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ABSTRACT

Small tributaries of the Great Lakes serve as important habitat during critical life stages of many fish species, though temporal and spatial dynamics of the assemblage that uses these systems are seldom investigated. This study quantifies larval and adult fish assemblages captured by fyke net and light traps among small tributary mouths of Green Bay, Lake Michigan. Ten tributaries harbored a total of forty-five species representing seventeen families, with the most abundant including spottail shiner (*Notropis hudsonius* (Clinton 1824)) in adult assemblages and white sucker (*Catostomus commersonii* (Lacepède 1803)) in larval assemblages. Larval fish assemblage structures differed over five biweekly sampling events in May and June. Adult fish assemblage structures varied among tributaries but not among spring, summer, and fall samples. Larval and adult species assemblages at these rivermouths are likely influenced by hydrology, habitat structure, and species-specific ecology. Water movement may transport larvae into rivermouths, as larval assemblages were dominated by species that spawn in coastal habitats. Adult species richness varied with longitude, with the greatest diversity in tributaries on the west shore. This investigation of fish assemblages highlights the spatial and temporal variation that occurs in these systems and their role in shaping fish populations in Green Bay.

KEY WORDS

Assemblage structure, freshwater fish, Great Lakes, habitat use, fish assemblages, spottail shiner, *Notropis hudsonius,* white sucker, *Catostomus commersonii*

INTRODUCTION

Tributary mouths are riverine ecotones which contribute to critical processes including material transport, ecosystem productivity, and wildlife population dynamics (Risser 1995; Ward and Wiens 2001). These strong gradients in habitat act as filters to dispersal, contributing to high variability of fish assemblages among rivermouths and along their connected waters (Czeglédi et al. 2016). In tributaries to the Great Lakes, the rivermouth gradient encompasses the lower reaches of the stream, the slower-flowing and semi-enclosed mouth area, and the adjacent nearshore habitat, including coastal wetlands (Larson et al. 2013). These habitats serve as refuges and high-quality foraging opportunities for many species, which influences the structure and function of coastal communities (Clark 1979; Jude and Pappas 1992; Larson et al. 2013).

The rivermouth transitional system contains optimal spawning and nursery habitats for many fish species (Goodyear et al. 1982; Mansfield 1984; Brazner and Beals 1997). The majority of Great Lakes fish species use rivermouths for part of their life cycle, including recreationally-important native fish species such as northern pike (*Esox lucius* Linnaeus, 1758), walleye (*Sander vitreus* (Mitchill, 1818)), and yellow perch (*Perca flavescens* (Mitchill 1814)) (Jude and Pappas 1992; Brazner et al. 2000; Sierszen et al. 2012). While the value of coastal wetlands in supporting fisheries is well-recognized (Wei et al. 2004; Sierszen et al. 2012), the influence of small tributaries on spawning and recruitment success may be overlooked (Mansfield 1984; Salas and Snyder 2010). For example, Höök et al. (2008) found that warmer water in Lake Michigan tributary mouths triggered earlier spawning and promoted higher growth

rates in young alewives (*Alosa pseudoharengus* (Wilson, 1811)) relative to those in colder nearshore areas.

Nearly all of Green Bay's tributaries harbor potential spawning areas for migratory fish including *E. lucius*, *P. flavescens, S. vitreus*, and lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) (Brazner 1997; Elliot and Gunderman 2004); however, little is known of the extent of fish assemblages' use of small tributary mouths in Green Bay. Most fisheries research conducted in Green Bay to date pertained to sport fish ecology (e.g. Jensen et al. 1982; Lehrer-Brey and Kornis 2014; Donofrio et al. 2017; Dembkowski et al. 2018). Relationships between fish assemblages, habitat, and landscape disturbance have primarily been investigated in wetlands on the west shore of Green Bay (Brazner 1997; Brazner and Beals 1997). Recent work documented the contemporary fish assemblage of lower Green Bay with a focus on the littoral and pelagic zones (Harris et al. 2018). Thus, there is uncertainty surrounding the current fish assemblages that use small tributary mouths in Green Bay, especially across the full spatial extent of the bay.

The objective of this study is to describe spatial and temporal patterns in larval and adult fish assemblages of lower-order tributary mouths of Green Bay. Since these rivermouths differ in habitat features and hydrologic connectivity with Green Bay, we expect differences in larval and adult assemblage structure among tributaries. We predict latitudinal variation in species richness along the trophic gradient of Green Bay, with tributaries to the highly eutrophic lower bay containing the greatest number of species (Brazner 1997). We also predict that both larval and adult assemblages will vary in structure between sampling events. In the spring, presence of migratory adult fish may increase diversity and change assemblage structure. Temporal shifts in larval fish assemblages will reflect variation in species-specific spawning and hatching patterns,

with species richness increasing over the sampling period to a maximum in late June as species hatch then reside in tributary mouths during early life stages (e.g., Nash and Geffen 1991; O'Brien et al. 2019).

MATERIALS AND METHODS

Study site

Green Bay is the largest embayment of Lake Michigan, with a watershed that covers approximately 40,000 km^2 (Bertrand et al. 1976; Klump et al. 2018). Average water depth in the bay varies from 2 meters at the south end to 29 meters in the north, with an associated gradient from hypereutrophic to oligotrophic conditions driven by nutrient and sediment inputs from the Fox River (Harris et al. 1987; Sager and Richman 1991; Althouse et al. 2014). Tributaries to Green Bay vary dramatically in size, from four large rivers (the Fox, Oconto, Peshtigo and Menominee Rivers) to a multitude of wadable streams (Dembkowski et al. 2018). During two survey efforts, we sampled ten small tributaries with watershed areas between 26.5 km^2 (Turtle Creek) and 79.0 km^2 (May Creek, Figure 1).

Fish assemblage surveys

Larval fish were collected in six lower-order tributaries with direct connection to Green Bay: Kirchner Creek, Mahon Creek, Red River, Sugar Creek, Turtle Creek, and Wequiock Creek (Figure 1). Four quatrefoil light traps (Secor et al. 1992) were set overnight in shallow water (≤1 m) in representative habitats of the rivermouth gradient. Chemical light sticks in the central chamber of each trap supplied a green light lure, and light traps fished for approximately twelve hours. Sampling occurred during five biweekly events in 2017. Event 1 occurred on May 3-11, event 2 occurred on May 15-22, event 3 occurred on May 23-30, event 4 occurred on June 1-7,

and event 5 occurred on June 19-27. Each tributary was sampled once per sampling event, except where site access was not obtained (Kirchner and Wequiock Creeks were not sampled during event 1) or sampling was repeated due to unusually low catch rates (Kirchner and Turtle Creeks were sampled twice in event 4). Captured fish larvae were anesthetized using eugenol and preserved in ethanol before identification to species (Auer 1982). Larval fish that were unidentifiable to species and juvenile fish according to size classes defined in Auer (1982) were removed from analysis (2.65% and 6.4% of total, respectively). Total length was recorded at the time of identification for 540 of 1 202 larvae, and for 83 juvenile fish captured.

Adult fish were captured in ten lower-order tributaries also directly connected to Green Bay: Big Creek, Kirchner Creek, Little River, Mahon Creek, May Creek, Red River, Samuelson's Creek, Sugar Creek, University Creek, and Wequiock Creek (Figure 1). Focal tributaries were sampled once during each of three seasonal sampling events in June 2014 ("summer"), September 2014 ("fall"), and March to April 2015 ("spring"). Modified fyke nets (4.8 mm mesh, box frame dimensions 1.2 x 1 m or 1 x 0.5 m depending on water depth) were deployed in the mouth of each tributary where water velocity and stream gradient diminished from the main channel up to the confluence with Green Bay. Two adjacent nets were deployed overnight, with one facing upstream and another facing downstream, to capture bidirectional fish movement (Brady et al. 2007). All fish collected were identified to species and measured for total length.

