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Title:

Influence of water-level variability on fish assemblage and natural reproduction following connectivity enhancement in a Typha dominated coastal wetland, USA

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Abstract:

We evaluated a wetland habitat modification strategy to contrast fish assemblage structure and the production of young-of-the-year (YOY) fish between different engineered habitats (i.e., spawning pool complexes and connectivity channels) relative to unmodified lateral channels in a large drowned river mouth tributary of the St. Lawrence River. Prior to habitat modifications, the coastal wetland was impaired by water level regulations, dominance of invasive hybrid cattail, *Typha* x *glauca*, that collectively replaced or created barriers to seasonally flooded spawning habitats important to fish. Connectivity enhancements provided fish access along a wetland habitat gradient from sedge-meadows to the deeper water robust emergent main-channel. Across an eight-year fish emigration dataset (2012, 2013, 2016-2021) more than 90% of all captured fish (N_{total} = 218,086 fish) were YOY and modified habitats outperformed the unmodified channels in total fish catch-per-unit-effort (CPUE) per year (both YOY and non-YOY). Spawning pool complexes had higher YOY species richness than unmodified channel habitats. Fish assemblage structure differed between the modified habitats, where connectivity channels and unmodified channels shared a more similar fish assemblage than spawning pool complexes. Modified habitats, however, supported warmer water and higher dissolved oxygen than the unmodified channels. Redundancy analysis and linear mixed-effect modeling with abiotic variables (hydrology, temperature and dissolved oxygen) showed significant effects on fish assemblage structure, species richness and CPUE of fish emigrating from the modified and unmodified habitats. Historic flooding in 2017 and 2019 was a primary driver of YOY fish production and fish assemblage structure, but also appeared associated with

near anoxic conditions systemwide. YOY fish for several species was inversely affected by floods at spawning pool complexes, however CPUE of YOY fish for these species appeared unaffected at the connectivity channels despite low dissolved oxygen. Diversified habitat structure (i.e., connectivity channels and spawning pool complexes) offers a management option to enhance habitat for fish that allowed compensatory effects on the capture of YOY fish of several species during floods. This multi-faceted outcome from the habitat modifications resulted in unique fish assemblages between the channelized and spawning pool habitat. A connectivity-based habitat enhancement strategy provides adaptability for an uncertain climatic and regulatory future for the Laurentian Great Lakes and St. Lawrence River.

Introduction:

Between Canada and the United States of America, water levels in the Laurentian Great Lakes typically follow an intra-annual pattern of rising water levels through the spring, peaking in mid-summer and declining into the winter (Farrell et al., 2010a). The period of rising water levels throughout the spring represents a spring flood pulse where spring flood waters inundate upslope or high-marsh habitats (Junk et al., 1989; Midwood and Chow-Fraser, 2012). Such hydrological patterns create natural disturbances where the timing, magnitude, and duration of water level fluctuations influence nearshore macrophyte assemblages (Keddy and Reznicek, 1986; Wilcox, 2004; Midwood and Chow-Fraser, 2012) and provides ephemeral connectivity pathways between littoral and upslope habitats (Bunn and Arthington, 2002; Carlson et al., 2016; Ward et al., 1999; Wilcox et al., 2008). Moreover, interactions between natural hydrology and geomorphology maintain the variety of coastal wetland types or hydro-geomorphic settings (Albert et al., 2005; Keough et al., 1999) that the majority of Laurentian Great Lakes fish use to complete life-history requirements (Jude and Pappas, 1992; Wie et al., 2004).

The magnitude and duration of the spring flood pulse in the Laurentian Great Lakes varies annually by Lake because of the combined effects of climatic variability and water level regulation. This would include the St. Lawrence River, the natural outlet of the Laurentian Great Lakes towards the Atlantic Ocean and ~21% of the world's surface freshwater, which became regulated following construction of the Robert-Moses Saunders Power Dam in 1959 (Farrell et al., 2010a; IJC, 2014). A consequence of regulated waters in the St. Lawrence River was the suppression of inter- and intra-annual hydrological variation relative to unregulated conditions (Farrell et al., 2010a; IJC, 2014). During regulated water levels, many coastal wetlands in the St. Lawrence River experienced significant increases in cover and density of the invasive cattail

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hybrid *Typha* x *glauca* (> 20 stems/m^2; Farrell et al., 2010a, Bansal et al., 2019), but its initial invasion is thought to be associated with an earlier period of land conversion and agricultural expansion (Rippke et al. 2010). The expanding *Typha* x *glauca* eventually created barriers to fish passage to lateral upslope habitats or completely replaced native sedge-meadow (*Carex* spp.) habitats used by spawning fish (Farrell, 2001; Farrell et al., 2010a; Wilcox and Bateman, 2018; Wilcox et al., 2008).

In response to degraded conditions and ecosystem function in coastal wetlands in the St. Lawrence River (Farrell et al., 2010a; Wilcox & Bateman, 2018; Wilcox et al., 2008), a multi-partner collaboration proposed to evaluate fish habitat enhancement strategies that modified the configuration of coastal wetlands impacted by *Typha* x *glauca* expansion (Massa and Farrell, 2020; Neveldine et al., 2019). The modifications were hypothesized to improve access to lateral upslope sedge-meadow habitats disconnected by *Typha* x *glauca* by excavating 'connectivity channels'. 'Spawning pool complexes' that created potholes of open-water spawning/nursery habitats were also excavated within monotypic stands of *Typha* x *glauca* (Massa and Farrell, 2020; Neveldine et al., 2019; Figure 1).

