instance, more species were generally collected at vegetated sites (i.e., S-006 and S-009) than those without vegetation which could indicate that fish use those habitats with greater prevalence. However, Pierce et al. [76] reported a positive association between gear efficiency and vegetation biomass for beach seines sampling fishes in lakes. Behaviorally, small-bodied fishes may spend most of their time in those habitats or move there to seek shelter from perceived threats [77], whereas fish in unvegetated habitats may be more likely to flee to open water, making them unavailable to sampling. Given the size of these rivers, the use of techniques employed in smaller systems to reduce emigration such as block netting were not feasible. Consequently, seine hauls are not from the exact same location at a given site and are not true replicates. As a result, we were unable to address detection probabilities for species in relation to the sampling gear or habitat characteristics. Further, characteristics of certain sampling sites may present challenges in sampling. Silt-bottomed sites may reduce mobility for scientists working the seine upstream relative to rocky-bottomed sites and differences in flow velocity may result in different speeds during seining. Additional study may be necessary to understand detectability of species at sites in relation to habitat use and gear efficiency.

Future work related to the fish community of the SCDRS may also benefit from inclusion of additional habitat characteristics and integration of multiple sampling gears. Factors discussed above such as flow velocity and channel morphology may be important factors in understanding habitat and fish community associations and may influence other habitat features. Additional factors found to influence species-site associations include river bottom slope or contour, depth, turbidity, and distance from shore [6,7]. Because our sampling was shore based and limited to wadable areas, comparable depths and distances to shore were sampled at all sites. However, slope and distance to the main channel may be more meaningful metrics to explain variability in fish species richness at our sample sites. Slope provides information on the transition to deep main-channel habitat and distance to the main channel provides information on the area of shallow water available to small and juvenile fishes. Additionally, areas with a greater distance between the bank and main channel provide more area for retention of drifting larvae [78]. Indeed, some of the highest species counts we observed were at sites with large distances between the riverbank and main channel (e.g., S-006, S-009, and S-010). Given that seining limits sampling to wadable stream segments with public access, the number of sampling sites possible were quite limited. Inclusion of additional sampling gears, such as boat-mounted electrofishing, may allow researchers to take a more randomized approach to site selection and enhance the amount of space that can be feasibly sampled. Using these methods, Francis et al. [19] were able to collect species undetected in our seine surveys. However, electrofishing has limitations in sampling fishes of interest in this study as small-bodied fishes are less susceptible to electrofishing [79]. Expansion and refinement of predictor variables to better explain species–habitat associations and enhanced sampling coverage may improve understanding of the community ecology of SCDRS fishes and better inform habitat restoration decisions.

This study provides guidance for establishment of tangible objectives for shallow water riparian habitat restoration by evaluating habitat associations with species richness and individual species. When setting fish community objectives, sites with high species richness could represent the maximum number of fish species restored or managed habitats could realistically support. Observed richness can be used to derive system specific goals for restoration projects directed at removing the loss of fish and wildlife habitat BUI in the St. Clair and Detroit River AOCs. Several at-risk, economically important, and invasive species were observed within the sampling area, sometimes with similar associations to habitat features. Restoration efforts that provide functional habitat for a broad number of species and life history stages will likely benefit both desirable native species and undesirable invasive species. For example, increasing aquatic vegetative cover to improve Centrarchidae populations without benefitting tubenose gobies is unrealistic because both taxa prefer vegetated areas [80]. Additionally, not all native fishes will benefit from increased macrophyte richness, such as those that require shallow sandy areas for reproduction and development. Understanding and evaluating tradeoffs associated with habitat restoration and community and individual species responses is likely a critical step when developing restoration goals and objectives.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/w13121616/s1, Table S1: Number of each fish species collected during a shoreline seine survey at sites in the St. Clair-Detroit River System 2013–2019. Table S2: Model selection results and model-averaged slope parameter estimates based on 256 candidate generalized linear mixed models to understand habitat associations of 33 fishes in the St. Clair and Detroit rivers based on a shoreline seine survey from 10 sites sampled 2013–2019. Column headings are predictor variables.

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Institutional Review Board Statement: All sampling and handling of fish during research are carried out in accordance with guidelines for the care and use of fishes by the American Fisheries Society (http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf) [accessed on 6 June 2021]).

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