Animals were cared for in accordance with guidelines of the *Guide for the Care and Use of Laboratory Animals* (National Research Council 2011) and *Guidelines for the Use of Fishes in Research* (American Fisheries Society 2014). This research was conducted according to State of

Wisconsin Scientific Collectors Permits awarded to P.S. Forsythe and reviewed and approved by the University of Wisconsin Green Bay Institutional Animal Use and Care Committee.

Data analysis

All fish captured in the set of traps deployed at a tributary mouth during a single sampling event were pooled into one sample. Species commonly pursued by commercial and recreational fishers are referred to as "targeted" species. All other species of native and introduced fishes are designated as "non-targeted" (Table 1, Table 2, Table 3). Species richness was the total number of species observed in a sample. Catch per unit effort (CPUE) was calculated for each species as number of individuals divided by total hours that the group of light traps of fyke nets fished overnight at a tributary. Differences in species richness and CPUE among events and tributaries were analyzed separately for larval and adult fish assemblages; univariate tests were run using either event or tributary as a factor due to limited sample size. Welch's one-way ANOVAs were used to compare mean species richness among sampling events and tributaries, with species counts square root-transformed to meet assumptions of normality of residuals. Variation in cumulative CPUE among sampling events and tributaries was tested using a Kruskal-Wallis test on log-transformed CPUE of adult fish among seasons, and Welch's one-way ANOVA was used to identify differences in CPUE of adult fish among tributaries and differences in CPUE of larval fish among tributaries and events. Pearson correlations between species richness and latitude or longitude were used to identify spatial gradients.

Adult fish which undergo spawning migrations were classified according to David (2019) (Table 3). Differences in mean relative abundance of adult migratory fish among tributaries and

147 sampling events were identified using Welch's one-way ANOVA. Welch's one-way ANOVA
148 followed by a Games-Howell test were used to compare larval and juvenile white sucker
149 (*Catostomus commersonii* (Lacepède, 1803)) and *P. flavescens* total lengths among sampling
150 events to illustrate differences in length distributions and relative abundance over the sampling
151 season between two species of contrasting life history strategy. Since *P. flavescens* spawn in the
152 pelagic zone while *C. commersonii* use the nearshore or tributary habitats, these species are
153 subjected to different environmental conditions during early life stages that affect timing of hatch
154 and arrival in the tributary mouth (Childress et al. 2016; Froese and Pauly 2019).

155 Principal coordinates analysis (PCoA) was used to visualize differences in assemblages,
156 as distances are preserved accurately in ordination space (Gower 2005). PCoA was based on
157 Bray-Curtis matrices of CPUE for each sample, including rare species. A permutational
158 multivariate ANOVA (PERMANOVA) was used to identify differences in fish assemblage
159 structure between streams and sampling events (Anderson 2001). Adult and larval assemblages
160 were analyzed separately, with two single-factor models run for stream and sampling event.
161 PERMANOVA with 5,000 permutations was conducted on Bray-Curtis dissimilarity matrices of
162 CPUE of each species, and multivariate dispersion was examined for each factor. Similarity
163 percentage analysis (SIMPER) was used to quantify species contributions to dissimilarity among
164 streams and sampling events (Clarke 1993).

165 Procrustean Rotation Analysis (PRA) was used to test for a spatial effect on adult and
166 larval assemblage structures. For each life stage, PRA was used to superimpose the first two axis
167 scores from PCoA on the geographic coordinates of the sampling location, using rotating and
168 scaling to find the best fit between these two ordinations (Peres-Neto and Jackson 2001). ProTest

was used to determine statistical significance of the Procrustean fit through random permutation, where a significant result indicates that variation in geographic coordinates corresponds to the variation in fish assemblages in ordination space (Jackson 1995). Data was analyzed in R version 3.5.3 (R Core Team 2019) using the 'vegan' package (Oksanen et al. 2018) for PERMANOVA, SIMPER, and PRA, and 'userfriendlyscience' package for Games-Howell test (Peters 2018). Assumptions of all statistical analyses were met unless otherwise noted, and significance was assumed at $p<0.05$. Data are reported as mean ± standard deviation.

RESULTS

Larval fish assemblages

Over five sampling events, 1 202 larval fish and 83 juvenile fish were captured in six small tributaries. A total of fourteen species from seven families were encountered, with nine species captured in the larval stage and nine species captured in the juvenile stage (Table 1, Table 2). Species richness of larval assemblages was between one and six species per stream (Figure 2). The most abundant species were *C. commersonii* (32.1%), spottail shiner (*Notropis hudsonius* (Clinton, 1824)) (26.3%), and common carp (*Cyprinus carpio* Linnaeus, 1758) (23.9%), which accounted for the majority of the individuals captured (Table 1). Larvae of several species known to spawn in nearshore areas were collected in tributary mouths, including round goby (*Neogobius melanostomus* (Pallas, 1814)), *C. carpio*, and *P. flavescens* (Froese and Pauly 2019). The only targeted species captured was *P. flavescens*, which occurred in Kirchner Creek, Mahon Creek, Red River, Turtle Creek, and Wequiock Creek at the larval or juvenile stage. Nonnative species *C. carpio* and *N. melanostomus* comprised 27.3% of total CPUE.

High variability in species richness and CPUE of larval fish assemblages was evident. Total species richness summed across focal tributaries increased over time, with a maximum observed during event 4. However, median species richness did not vary significantly between events (Kruskal-Wallis test: $H_{[5]}$=2.71, p=0.745). Median species richness also did not vary significantly between tributaries over the six events (Kruskal-Wallis test: $H_{[4]}$=5.814, p=0.214), but varied from one species (Sugar Creek) and six species (Wequiock Creek). Similar patterns were observed in median CPUE, which varied extremely between samples but did not differ significantly between tributaries (Kruskal-Wallis test: $H_{[5]}$=3.742, p=0.587) or events (Kruskal-Wallis test: $H_{[4]}$=5.464, p=0.243). Average total CPUE was highest in event 5 (12.4±16.7 ind./hr.), event 2 (3.79±6.62 ind./hr.), and event 4 (5.94±9.84 ind./hr.). During these events, large numbers of single species were observed in a subset of tributaries; for example, *C. commersonii* were captured at high rates in Sugar Creek and Wequiock Creek in event 2 (Figure 2). Larvae were captured at the highest rate in tributaries on the southeast shore of Green Bay, where Red River (6.70±12.1 ind./hr.), Mahon Creek (6.59±13.9 ind./hr.) and Wequiock Creek (5.96±7.69 ind./hr.) had the highest average total CPUE.

Temporal trends in mean length and capture rate differed between two species of interest (Figure 3). *C. commersonii* were encountered during all five sampling events, and at least once in every tributary; mean total length differed significantly between events (Welch's one-way ANOVA: $F_{[4,218]}$=136, p<0.001). *C. commersonii* larvae captured in event 3 (10.6±3.15 mm) were smaller on average than those captured in events 1, 2, 4, and 5 (Games-Howell test: $t_{[19.29]}$=5.86, $t_{[14.75]}$=3.11, $t_{[22.82]}$=7.05, $t_{[26.97]}$=11.64; all p<0.05). Average length in event 2 (13.3±2.08 mm) was smaller than in events 1, 4, and 5 (Games-Howell test: $t_{[9.86]}$=5.59,

$t_{[117.31]}$=7.80, and $t_{[21.43]}$=11.19; all p<0.002). Significantly larger fish (37.4±10.0 mm), including many juveniles, were captured in event 5 compared to the previous four events (Games-Howell test: $t_{[23.13]}$=9.58, $t_{[21.43]}$=11.19, $t_{[26.97]}$=1.64, $t_{[23.23]}$=9.07; all p<0.001). *P. flavescens* were captured at the larval and juvenile stages during event 4 (14.8±2.43 mm) and as juveniles in event 5 (30.1±2.63 mm), with significantly larger fish captured in event 5 than event 4 (Welch's one-way ANOVA: $F_{[1,85]}$=425.5, p<0.001).