The modifications were engineered to accommodate the suppressed spring flood pulse prescribed for the St. Lawrence River (IJC, 2014; IJC, 2017) by maintaining littoral zonation and hydrological connectivity within the modified habitats (Humphries et al., 1999; Junk et al., 1986; King et al., 2003; Tockner, et al., 2000). Because the modified habitats differed in design (i.e., connectivity channels vs. spawning pool complexes), we contrasted fish assemblage structure between the two types of habitat modifications relative to unmodified reference channels. Modified habitats were predicted to function as suitable early-life habitats that were at least equitable in quality to unmodified reference habitats (Dionne et al., 1999; Massa and Farrell,

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2019; Moyer et al., 1995; Neveldine et al., 2019; Williams and Zelder, 1999). Evaluating the effectiveness of habitat enhancements in providing high quality fish habitat is essential to the future application of similar engineered habitats in the St. Lawrence River and Laurentian Great Lakes degraded by the spread of invasive emergent vegetation.

Finally, we tested the influence of hydrology, temperature and dissolved oxygen on species diversity and catch-per-unit-effort (CPUE) of young-of-the-year (YOY) and non-YOY fish captured emigrating from the modified and unmodified habitats over an eight-year period. Spawning behaviours and nursery habitat condition for many fish are adapted to natural hydrological patterns (Bunn and Arthington, 2002; Junk et al., 1989; Lytle and Poff, 2004; Poff et al., 1997). Across our eight-year dataset, water levels in the upper St. Lawrence experienced all time highs through the spring and summer of 2017 and 2019 (Carter and Steinschneider, 2018; Gronewald and Rood, 2019), and uncharacteristic lows in 2012, 2016 and 2021. Thus, evaluating relationships between hydrology and nearshore fish assemblage structure will help determine the functional sustainability and ecological resilience of engineered modifications as spawning and nursery habitats (Erwin, 2009; Peterson et al., 1998; Poff, 2018), and guide future water level regulation plans.

Methods

Study Site Description:

Our study focused on modified habitats excavated in French Creek, a drowned river mouth tributary in the Thousand Islands Region (Clayton, NY) of the upper St. Lawrence River (USLR) (Figure 1). Most of French Creek's watershed (930-ha) is administered as a 'wildlife management area' by the New York State Department of Environmental Conservation

(NYSDEC), but the sub-watershed includes agricultural land use (Massa and Farrell, 2020). The mainstem of French Creek (>12 km long) flows into French Bay that interfaces the USLR proper (Figure 1), and was a priority for habitat enhancement to promote northern pike (*Esox lucius*) YOY production (Massa and Farrell, 2020; Neveldine et al., 2019). Northern pike populations in the St. Lawrence River have demonstrated poor year-class strength (Smith et al., 2007), and inaccessibility to seasonally flooded habitats (e.g., sedge-meadows) caused by *Typha* x *glauca* expansion is believed to contribute to reduced recruitment (Farrell, 2001; Farrell et al., 2006)

Modifications/Enhancement

Connectivity channels were completed in French Creek with an aquatic excavator to reconnect the main stem of French Creek to lateral sedge-meadow habitats disconnected by *Typha* x *glauca* expansion (Massa and Farrell, 2020; Neveldine et al., 2019; Figure 1). The design of connectivity channels included slight meanders, with a channel width between one and two meters, and 0.5 m depth. The mechanical head of the aquatic excavator side-cased spoil into the riparian and floodplain zones of each connectivity channel, which allowed the newly exposed native seedbank to recolonize the habitat (Neveldine et al., 2019). When more than one connectivity channel reconnected the same patch of sedge-meadow habitat to the main stem of French Creek, the connecting channels were grouped into an ecological complex that were considered independent from other complexes (Figure 1). Between 2008 and 2010, three complexes of connectivity channels were installed at French Creek which renewed access to three sedge-meadow habitats (0.15, 0.32 and 0.85 Ha/sedge-meadow habitat; Neveldine et al., 2019).

In the winter of 2012, spawning pool complexes were installed at French Creek with an amphibious long-arm excavator. Spawning pool complexes consisted of a group of relatively

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small pools (mean (±SD): 0.04 ± 0.04 Ha/ individual spawning pool) interconnected by short

channels excavated within large monotypic stands of *Typha* x *glauca* (Figure 1). Spoil from the

excavated spawning pools was deposited as small mounds adjacent to pools (< 1.0-m height) on

the monodominant *Typha* x *glauca*. Depth of spawning pools approximated 0.5-m, and the

dimensions of channels that connected adjacent spawning pools were similar in depth and width

to the connectivity channels (Massa and Farrell, 2020; Neveldine et al. 2019). Groups of

interconnected spawning pools were considered an independent ecological complex when

movement between adjacent spawning pools did not require using the mainstem of French Creek

(Massa and Farrell, 2020; Neveldine et al., 2019; Figure 1). Spawning pool complexes were

made up of three to six individual spawning pools, and the number of outlets connecting a

spawning pool complex to the mainstem of French Creek varied between two and six. Seven

independent spawning pool complexes were installed in French Creek (Figure 1), but, between

one and five spawning pool complexes were surveyed for fish, a given year.

Lateral channels that resisted *Typha* x *glauca* expansion in French Creek represented

available unmodified habitat for fish (Neveldine et al., 2019; Massa and Farrell, 2020); were

considered reference habitats and termed unmodified channels (Keough et al., 1999; Neveldine

et al., 2019; Figure 1). The unmodified channels had similar wetted width and depth to the

connectivity channels and provided the primary natural connectivity to upslope sedge-meadow

habitats prior to excavating the modified habitats. In total, 11 unmodified channels were

surveyed over the study. Each year, between three and nine unmodified channels were surveyed

for an approximate 1:1 ratio of modified-to-unmodified habitats surveyed. The unmodified

channels were considered the best available secondary-lateral habitat for fish and provided an

internal standard within French Creek to evaluate differences in fish assemblages among habitat

types that was deemed more appropriate than using reference habitats outside the study site (Keough et al., 1999; Neveldine et al., 2019).