Stream assemblages were indistinguishable, but distinct clusters of assemblages are apparent among sampling events (Figure 4, Figure 5). Larval fish assemblages differed significantly among events (PERMANOVA: $F_{[4,14]}$=1.931, p=0.004) but did not differ among streams (PERMANOVA: $F_{[5,13]}$=0.952, p=0.546). A few key species drove the observed differences among events. Variation in CPUE of *C. commersonii* explained the greatest proportion of dissimilarity between events 1 and 2 (69.7±34.6%), 1 and 3 (39.1±22.9%), 1 and 4 (32.9±28.3%), 2 and 3 (67.1±27.5%), 2 and 4 (41.1±30.4%), 2 and 5 (37.5±32.4%), and 3 and 4 (31.6±25.2%). Capture of large numbers of *C. carpio* in event 4 explained a moderate proportion of the differences in assemblage structure between event 4 and event 1 (20.9±32.9%), event 2 (16.4±28.3%), event 3 (20.4±31.6%), and event 5 (17.1±23.4%). There was no significant spatial gradient in assemblage structures (ProTest: Procrustes sum of squares=0.939, p=0.539).

Adult fish assemblages

A total of 5 509 fish were caught over three sampling seasons, representing 44 species in 17 families. The observed variation in total lengths indicates use of rivermouths by both adults and juveniles of many species (Table 3). Family Cyprinidae was most abundant and was represented by the greatest number of species (Table 3). The most abundant species across all 10

tributaries was *N. hudsonius* (66.2% of total catch), due to capture of a school of 3 085 fish in Mahon Creek in summer 2014, when the highest CPUE was observed (131.29 ind./hr.). The majority of adult fish captured belonged to 31 non-targeted species (90.2%; Table 3). Thirteen targeted species constituted only 9.8% of the individuals captured by fyke net, but a targeted species was the most abundant in five of the ten tributaries' assemblages. With the Mahon Creek outlier removed, CPUE of assemblages did not differ between seasons (Kruskal-Wallis test: $H_{[2]}$=3.388, p=0.184) or between streams (Welch's one-way ANOVA: $F_{[9,19]}$=1.29, p=0.304).

Species richness of these assemblages varied; in fall 2014, only one species was observed in May Creek while 16 species were documented in Mahon Creek (Figure 6). Mean species richness did not differ significantly between tributaries (Welch's one-way ANOVA: $F_{[9,20]}$=1.76, p=0.139) or between seasons (Welch's one-way ANOVA: $F_{[2,27]}$=1.32, p=0.284). There were no associations between species richness and latitude or longitude (Pearson correlation coefficient: r= -0.032, p=0.895; r=0.246, p=0.311, respectively).

Migratory species were common (68.7±31.6%) and accounted for most of the catch in 9 of 30 samples (Table 3). Mean proportion of migratory fish did not differ between tributaries (Welch's one-way ANOVA: $F_{[9,20]}$=1.26, p=0.315), but varied significantly between some seasons (Welch's one-way ANOVA: $F_{[2,27]}$=4.02, p=0.030). A greater proportion of migratory fish were collected in spring (84.4±25.1%) than in fall (51.1±35.2%; Games-Howell test: $t_{[17.35]}$=2.71, p=0.037). Presence of migratory fish in summer was not significantly different than presence in spring (Games-Howell test: $t_{[17.22]}$=1.62, p=0.262) or fall (Games-Howell test: $t_{[17.99]}$=1.24, p=0.448). Spring adult fish assemblages contained targeted species undergoing spawning migrations including *E. lucius*, *P. flavescens*, and *S. vitreus* (Figure 6).

Fish assemblages were more strongly clustered by tributary than by sampling event (Figure 7, Figure 8). Sampling season had no influence on fish assemblage structure (PERMANOVA: $F_{[2,27]}$=1.260, p=0.113). Adult fish assemblages differed significantly between at least two tributaries (PERMANOVA: $F_{[9,20]}$=1.230, p=0.039), but was confounded by potential violation of the assumptions of equal multivariate dispersion among tributaries. This assumption appeared met by statistical tests (ANOVA: $F_{[9,20]}$=0.1919, p=0.993), but was suspect based on visual examination of the data. PRA followed by ProTest indicated an effect of geographic location on assemblage structure (Procrustes sum of squares=0.893, p=0.006). For example, Big Creek and Samuelson's Creek are neighbors in ordination space and in Green Bay (Figure 1, Figure 7). These two tributaries to Sturgeon Bay both contained rainbow trout (*Oncorhynchus mykiss* (Walbaum 1792)), *N. melanostomus*, bowfin (*Amia calva* Linnaeus, 1766) and rock bass (*Ambloplites rupestris* (Rafinesque, 1817)), which were rarely captured in other focal tributaries. Most tributaries along the southeast shore of the bay, including Mahon Creek, Red River and Wequiock Creek, were similar in assemblage structure (Figure 7). However, Sugar Creek has a distinct fish assemblage from Red River, its closest neighbor, and is more like University Creek on the opposing shore (Figure 1). Both Sugar and University Creek contained banded killifish (*Fundulus diaphanus* (Lesueur 1817)), bluegill (*Lepomis macrochirus* Rafinesque, 1810*),* and northern redbelly dace (*Chrosomus eos* Cope, 1861), which were relatively rare in this survey (Table 3).

DISCUSSION

While species richness varied widely at individual streams during a sampling event, the cumulative species richness across all small tributary mouths in Green Bay was high.

Considering larval, juvenile, and adult fish, we documented forty-five species using these tributaries during at least one life stage. Across all sampling efforts, an average of 8.28 species were observed using each tributary. Brazner (1997) documented a total of 47 species in coastal wetlands across the latitudinal gradient of Green Bay, with an average species richness of 21.4. We captured 37 of the 54 species of the contemporary fish assemblage of lower Green Bay in small tributary mouths (Harris et al. 2018). Diversity is likely higher than reported in this study, since the passive gear types used may lead to under-representation of rare, patchily distributed, or less-mobile species (Salas and Snyder 2010; Porreca et al. 2013; Francis et al. 2014; Wedderburn 2018). Species-level identification of larval fish is difficult, and species differ in catchability due to duration of the larval stage, microhabitat use, and degree of phototaxis (Trebitz et al. 2009; Pritt et al. 2014). While duration of ichthyoplankton sampling was shorter than in other studies from Great Lakes coastal habitats (e.g. Nash and Geffen 1991; Tanner et al. 2004; Tucker et al. 2019), we feel we have adequately captured trends in larval assemblages given the observed peak in species richness in June and July, followed by a decrease in CPUE in event 5. Later samples, which were not included in this analysis, showed strong decreases in CPUE and rapidly changing habitat conditions as water warmed and shell beds shifted, blocking several rivermouths.

Larval fish diversity and the relative abundance of non-native species are indicators of ecological integrity of nursery habitats, given the environmental requirements of many species during early life stages (Ramos et al. 2012; Mapes et al. 2015). Species richness of larval fish assemblages was relatively low in comparison to other coastal areas of the Great Lakes, given the high productivity of Green Bay. Embayments of relatively less-productive Lake Ontario had

larval assemblages of three to six species (Klumb et al. 2003), and embayments of northern Lake Huron contained between 9 and 12 taxa (Höök et al. 2001). Pentwater Marsh, a drowned river mouth wetland on the east shore of Lake Michigan, contained 18 taxa of larval fish dominated by green sunfish (*Lepomis cyanellus* Rafinesque, 1819), *C. carpio* and various cyprinid species (Chubb and Liston 1986). Despite collection of targeted and migratory species in tributary mouths during spawning periods, catch rates of these species were low at the larval stage, and two of the five most abundant species were non-native. Restoring habitat, prey availability and water quality in small tributary mouths may improve populations of targeted species, as larvae in tributary mouths can grow and develop faster more successfully than fish in harsher environments due to abundant food sources and habitat (Eadie and Keast 1984; Benson and Magnuson 1992; Oele et al. 2019).

Temporal variation in larval assemblages is shaped primarily by adult spawning behaviors (Miller 2002). For tributary-spawning fish such as *C. commersonii*, habitat quality and temperature regime within a stream contribute to variation in hatch timing and success (Childress et al. 2016). Total lengths of *C. commersonii* larvae were similar across the first four sampling events and showed variation in timing among tributaries, indicating that larvae originated from multiple hatching or spawning events. Pelagic-drifting larvae like *P. flavescens* exhibit stronger synchrony at lake- and basin-wide scales, driven by climatic trends at these larger spatial extents (Redman et al. 2011; Honsey et al. 2016). *P. flavescens* appeared to be coming from one open-bay population, as they formed two distinct, clustered size classes which increased in length over time. Larval and juvenile behaviors also play a role in timing of encounter at tributary mouths. *C. commersonii* drift passively into rivermouths from upstream during the larval stage, while *P.*

322 *flavescens* migrate from open water into shallow coastal areas including tributary mouths after
323 maturing for roughly 30 days (Corbett and Powles 1986; Post and McQueen 1988).
324 Lack of a spatial pattern in larval assemblages is surprising given the structural diversity
325 of focal tributaries but can be partly explained by the hydrology of Green Bay. Counterclockwise
326 water circulation in lower Green Bay is driven by prevailing southwest winds, rightward drift of
327 the Coriolis effect, and bathymetry of the bay (Miller and Saylor 1985; Lathrop et al. 1990).
328 Wind-driven seiche also causes significant tide-like fluctuations in water level within the Great
329 Lakes (Trebitz 2006). Water driven by currents and seiche can push larvae that hatch offshore
330 into tributary mouths, especially during passive larval drift (Höök et al. 2006). Many of the
331 species that were found in the highest abundance in our survey (*C. carpio*, *C. commersonii*) can
332 spawn in coastal or nearshore areas (Froese and Pauly 2019). Larval transport into these tributary
333 mouths appears to play a larger role in shaping ichthyoplankton assemblages than local spawning
334 and hatching in the rivermouth or upstream area.
335 Assemblage structure of adult fish varied among tributaries and along a spatial gradient,
336 likely due to local habitat structure (Smith and Simpkins 2018). The absence of a latitudinal
337 trend in species richness indicates the greater importance of tributary-scale variation in habitat
338 quality than the bay-wide gradient in trophic state (Smith and Magnuson 1990; Brazner 1997).
339 Lack of a seasonal effect on species richness and assemblage structure shows lack of significant
340 turnover in assemblages throughout the year and reinforces the importance of local habitat at
341 tributary mouths. Diverse habitats increase the variety of available resources, supporting more
342 diverse fish assemblages (Eadie and Keast 1984). For example, the cluster of fish assemblages in
343 Mahon Creek, Red River and Wequiock Creek may be driven partly by these streams' relatively

large, slow-moving mouths that include protected wetland areas.. However, results of this analysis should be interpreted with caution given relatively small sample size and potential violation of statistical assumptions, since in this case, PERMANOVA and SIMPER are sensitive to differences both between and within groups (Warton et al. 2012).

Three broad functional groups were encountered: migratory fish during spawning movements, predators foraging, and residents of the stream or river mouth, as described by Jude and Pappas (1992). Spawning migrations in fish are often cued by changing light and temperature regimes, with habitat availability influencing fish use of the stream (Jonsson 1991). Many of the fishes that use these streams during spawning events may also forage alongside fish from the nearshore zone. For example, *A. calva* migrate up tributaries to spawn during spring, but also make significant post-spawn movements around coastal habitats (Daniels 1993; Midwood et al. 2018). These foragers are driven by the relatively high availability of prey and suitable habitat in these productive areas (Jude and Pappas 1992; MacKenzie et al. 2004). Resident species assemblages are also structured by habitat quality in tributary mouths, including macrophyte cover and water quality, and are influenced by predator-prey dynamics (Sharma and Jackson 2007). This group includes species that favor either stream or coastal habitats and are likely making the smallest-scale movements around the stream, such as Iowa darter (*E. exile* (Girard 1859)) or black bullhead (*Ameiurus melas* (Rafinesque, 1820)) (Jude and Pappas 1992).

Though understudied, small tributary mouths serve an important role in the ecosystem of Green Bay. These coastal areas have been named “centers of organization” for the fish assemblage, as they have disproportionately high contributions to spawning, rearing, and foraging compared to their relatively small spatial extent (Steedman and Regier 1987). We

366 observed fish assemblages that were dynamic over time and among adjacent tributaries,
367 however, these tributary mouths are vulnerable to anthropogenic degradation and invasive
368 species (Poe et al. 1986; Brazer 1997; Trebitz et al. 2009). Small tributary mouths, including
369 those in this study, should be recognized as a key component of Great Lakes ecosystems and a
370 valuable opportunity for restoration of critical spawning and nursery habitats for diverse fish
371 species.

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664 **FIGURE CAPTIONS**

665 Fig. 1 (a) Location of the 10 lower order tributaries of Green Bay from which fish assemblage
666 data using fyke nets were collected during summer and fall 2014 and spring 2015:
667 University Creek (UNC); Little River (LIR); Kirchner Creek (KIC); Mahon Creek
668 (MHC); Wequiock Creek (WEC); Red River (RER); Sugar Creek (SUC); May Creek
669 (MYC); Samuelson's Creek (SAC); and Big Creek (BIC). Tributaries demarcated with an
670 asterisk were also sampled using light traps to collect juvenile fish in 2017. Turtle Creek
671 (TUC) was only sampled by light trapping. Figure was created in ArcMap version 10.6.1
672 using shapefiles from the Wisconsin Department of Natural Resources (2018, 2019). (b)
673 Aerial images of the mouths of SUC, RER, and MHC where sampling occurred.

674 Fig. 2 CPUE of larval fishes captured in quatrefoil light traps over five sampling events in Green
675 Bay rivermouths (Figure 1). Larval fishes from multiple light traps set overnight in
676 representative habitats were pooled into one composite sample for each tributary. For
677 tributary abbreviations, see Figure 1.

678 Fig. 3 Larval and juvenile (a) white sucker (*Catostomus commersonii* (Lacepède, 1803)) and (b)
679 yellow perch (*Perca flavescens* (Mitchill 1814)) total length distributions across sampling
680 events in Green Bay rivermouths. Gray lines indicate the division between larval and
681 juvenile fish lengths (Auer, 1982). (c) *Catostomus commersonii* and (d) *P. flavescens*
682 CPUE during each event.