Fish Survey

Surveys for emigrating fish followed the same netting protocol described in Neveldine et al. (2019) and Massa and Farrell (2020). Emigration nets had three 60-cm diameter hoops connected with 2.54-cm throats. Mesh size of the net was 1.6-mm and the net opening attached to a panel 366-cm in length and 122-cm in height that was buoyed by floats and stretched with a lead core line. Three reinforcing rods were used to deploy the net at the channel outlet opening; two rods stretched the wings across the channel outlet opening and the third set the cod end downstream of the channel. Each net spanned the entire channel outlet opening to restrict the catch to out-migrating fish by blocking passage of immigrating fish into the channel. Nets were also set at approximately the same location within the channel outlet each year. For most years, emigration nets fished the entire water column of the outlet channel. In 2017 and 2019, when high water levels exceeded the 122 cm net height, nets were fished at mid-depth in the water column at approximately the same location from other years.

Emigration surveys started most years by mid-June, approximately two months after northern pike completed their tributary spawning run (e.g., by mid-April) as to not to interfere with northern pike spawning. Emigration nets were set between 12 and 31 days depending on the year. The longer surveys corresponded to the earliest years that habitats were netted (2012-2013) and became shorter when survey effort was optimized to encompass peak emigration of YOY northern pike (Massa and Farrell, 2020; Neveldine et al., 2019). Within years, consistent survey effort (i.e., net-nights) was used at each habitat-type complex.

Emigration nets were checked daily throughout the survey period, and all fish caught were identified to lowest taxonomic level, categorized by life-stage base on species length (YOY or non-YOY) and counted (Table 1). After processing, fish were released in the mainstem of French Creek to continue emigrating, and we assumed that released fish were not recaptured. Fish were never anesthetized because of a short handling time (<30 s). The care and use of experimental animals complied with New York State animal welfare laws, and all fieldwork was conducted under the scientific collectors permit NYSDEC-Scientific-#354 and the IACUC project approval #140202.

At each net check, water temperature (°C) and dissolved oxygen concentration (mg/L) were measured with a YSI ProODO® (Optical sensor) from the surface, mid-depth, and near the substrate of the water column. Temperature and dissolved oxygen were averaged among depth profile measurements to obtain representative daily estimates, which were then averaged over the survey period per year at each independent complex. Measurements for dissolved oxygen and temperature generally occurred between 0830 and 1200 each day.

Emigration surveys in French Creek occurred at all three habitat-types (i.e., connectivity channels, spawning pool complexes and unmodified channels) in 2012, 2013, and between 2016 and 2021. Connectivity channels were not surveyed in 2014 and 2015, and those years were excluded from the dataset. At minimum, each year included in the dataset had fish capture and environmental information from complexes of all three habitat-types; however, data from the 2012, 2013 and 2020 surveys were represented by a single spawning pool complex.

For each spawning pool complex surveyed, between two and four emigration net locations were randomly selected and nets were placed at the outlets connecting spawning pools to the mainstem of French Creek. The number of nets used per spawning pool complex was

proportional to the number of available outlets. In contrast, at connectivity channels and

unmodified channels, emigration nets covered all outlets. To account for fish that emigrated

through unnetted outlets at spawning pool complexes, we assumed that fish only used outlets for

movements and were equally distributed among all spawning pool outlets. The total number of

fish caught at a spawning pool complex for each year was divided by the number of outlets

netted. The quotient was multiplied by the total number of outlets available to be netted to

estimate the total abundance of fish emigrating from the entire spawning pool complex (Massa

and Farrell, 2020).

Habitat digitization

Orthoimagery of French Creek was downloaded from the New York State Interactive

Mapping Gateway (https://orthos.dhses.ny.gov//). Orthoimagery represented spring conditions

(April/May; source 4-band at resolutions of 30.5 or 15.2 cm) and were available for the years

2015 and 2020. The open-water habitat (Ha) observed at each habitat-type (spawning pool,

connectivity channel or unmodified, maximum scale of 1:1000) was digitized visually in QGIS

(version 3.16.11-Hannover) for both years. Areas of open-water at each habitat-type was

considered representative of available fish habitat. The high density of *Typha* x *glauca* stem (>

20 stems/m^2; Farrell et al., 2010a; Neveldine et al. 2019) that delineates the habitat-types was

assumed a barrier to fish movement into the *Typha* x *glauca* matrix (Farrell, 2001; Farrell et al.,

2006).

Locations where emigration nets were set delineated the outlet boundary of each habitat-

type and was assumed to represent available fish habitat surveyable. The mainstem-distance of

each habitat-type was also measured from the centroid of a habitat-type to the outlet of French

Creek into French Bay (at the Rte. 12E bridge; Figure 1) to examine longitudinal effects (i.e., distance) on fish capture.

Between the 2015 and 2020 orthoimagery of French Creek, large mats of *Typha* x *glauca* became dislodged from the riparian habitat that borders the mainstem of French Creek. At three spawning pool complexes, a dislodged Typha mat altered the border with the original excavation. As a result, individual spawning pools exposed to the mainstem of French Creek were functionally separated from the complex due to loss of hydrologic connectivity (Figure 2). The most extreme example involved a spawning pool complex that lost up to 66% of its open-water habitat between 2015 and 2020 (Figure 2). Spawning pool complexes that remained intact, however, had near identical area measurements between the two years measured (2015 and 2020). Connectivity channels and unmodified channels showed a slight increase in open-water habitat in 2020 relative to 2015 due to water level variation. Netting crews adapted to changes in habitat reconfiguration and modified netting locations to ensure remnant outlets were sampled at the impacted spawning pool complexes.