683 Fig. 4 Principal coordinates analysis of larval fish assemblages of small tributary mouths over
684 five sampling events with percentage of variation explained indicated for each axis.
685 CPUE for nine species was compared using Bray-Curtis distance matrices, with ellipses

686 of 1 standard error around centroids for each tributary. Tributaries did not differ
687 significantly in assemblage structure. For tributary abbreviations, see Figure 1.
688 Fig. 5 Principal coordinates analysis of larval fish assemblages of six small tributary mouths,
689 grouped by biweekly sampling event with percentage of variation explained indicated for
690 each axis. CPUE for nine species was compared using Bray-Curtis distance matrices. The
691 centroid for each event is labeled within an ellipse of 1 standard error, except where
692 sample size was insufficient for event 1. Assemblage structure differed significantly
693 between at least two events. For tributary abbreviations, see Figure 1.
694 Fig. 6 CPUE of adult fish captured using fyke nets during three standardized seasonal samples at
695 ten rivermouths in Green Bay (Fig. 1). For tributary abbreviations, see Figure 1.
696 Fig. 7 Principal coordinates analysis of adult fish assemblages of ten small tributaries over three
697 sampling events with percentage of variation explained indicated for each axis. Bray-
698 Curtis distance was used to compare catch per unit effort, with ellipses of 1 standard error
699 around centroids for each tributary. There were significant differences in assemblage
700 structure between at least two tributaries. For tributary abbreviations, see Figure 1.
701 Fig. 8 Principal coordinates ordination of adult fish assemblages during three seasonal sampling
702 events at ten small tributaries with percentage of variation explained indicated for each
703 axis. Bray-Curtis distance was used to compare catch per unit effort, with ellipses of 1
704 standard error around centroids for each sampling event. There were no significant
705 differences in assemblage structure between seasons.

TABLE 1 Larval fish collected using light traps in six tributaries over five sampling events, with introduced species represented by bold text.

Family	Species	Total catch (*n*)	Length range (mm)	Event	Targeted
Catostomidae	White sucker (*Catostomus commersonii*)	393	5-22	1-5	
Clupeidae	Gizzard shad (*Dorosoma cepedianum*)	14	18-20	5	
Cyprinidae	**Common carp (*Cyprinus carpio*)**	308	4-14	4, 5	
	Emerald shiner (*Notropis atherinoides*)	18	-	3	
	Spottail shiner (*Notropis hudsonius*)	337	6-16	4, 5	
	Bluntnose minnow (*Pimephales notatus*)	8	5	4	
	Fathead minnow (*Pimephales promelas*)	3	4.9-6.3	4	
Gobiidae	**Round goby (*Neogobius melanostomus*)**	48	6-10	5	
Percidae	Yellow perch (*Perca flavescens*)	73	10-20	4	X

TABLE 2 Juvenile fish collected using light traps in six tributaries over five sampling events.

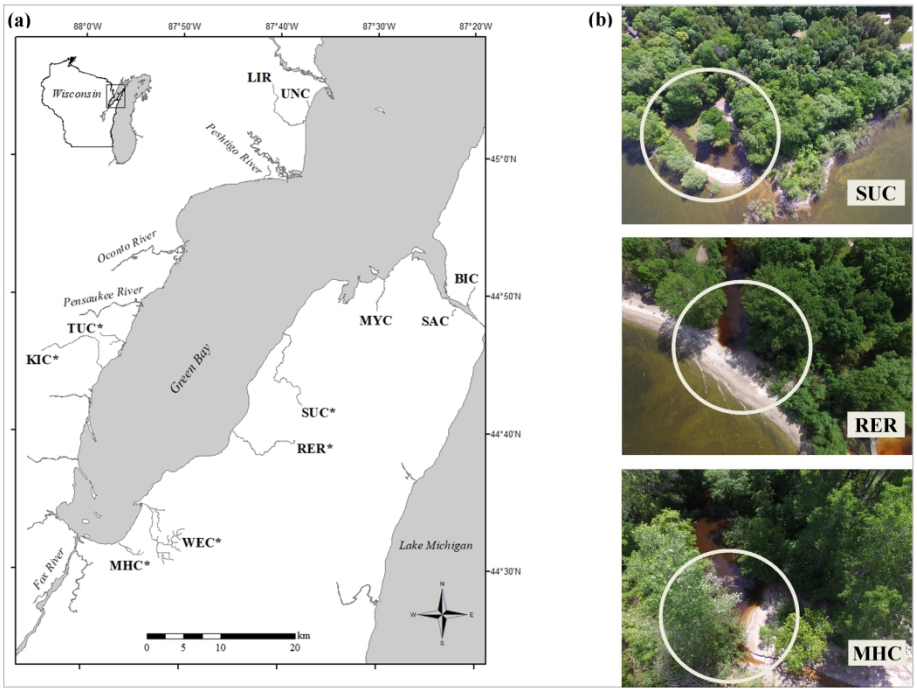
Family	Species	Total catch (*n*)	Length range (mm)	Event	Targeted
Catostomidae	White sucker (*Catostomus commersonii*)	19	32-46	5	
Centrarchidae	Bluegill (*Lepomis macrochirus*)	2	13-15	5	X
Clupeidae	Gizzard shad (*Dorosoma cepedianum*)	42	21-25	5	
Cyprinidae	Common shiner (*Luxilus cornutus*)	2	52-57	4	
	Spottail shiner (*Notropis hudsonius*)	1	20	5	
Esocidae	Northern pike (*Esox lucius*)	1	48	4	X
Percidae	Iowa darter (*Etheostoma exile*)	1	29	5	
	White bass (*Morone chrysops*)	1	21	5	X
	Yellow perch (*Perca flavescens*)	14	20-36	4, 5	X

TABLE 3 Fish species captured by fyke nets over three sampling seasons in ten tributaries, with introduced species represented by bold text and migratory species designated by David et al. (2015).

Family	Species	Total catch (*n*)	Length range (mm)	Season	Targeted	Migratory
Amiidae	Bowfin *(Amia calva)*	28	169-599	Summer, Fall		X
Catostomidae	White sucker *(Catostomus commersonii)*	310	27-486	Spring, Summer, Fall		X
	Bigmouth buffalo *(Ictiobus niger)*	1	32	Summer		X
Centrarchidae	Rock bass *(Ambloplites rupestris)*	17	54-235	Spring, Summer, Fall	X	
	Green sunfish *(Lepomis cyanellus)*	177	24-122	Summer, Fall	X	
	Pumpkinseed *(Lepomis gibbosus)*	17	37-141	Summer, Fall	X	
	Bluegill *(Lepomis macrochirus)*	9	64-160	Summer, Fall	X	
	Smallmouth bass *(Micropterus dolomieu)*	5	33-570	Summer, Fall	X	X
	White crappie *(Pomoxis annularis)*	22	64-81	Fall	X	
	Black crappie *(Pomoxis nigromaculatus)*	45	51-108	Fall	X	
Clupeidae	Alewife *(Alosa pseudoharengus)*	15	100-179	Summer		
	Gizzard shad *(Dorosoma cepedianum)*	21	30-442	Spring, Fall		
Cyprinidae	Northern redbelly dace *(Chrosomus eos)*	2	44-59	Spring		
	Common carp *(Cyprinus carpio)*	28	79-720	Spring, Summer, Fall		X
	Common shiner *(Luxilus cornutus)*	102	45-185	Spring, Summer, Fall		X
	Golden shiner *(Notemigonus crysoleucas)*	13	70-135	Fall		
	Emerald shiner *(Notropis atherinoides)*	298	26-112	Spring, Summer, Fall		X
	Spottail shiner *(Notropis hudsonius)*	3649	27-146	Spring, Summer		X

	Bluntnose minnow *(Pimephales notatus)*	111	27-87	Spring, Summer, Fall		
	Fathead minnow *(Pimephales promelas)*	26	32-76	Spring, Summer, Fall		
	Longnose dace *(Rhinichthys cataractae)*	1	90	Fall		X
	Creek chub *(Semotilus atromaculatus)*	26	37-167	Spring, Summer, Fall		
Esocidae	Northern pike *(Esox lucius)*	83	57-917	Spring, Summer, Fall	X	X
	Muskellunge *(Esox masquinongy)*	2	1180-1285	Spring	X	X
Fundulidae	Banded killifish *(Fundulus diaphanus)*	11	47-69	Spring, Summer, Fall		
Gasterosteidae	Brook stickleback *(Culaea inconstans)*	39	23-97	Spring, Summer		
Gobiidae	**Round goby *(Neogobius melanostomus)***	86	27-96	Spring, Summer, Fall		X
Ictaluridae	Black bullhead *(Ameiurus melas)*	47	56-330	Spring, Summer, Fall		
	Yellow bullhead *(Ameiurus natalis)*	1	76	Fall		
	Brown bullhead *(Ameiurus nebulosus)*	31	39-219	Fall		
	Channel catfish *(Ictalurus punctatus)*	5	542-681	Summer, Fall		
Lepisosteidae	Longnose gar *(Lepisosteus osseus)*	1	646	Summer		X
	Shortnose gar *(Lepisosteus platostomus)*	10	485-658	Summer		X
Lotidae	Burbot *(Lota lota)*	3	90-143	Summer, Fall		X
Percidae	Iowa darter *(Etheostoma exile)*	1	41	Spring		
	Johnny darter *(Etheostoma nigrum)*	1	48	Spring		
	Yellow perch *(Perca flavescens)*	139	36-254	Spring, Summer, Fall	X	X
	Log perch *(Percina caprodes)*	36	60-481	Spring, Summer, Fall		X
	Walleye *(Sander vitreus)*	22	152-569	Spring, Summer, Fall	X	X

Percopsidae	Trout perch *(Percopsis omiscomaycus)*	17	85-145	Spring, Summer		X
Salmonidae	**Rainbow trout *(Oncorhynchus mykiss)***	3	134-454	Spring, Summer	X	X
	Lake trout *(Salvelinus namaycush)*	1	424	Summer	X	X
Sciaenidae	Freshwater drum *(Aplodinotus grunniens)*	2	61-112	Summer		X
Umbridae	Central mudminnow *(Umbra limi)*	45	28-113	Spring, Summer, Fall		



(a) Location of the 10 lower order tributaries of Green Bay from which fish assemblage data using fyke nets were collected during summer and fall 2014 and spring 2015: University Creek (UNC); Little River (LIR); Kirchner Creek (KIC); Mahon Creek (MHC); Wequiock Creek (WEC); Red River (RER); Sugar Creek (SUC); May Creek (MYC); Samuelson's Creek (SAC); and Big Creek (BIC). Tributaries demarcated with an asterisk were also sampled using light traps to collect juvenile fish in 2017. Turtle Creek (TUC) was only sampled by light trapping. Figure was created in ArcMap version 10.6.1 using shapefiles from the Wisconsin Department of Natural Resources (2018, 2019). (b) Aerial images of the mouths of SUC, RER, and MHC where sampling occurred.

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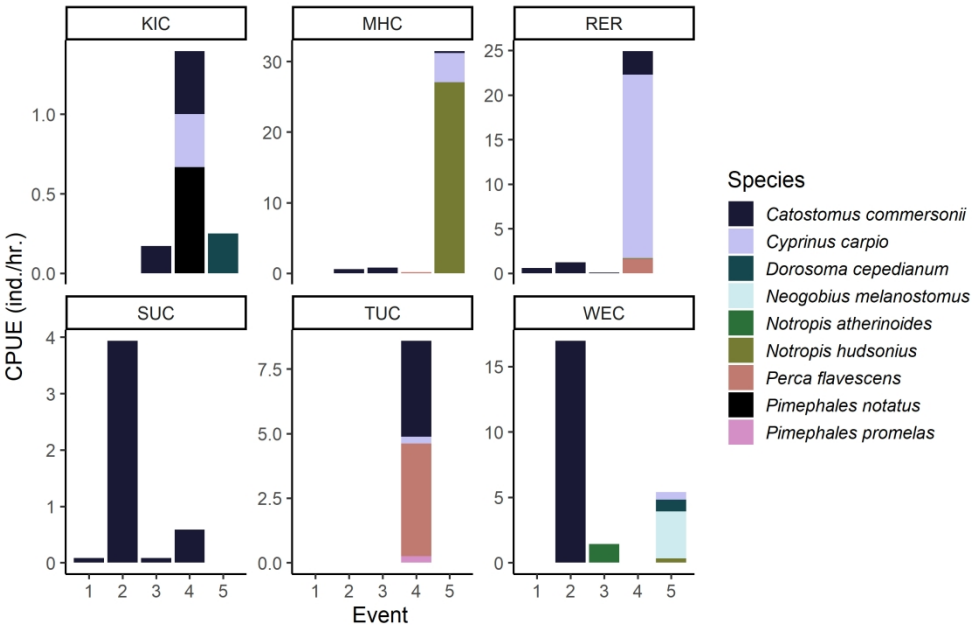

CPUE of larval fishes captured in quatrefoil light traps over five sampling events in Green Bay rivermouths (Figure 1). Larval fishes from multiple light traps set overnight in representative habitats were pooled into one composite sample for each tributary. For tributary abbreviations, see Figure 1.

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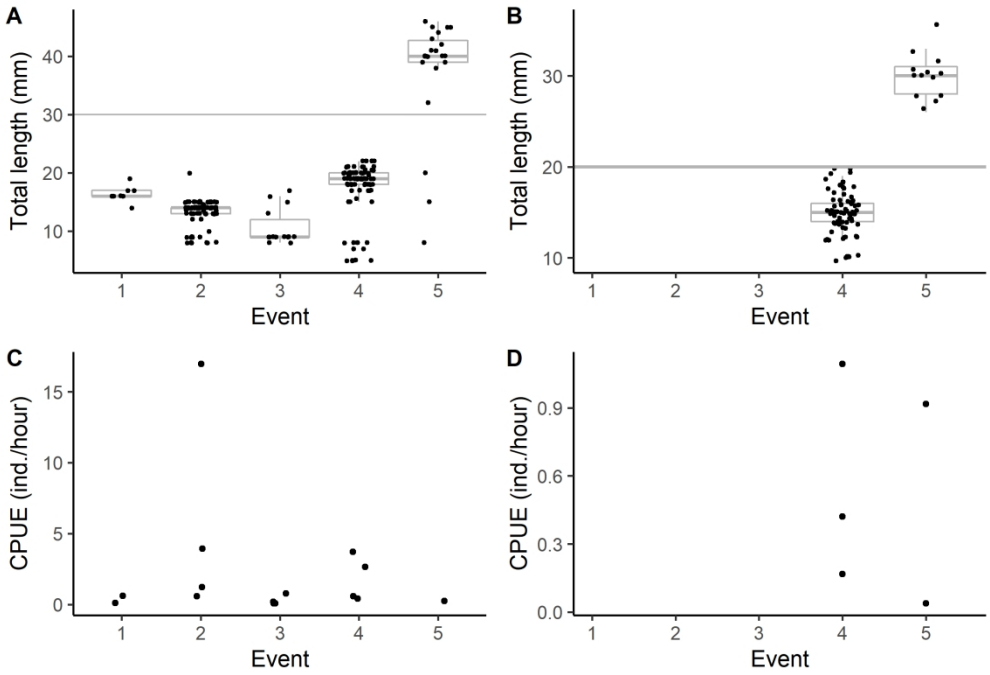

Larval and juvenile (a) white sucker (*Catostomus commersonii* (Lacepède, 1803)) and (b) yellow perch (*Perca flavescens* (Mitchill 1814)) total length distributions across sampling events in Green Bay rivermouths. Gray lines indicate the division between larval and juvenile fish lengths (Auer, 1982). (c) Catostomus commersonii and (d) P. flavescens CPUE during each event.