Data handling

Fish capture data was first expressed as a CPUE by taking the number of fish captured at a complex and dividing it by the duration of the netting survey (i.e., net-nights) each year. CPUE data were then corrected to account for differences in open-water area available to fish among the habitat-types by dividing the CPUE by the open-water area (Ha) measured per complex. Hereafter we refer to our area corrected CPUE as simply $CPUE_{area}$. Estimates of open-water area were measured from the 2015 orthoimagery and considered representative of available fish habitat during the 2012, 2013, 2016 and 2017 surveys, whereas open-water area measured from the 2020 orthoimagery represented available fish habitat from 2018 to 2021.

Prior to analysis, fish data were divided by size into putative age-classes representing YOY and non-YOY fishes (Table 1). The YOY fish assemblage was assumed representative of the quality and suitability of early-life habitats (Mapes et al., 2015; Pritt et al., 2015), while non-YOY fish were assumed to be representative of the adult resident or post-spawn fish community that occupy the habitat-types for purposes other than reproduction.

Within the YOY and non-YOY fish assemblages, fish that were identified to species were used to estimate species diversity metrics. Cumulative fish species diversity was assessed among the habitat-types using rarefaction curves (Chao et la., 2014) with "iNEXT Online" (https://chao.shinyapps.io/iNEXTOnline/; Chao et al., 2016), whereas yearly mean fish species richness was evaluated among the habitat-types using linear mixed-effect modeling to determine which of environmental variables best explained patterns in species richness.

Prior to evaluating fish assemblage structure, taxa that were not identified to species were assigned to categories (Table 1). All larval Cyprinidae were combined into a YOY Cyprinidae category. A *Lepomis* category combined abundances of YOY pumpkinseed *Lepomis gibbosus* and YOY bluegill *Lepomis macrochirus*. When YOY taxa were infrequently encountered among all habitat-types (< 10% occurrence; Infante et al., 2009; Schilling et al., 2009) they were grouped into an 'other' category (Table 1).

A similar approach was taken with the non-YOY fish assemblage. Taxa with the potential to reach 300 mm total length were considered to be 'large-bodied adults' (L.B.A.), which were caught by nets with a capture efficiency targeting smaller sized fish (net throat diameter = 25.4-mm). Cyprinidae species encountered at > 10% of all habitat-types were left as standalone species (n = 5), whereas all other Cyprinidae (n = 11) were combined into an 'other Cyprinidae' (CYP) category. Iowa darter *Etheostoma exile* and tessellated darter *E. olmstedi* were grouped

into a 'Darter' category, while round goby *Neogobius melanostomus*, tubenose goby *Proterorhinus semilunaris*, and rudd *Scardinius erythrophthalmus* were categorized as 'Exotics' to the Laurentian Great Lakes. Finally, a non-YOY 'Other' category combined the remaining non-YOY taxa that were infrequently encountered (≤ 10% of all habitat-types; Table 1).

Environmental variables used to explore patterns in fish assemblage structure included mean-daily water column dissolved oxygen and water temperature which were averaged across the survey period for each habitat-type complex per year. The mainstem distance of each habitat type to French Bay was included to account for spatial differences in the location of modified habitats (Figure 1). Connectivity channels were clustered within at 1.5 km reach of French Creek located between 7.0 and 8.5 km upstream of French Bay. Spawning pool complexes were excavated downstream of the connectivity channels between 1.5 and 5.6 km upstream of French Bay. Locations of unmodified channels occurred between 0.6 to 9.2 km upstream of French Bay and provided spatial overlap with all the modified habitats (Figure 1). Habitat-type was included as a categorical factor to examine differences in assemblage structure between the modified habitats relative to unmodified reference channels.

Daily water level measurements (meters above International Great Lakes Datum; mIGLD) were downloaded from the NOAA monitoring station located in Alexandria Bay, NY (ABAN6–8311062; https://tidesandcurrents.noaa.gov/waterlevels.html?id=8311062). Seasonal and annual water level fluctuations recorded from Alexandria Bay were assumed representative of the hydrological conditions in the USLR that includes French Creek (Alexandria Bay is located approximately 20-km downstream of French Creek). For each year, daily water levels were averaged between 15-March and 15-April to represent water levels during the spawning period for northern pike to access sedge-meadows habitats (Massa and Farrell, 2020; Neveldine

et al., 2019); hereafter referred to as WLSpring (Figure 3a). The change in water level between WLSpring and when emigration surveys were run in mid-June (i.e., mean June water levels) was assumed to represent the strength of each year's flood pulse (ΔWL). ΔWL was calculated as the difference between mean June water levels and WLSpring, where values for ΔWL indicate relative rates of change in water levels between spring water levels and the emigration period. Negative values for ΔWL suggest habitat contraction because of water level drawdown (Neveldine et al., 2019), whereas positive values for ΔWL suggest an expansion of the wetted area (Figure 3b). No relationship was found between WLSpring (15-March to 15-April) and ΔWL (Pearson R = -0.021, p = 0.939, df = 14), and were treated as independent continuous variables to describe interannual hydrology for the USLR (Figure 3).

Statistical Analysis

Redundancy Analysis (RDA) was used to model assemblage structure of YOY and non-YOY fish against environmental predictors. RDA is a direct gradient ordination technique that can accommodate qualitative factors (Legendre and Legendre, 1998). All continuous environmental variables were centered to 0 mean and standardized to 1 standard deviation prior to analysis. Dissolved oxygen and ΔWL showed the strongest collinearity among environmental predictors (-0.53), but both were included in the analysis. Fish community data was Hellinger transformed prior to analysis, and the forward stepwise procedure in the R package "Vegan" (R version 4.1.3) was used to identify which linear combination of explanatory variables best described fish assemblage structure. Permutation tests (1000 permutations) were used to evaluate the significance of the forward-selected model, and the significance of marginal terms effects. The RDA analysis assumed a linear additive model to explain variation between the environmental predictors and fish community structure.

Potential interactions between environmental variables and habitat-type on overall mean fish $CPUE_{area}$ and yearly species richness were examined with linear-mixed effect models (LMM) in lmerTest (version 3.0–1; Kuznetsova et al., 2017) (R package lme4 version 1.1–17; Bates et al., 2015). Habitat-types were set as a random intercept to account for repeated-measures, and year was set as a random slope to account for interannual variability. Environmental predictors (dissolved oxygen, temperature, WLSpring, ΔWL and mainstem distance), which were also centered to zero mean and one standard deviation, were set as fixed factors. Akaike information criterion (AIC) was used to evaluate the strength of candidate models against a null model with only random slope and intercept. Models within 2 units of the lowest AIC score were considered equal in the models' ability to describe the data, but the model with the fewest terms was considered parsimonious with the least bias. Fish $CPUE_{area}$ data were $\log_{10}$ (n+1) transformed to normalize the data prior to analysis. Species richness data were not transformed. In addition, we used the same LMM structure to model the influence of hydrology and habitat-type on patterns of untransformed dissolved oxygen and temperature data.

Results

We caught 218,086 fish emigrating from lateral habitats (modified, n = 8; unmodified, n = 11) over eight-years at French Creek. Non-YOY fish were represented by 19,468 individuals among 40 species, whereas YOY fish accounted for more than 90% of the cumulative catch (198,616 fish) and were represented by 23 species.

Rarefaction curves demonstrated that cumulative non-YOY species richness was similar among the three habitat-types with similar inflection points and overlapping 95% confidence intervals (Figure 4a). A total of 33 species were identified at the unmodified channels, 29 species from connectivity channels and 28 non-YOY species at spawning pool complexes over the eight-

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years. Rarefaction curves for YOY fish indicated that a larger number of YOY species (n = 19) emigrated from spawning pool complexes, relative to the connectivity (n = 14) and unmodified channels (n = 13) over eight-years. Confidence intervals (95% CI) around species richness rarefaction curves overlapped between the connectivity channels and unmodified channels, but curves for the channelized habitats were below the 95% CI observed for spawning pool complexes (Figure 4b).

Based on the cumulative catch across years, the relative abundance of non-YOY fish appeared more similar between the connectivity channels and unmodified channels relative to spawning pool complexes (Figure 5a). Central mudminnow, *Umbra limi,* was the most commonly encountered non-YOY fish at both the connectivity channels and unmodified channels and accounted for 41% and 37% of the total catch across years, respectively. Central mudminnow at spawning pool complexes represented only 4% of the total catch (Figure 5a). In contrast, spawning pool complexes were dominated by Tadpole Madtom, *Noturus gyrinus*, representing 75% of all non-YOY fish caught at spawning pool complexes. Tadpole Madtom accounted for approximately 1% of the total catch at connectivity channels and unmodified channels (Figure 5a).

YOY largemouth bass, *Micropterus salmoides,* made up 81% of all captured YOY across all habitat-types and years in French Creek (Figure 5b). YOY largemouth bass were consistently dominant among the habitat-types, making up 88% of the total catch at connectivity channels, 79% at spawning pools and 70% at unmodified channels. When YOY largemouth bass were removed to examine relative abundance among the remaining species (with 37,419 individuals; Figure 5c), YOY brown bullhead, *Ameiurus nebulosus,* made up a larger proportion of the catch at spawning pool complexes (42%) relative to connectivity channels (12%) and unmodified

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habitats (4%). Bowfin, *Amia calva,* was the most common YOY fish captured at connectivity

channels (51%) and unmodified channels (54%) but accounted for 19% of the catch at spawning

pool complexes, after excluding YOY largemouth bass (Figure 5c).

The influence of environmental variables on the non-YOY and YOY fish assemblage

structure were evaluated with redundancy analysis. Forward stepwise selection found that a

linear combination of habitat-type, WLSpring, ΔWL, and mainstem distance of the habitat-types

was a significant model ($F_{5,92}$ = 7.509, p = 0.001, adj.r^2 = 0.251) that explained 29% of the

variation in the non-YOY data (Figure 6a). Effects of the selected variables were all significant

(p < 0.02). The first RDA axis explained 21.8% of the variation and was interpreted to describe

fish associated with spawning pool complexes and positive association with spring water levels

and ΔWL. Distance of each habitat-type to the mainstem was negatively associated with the first

RDA axis and was considered a proxy for the upstream location of the connectivity channels.

Non-YOY central mudminnow and tadpole madtom had the strongest species scores on the first

RDA axis (-0.929 and 0.534, respectively) and generally aligned with the group centroids for the

channelized habitats and spawning pool complexes, respectively (Figure 6a). The second RDA

axis accounted for only 4% of the variation in the non-YOY data and was not explored further.

RDA on the YOY fish assemblage included largemouth bass. Forward stepwise selection

found that the linear combination of habitat-type, dissolved oxygen, WLSpring and ΔWL were a

significant fit ($F_{5,92}$ = 5.661, p = 0.001, adj.r^2 = 0.235) and explained 23.5% of the variation in

the YOY data (Figure 6b). Main-effects of the selected variables were all significant ($p \leq 0.048$).