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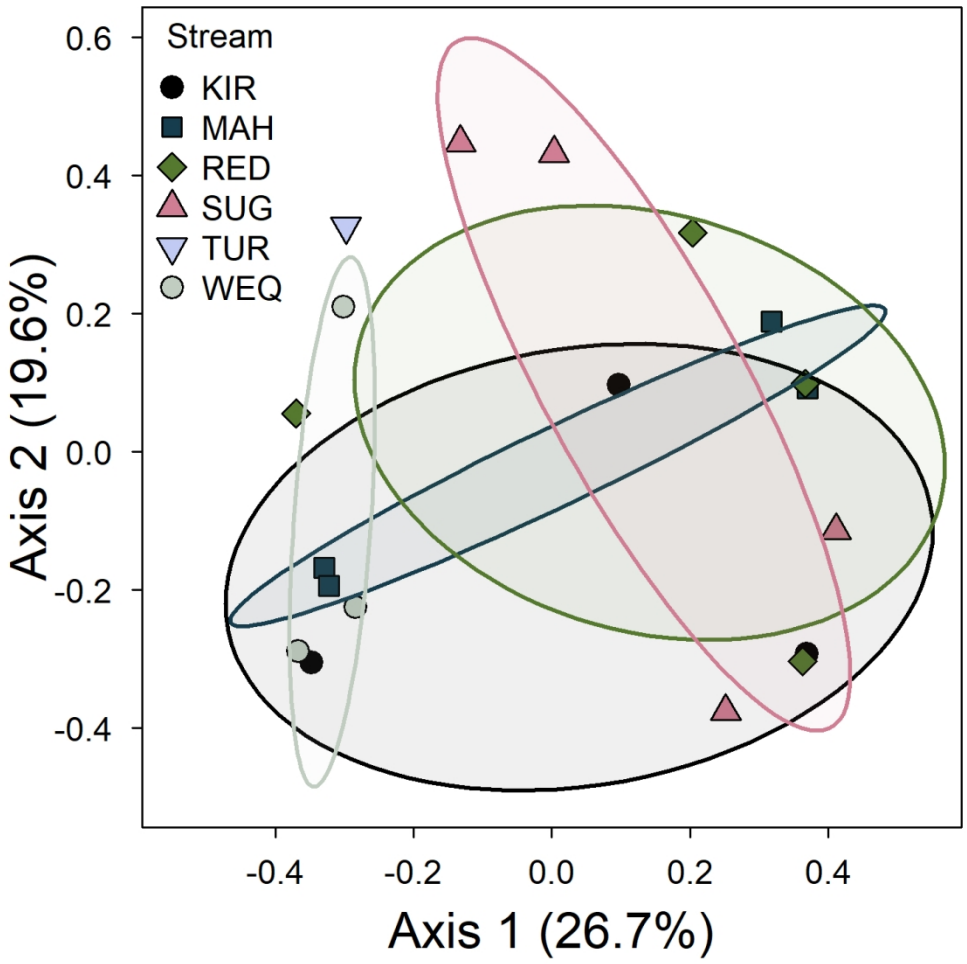

Principal coordinates analysis of larval fish assemblages of small tributary mouths over five sampling events with percentage of variation explained indicated for each axis. CPUE for nine species was compared using Bray-Curtis distance matrices, with ellipses of 1 standard error around centroids for each tributary. Tributaries did not differ significantly in assemblage structure. For tributary abbreviations, see Figure 1.

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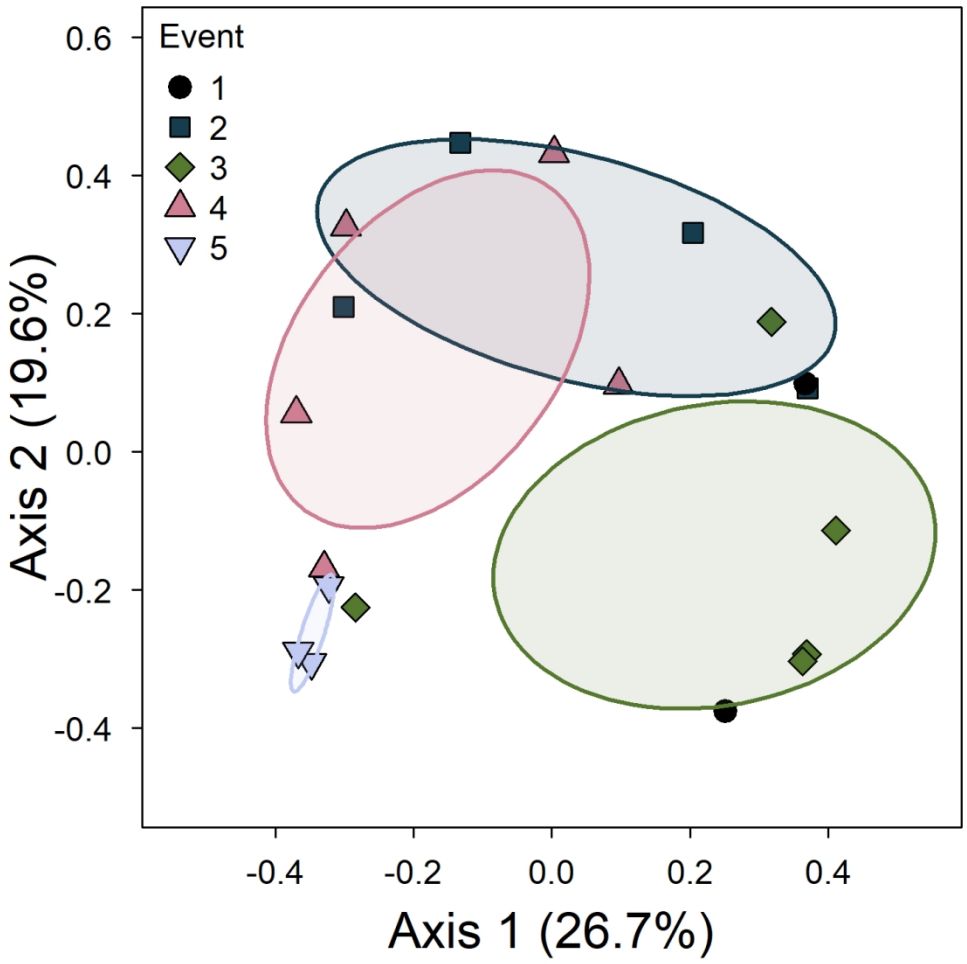

Principal coordinates analysis of larval fish assemblages of six small tributary mouths, grouped by biweekly sampling event with percentage of variation explained indicated for each axis. CPUE for nine species was compared using Bray-Curtis distance matrices. The centroid for each event is labeled within an ellipse of 1 standard error, except where sample size was insufficient for event 1. Assemblage structure differed significantly between at least two events. For tributary abbreviations, see Figure 1.