The first RDA axis explained 14.5% of variation and was associated with habitat-type and

hydrological variability. Spawning pool complexes and dissolved oxygen were negatively

associated with the first RDA axis, whereas ΔWL and WLSpring had positive associations. YOY

largemouth bass and YOY northern pike oriented on opposite ends of the first RDA axis. YOY

northern pike and Lepomis showed a positive association with the hydrologic variables, whereas

YOY largemouth bass and YOY brown bullhead were associated with the spawning pool

complexes, higher dissolved oxygen and low ΔWL (Figure 6). The second RDA axis explained

only 5% of the variation and was not explored further.

Linear mixed-effect modeling (LMM) and AIC model selection identified that habitat-

type and both hydrological variables (WLSpring and ΔWL) were among the most important

predictors of $CPUE_{area}$ and yearly species richness for the non-YOY and YOY fish assemblages

(Table 2), while temperature, DO and distance to the mainstem did not contribute significantly to

the model. $CPUE_{area}$ of non-YOY fish was best described (lowest AIC and fewest terms) by a

model with a significant effect of habitat-type ($F_{2,17} = 11.218$, $p < 0.0008$) and weak interaction

between habitat-type and ΔWL ($F_{2,81} = 2.708$, $p = 0.07$; Table 2). Pairwise comparisons using the

Tukey method found higher $CPUE_{area}$ of non-YOY fish at connectivity channels and spawning

pool complexes than unmodified channels ($p < 0.02$) (Figure 7a).

The best model describing $CPUE_{area}$ of YOY fish included a significant effect of habitat-

type ($F_{2,16} = 23.076$, $p < 0.0001$) and significant interaction between WLSpring and ΔWL ($F_{1,81} =$

7.584, $p = 0.007$; Table 2). Higher $CPUE_{area}$ of YOY fish occurred from connectivity channels

and spawning pools relative to unmodified channels (Tukey: $p < 0.005$; Figure 7b). Effects of

WLSpring and ΔWL were not significant at $α = 0.05$ ($p > 0.06$) but had positive coefficients.

Their interaction, however, carried a significant negative coefficient (-0.364; Figure 7b). The

negative coefficient from the WLSpring and ΔWL interaction appeared driven by lower

$CPUE_{area}$ of YOY fish from the modified habitats when the product between the hydrological

variables was maximized (Figure 7b). We interpret the YOY fish $CPUE_{area}$ response to the

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WLSpring and ΔWL interaction to describe years where water levels peaked in early-spring (WLSpring) and declined afterwards (i.e., negative ΔWL value). Spring water level itself had no apparent effect on $CPUE_{area}$ of YOY largemouth bass. $CPUE_{area}$ of YOY largemouth bass were best described by a significant habitat-type and ΔWL interaction ($F_{2,79} = 8.015$, $p = 0.0007$; Figure 7c). $CPUE_{area}$ of YOY largemouth bass emigrating from spawning pool complexes were negatively impacted during years of rising ΔWL compared to the unmodified channels, whereas densities of YOY largemouth bass increased in response to higher ΔWL at the connectivity channels (Figure 7c; Figure 6b).

Non-YOY species richness was described by significant effects of habitat-type ($F_{2,20} = 6.731$, $p = 0.006$), a negative association with WLSpring ($F_{1,82} = 6.040$, $p = 0.02$), a positive association with ΔWL ($F_{1,79} = 21.418$, $p < 0.0001$), and a negative interaction coefficient between WLSpring and ΔWL ($F_{1,81} = 13.784$, $p = 0.0004$; Figure 8a; Table 2). Non-YOY species richness was higher at spawning pool complexes relative to unmodified habitats (Tukey: $p = 0.015$) across years. Non-YOY species richness did not differ between the connectivity channels and either the unmodified channels (Tukey: $p = 0.106$) and spawning pool complexes (Tukey: $p = 0.811$; Figure 8a).

YOY species richness was described by significant effects of dissolved oxygen ($F_{1,89} = 5.148$, $p = 0.03$), habitat-type ($F_{2,61} = 13.012$, $p < 0.0001$), and a significant interaction between WLSpring and ΔWL ($F_{1,86} = 17.737$, $p < 0.0001$; Figure 8b; Table 2). YOY species richness was positively associated with dissolved oxygen, and negatively associated with the WLSpring x ΔWL interaction term. Tukey pairwise comparison indicated higher YOY species richness at spawning pool complexes relative to unmodified channels ($p < 0.001$) across years. Yearly YOY

species richness did not differ between connectivity channels and spawning pool complexes ($p = 0.124$), or between connectivity channels and unmodified channels ($p = 0.096$; Figure 8b).

Although dissolved oxygen and water temperature were rarely identified in the RDA models describing fish assemblage structure, each variable showed significant effects of hydrological variability and habitat-types. Patterns in temperatures were best described by an interaction between habitat-type and ΔWL ($F_{2,73} = 5.833$, $p = 0.004$) and a positive main-effect of WLSpring ($F_{1,80} = 9.702$, $p = 0.003$; Figure 9a). Across years, similar temperatures were observed between the modified habitats (Tukey; $p = 0.181$) which were significantly warmer than temperatures in the unmodified channels ($p < 0.02$; Figure 9a). Differences in temperature among the habitat-types, however, were most pronounced at low ΔWL values and converged towards a uniform thermal regime ($\sim 20°C$) at peak ΔWL (Figure 9a).

Dissolved oxygen was described by a simple additive model with effects of habitat-type ($F_{2,19} = 6.612$, $p = 0.006$) and ΔWL ($F_{1,80} = 56.426$, $p < 0.0001$). Among habitat-types, higher concentrations of dissolved oxygen (mg/L) were found at spawning pool complexes relative to unmodified channels (Tukey: $p = 0.008$; Figure 9b). Dissolved oxygen was however similar between connectivity channels and unmodified channels (Tukey: $p = 0.559$) and between connectivity channels and spawning pool complexes (Tukey: $p = 0.164$). Across habitat-types, dissolved oxygen declined with increasing ΔWL, and during peak ΔWL dissolved oxygen ranged between mild-hypoxia (< 4.0 mg/L) and anoxia (< 1.0 mg/L) among habitat-types (Figure 9b).