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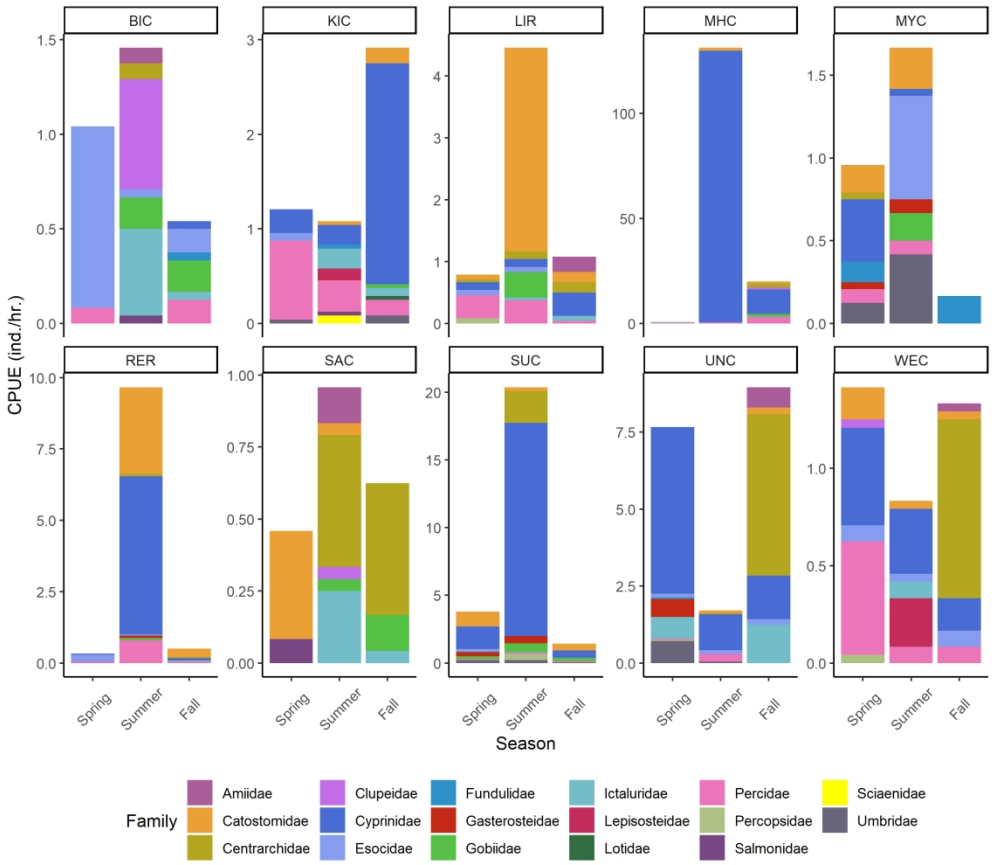

CPUE of adult fish captured using fyke nets during three standardized seasonal samples at ten rivermouths in Green Bay (Fig. 1). For tributary abbreviations, see Figure 1.

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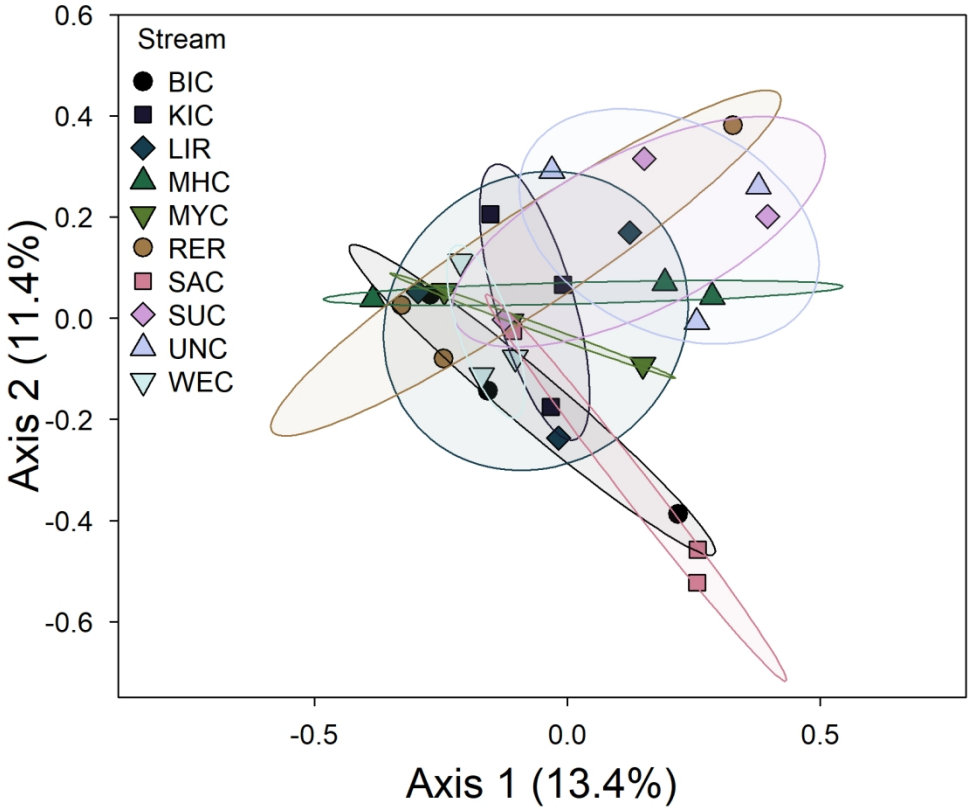

Principal coordinates analysis of adult fish assemblages of ten small tributaries over three sampling events with percentage of variation explained indicated for each axis. Bray-Curtis distance was used to compare catch per unit effort, with ellipses of 1 standard error around centroids for each tributary. There were significant differences in assemblage structure between at least two tributaries. For tributary abbreviations, see Figure 1.

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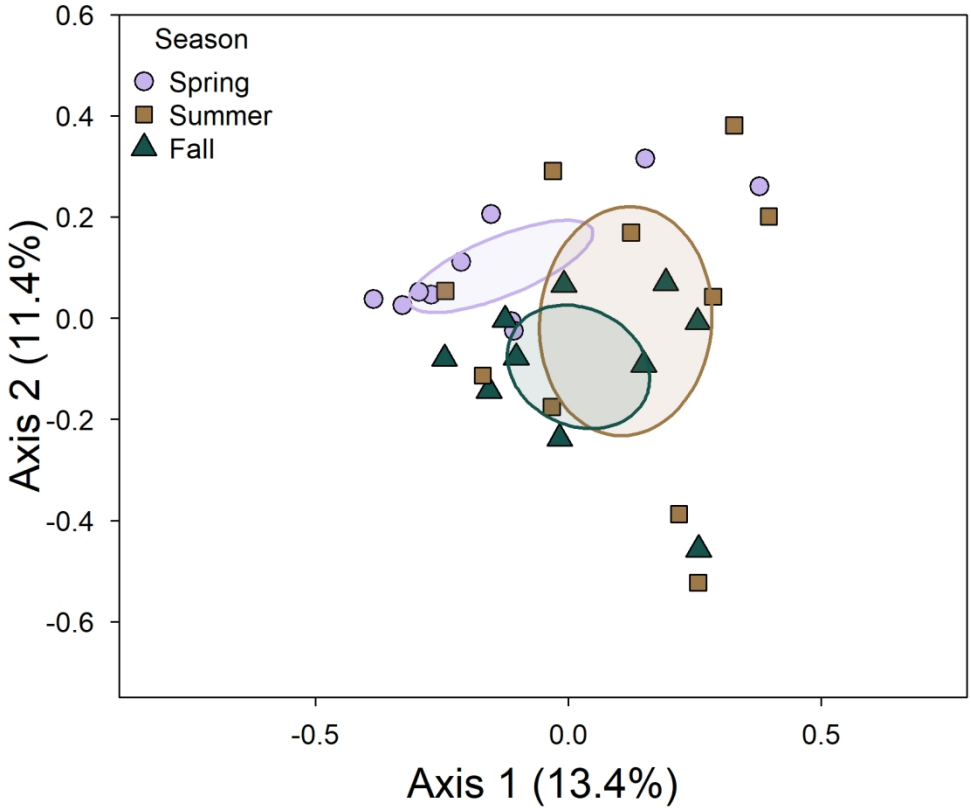

Principal coordinates ordination of adult fish assemblages during three seasonal sampling events at ten small tributaries with percentage of variation explained indicated for each axis. Bray-Curtis distance was used to compare catch per unit effort, with ellipses of 1 standard error around centroids for each sampling event. There were no significant differences in assemblage structure between seasons.

152x127mm (300 x 300 DPI)