Discussion

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The habitat modifications applied in the USLR increased the extent of and renewed connectivity to suitable early-life habitat for fish impacted by *Typha* x *glauca* expansion. The modified habitats outperformed the unmodified habitats in CPUE$_{area}$ of fish per year (YOY and non-YOY) and spawning pool complexes supported higher YOY species richness (yearly and rarefaction curve estimates) than the unmodified channel habitat. Spawning pool complexes and connectivity channels tended to be warmer and have higher dissolved oxygen than the unmodified channels. Ground water infiltration at the unmodified channels from the Frontenac Spring Aquifer (Neveldine et al., 2019) likely caused the cooler temperatures and lower dissolved oxygen (i.e., lower quality fish habitat; Mapes et al., 2015; Pritt et al., 2015) relative to the modified habitats, and may maintain channel morphology.

Despite these environmental differences between the modified (spawning pool complex and connectivity channel) and unmodified habitats, the physical attributes of the habitat (i.e., open-water pools vs. channelized habitats) had an overriding influence on the fish assemblage composition (Meadore and Carlisle, 2007). Connectivity channels complemented the fish assemblage associated with the unmodified channels (e.g., non-YOY central mudminnow and YOY bowfin). Despite similar fish assemblages, the warmer water temperatures and slightly higher dissolved oxygen at the connectivity channels corresponded with higher CPUE$_{area}$ of emigrating fish than the unmodified channels (Mapes et al., 2015; Massa and Farrell, 2020; Pritt et al., 2015).The spawning pool complexes in contrast supported high-quality early-life habitats (higher dissolved oxygen and warmer temperatures) that were used by taxa underrepresented in the channelized habitats (e.g., non-YOY tadpole madtom, YOY brown bullhead).

Although the modified habitats supported conducive environmental conditions for higher CPUE$_{area}$ of YOY fish, patterns in dissolved oxygen, temperature and fish assemblage structure

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were inextricably linked, often interactively, with ΔWL and interannual spring water levels (Carlson et al., 2016; Gathman and Burton, 2011; Linhoss et al., 2012). At peak ΔWLs, which corresponded with historic flooding in the USLR and Lake Ontario in 2017 and 2019 (Carter and Steinschneider, 2018; Gronewald and Rood, 2019), temperature differences among habitat-types were lost. Along the ΔWL gradient, temperatures at unmodified channels increased slightly relative to lower ΔWL years. Temperatures at connectivity channels declined slightly, while temperatures at spawning pool complexes declined with higher ΔWL to create a uniform thermal regime (~20°C) among habitat-types at peak ΔWLs. Peak ΔWLs also had a uniform decline in dissolved oxygen among all habitat-types that ranged from mild-hypoxia (< 4.0 mg/L) to anoxia (< 1.0 mg/L).

The cause for the negative relationship between ΔWL and dissolved oxygen is contrary to established relationships between other abiotic factors (e.g., flow and temperature) and dissolved oxygen (He et al., 2011). Temperature had no apparent influence on patterns in dissolved oxygen. Spawning pool complexes supported higher temperatures and dissolved oxygen relative to unmodified channels during low ΔWL years. During high ΔWL years, temperatures and dissolved oxygen declined in tandem at spawning pool complexes. The lack of relationship between temperature and dissolved oxygen suggested that respiration exceeded primary productivity, but the mechanism regulating this effect requires more detailed investigation (Post et al., 2018). The extreme flood waters may facilitate increased transport of dissolved organic carbon and other nutrients from newly inundated upslope habitats, or from the Typha litter itself, into coastal areas resulting in elevated microbial respiration (Williamson et al. 1999; Brothers et al. 2014; Su et al., 2007; Han et al., 2018). Although not measured in the current study, water clarity was also notably lower in 2017 and 2019 than the other years, presumably from added

runoff related to the floods (J.P. Leblanc, Pers. obs.). The elevated turbidity during the flood-years may have reduced the photosynthetic capacity of the system by limiting light exposure to algae and macrophytes. The precise mechanism(s) responsible for the low dissolved oxygen in French Creek during the floods is uncertain, but could result from heterotrophic-biogeochemical interactions. We suspect, however, that the extreme flood waters precipitated the subsequent biogeochemical process resulting in low dissolved oxygen in 2017 and 2019.

Similar patterns of dissolved oxygen deficits with elevated water levels were observed at other coastal habitats in the USLR surveyed over the same time period as the present study (unpublished data), and in Georgian Bay, Lake Huron, following uncharacteristically high water-levels (P. Chow-Fraser, Pers. Comm.). High flow rates in Savanah River (southeastern U.S.A) during a flood caused by 1000-year rainstorm also resulted lower dissolved oxygen relative to normal flow rates (Post et al., 2018). Hypoxia associated with extreme hydrological events (Post et al., 2018, this study) may be a novel climate induced stressor on freshwater systems. The frequency of extreme hydrological events (floods and droughts) is expected to increase with climate change (Marengo and Espinoza, 2016; Trenberth, 2011). Coupled with an overall deoxygenation of temperate freshwater lakes because of rising water temperatures (Jane et al., 2021) and eutrophication (Bhagowati and Ahamad, 2019), the severity of dissolved oxygen depletion caused by extreme hydrological events could be magnified. Our results suggest that dissolved oxygen in nearshore coastal habitats was influenced more by extreme hydrological events than temperature and was consistent with patterns in dissolved oxygen and temperature observed by Post et al. (2018) in the Savanah River in response to significant flooding.

Exposure to hypoxic conditions during high ΔWL years undoubtedly created a stressful environment for fish (Breitburg et al., 1999; Wu, 2009). However, based on fish CPUE$_{area}$

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estimates, certain YOY species (e.g., northern pike) showed a positive response to high WLSpring and ΔWL despite near anoxic conditions. CPUE$_{area}$ of YOY largemouth bass suggested limited production of YOY at spawning pool complexes during high ΔWL years, but CPUE$_{area}$ of YOY largemouth bass were positively related to ΔWL at the channelized habitats that also experienced low dissolved oxygen. Thus, it is difficult to attribute patterns in catches of YOY fish solely to reduced concentrations of dissolved oxygen, but rather as an interaction between the habitat-types, hydrodynamics, and adaptations to low oxygen environments.

Because spawning pool complexes were bordered by dense *Typha* x *glauca*, access to inundated riparian habitat during years with high WLSpring and ΔWL may be limited for nest building species (e.g., largemouth bass; Schrank and Lishawa, 2019). Spawning pools may be considered analogous to a series of deep ponds when water levels were at historic highs in the USLR, and may be avoided by species that prefer shallower nesting habitat (Havens et al., 2005; Maceina and Bettoli, 1998; Stuber et al., 1982), but was suitable for broadcast spawning species (e.g., northern pike) that use a wide range of spawning depths (up to 6-m; Farrell et al., 2006). The connectivity channels and unmodified channels, in contrast, maintained a shallower depth gradient relative to spawning pool complexes as flood waters inundated the riparian sedge-meadow habitat. The channelized habitats, which provided connectivity to sedge-meadow habitats, likely maintained sufficiently shallow habitat used by both nest building (largemouth bass; Garvey et al., 2000; Havens et al., 2005) and broadcast spawning species (northern pike; Cottrell et al., 2021; Foubert et al., 2020; Neveldine et al., 2019; Oele et al., 2018) during high and low water level years.

Spring water levels and the magnitude of the flood pulse interact to influence accessibility to spawning habitats and to connect spawning and nursery areas (Cooper et al.,

2008; Mingelbier et al., 2008; Neveldine et al., 2019). Low water levels during the spawning period not only limits access to spawning habitat but reduces the extent of available habitat for spawning fish (Farrell, 2001). If ΔWL declines after the spawning period, as was the case in 2012 and 2016, water connections between spawning and nursery areas may be reduced or lost, potentially stranding eggs or newly hatched larvae in upslope habitats leading to poor natural reproduction (Mingelbier et al., 2008; Neveldine et al., 2019; Massa and Farrell, 2020). When WLSpring and ΔWL were both high, fish could access inundated spawning habitats and YOY could exploit resources within an expanding habitat afforded by rising water levels which maintain reliable emigration routes (Casselman and Lewis, 1996; Cottrell et al., 2021; Farrell et al., 2006; Mingelbier et al., 2008, Foubert et al. 2019). However, during peak ΔWL years, the benefits of sustained hydrological connectivity may be offset by hydrologically induced hypoxia.

Fish condition was not evaluated in the study. Exposure to low dissolved oxygen during the nursery period can have consequential physiological impacts on fish that reduces post-nursery survival and recruitment (Wu, 2009). Duration of fish exposure to hypoxic conditions will also influence their physiological stress. Because we measured temperature and dissolved oxygen at the channel outlets of the habitat-types, we assumed a uniform distribution in environmental conditions throughout the habitat-types. However, refugia of dissolved oxygen may exist within the modified and unmodified habitats, and the presence of dissolved oxygen refugia could alleviate the severity of hypoxia induced stress experienced by fish.

We also observed a high prevalence of fish species that are known for tolerance of low dissolved oxygen conditions including air breathing fishes (e.g., bowfin and central mudminnow). Bowfin were the third most common YOY fish captured emigrating among all habitat types, whereas central mudminnow were among the most common non-YOY fish

encountered at the connectivity channels and unmodified habitats in French Creek. The strong representation of fishes adapted to low dissolved oxygen in French Creek would be expected in habitats influenced by frequent bouts of hypoxia or anoxia.

Many of these fish species tolerant to low dissolved oxygen also appeared to use the secondary lateral habitats (i.e., modified and unmodified habitats) in French Creek differently. Non-YOY central mudminnow and YOY bowfin were consistently overrepresented at the channelized habitats (i.e., connectivity channels and unmodified habitats). In contrast, non-YOY tadpole madtom, *Noturus gyrinus*, which are meso-tolerant to low dissolved oxygen (Tang et al., 2020), were captured near-exclusively at spawning pools. These observations may suggest that the structural properties of the habitat (channels vs. pools) was a stronger selective force than the environmental conditions (e.g., dissolved oxygen) lateral to the mainstem of French Creek (Meador and Carlisle, 2007).

Central mudminnow and tadpole madtom are strongly associated with high densities of macrophytes in the water column (Henning et al., 2014). However, the channelized habitats had similar representation of central mudminnow despite significant differences in the cover of submersed aquatic vegetation between the connectivity channels and unmodified habitats (Neveldine et al., 2019). Tadpole madtom, which were encountered almost exclusively at spawning pools, also prefer heavily-vegetated slow-moving backwater habitats similar to oxbow wetlands (Henning et al., 2014; Wilson et al., 1999) and un-channelized reaches of tributaries (Meneks et al., 2003). The spawning pool complexes in French Creek shared analogous characteristics with oxbow wetlands (e.g., relatively large sections of open-water lateral of the mainstem of the tributary) favoured by tadpole madtom (Wilson et al., 1999). Consistent with our results from French Creek, tadpole madtom were also encountered less frequently at

channelized reaches within the Red River basin, Minnesota, USA than at un-channelized reaches (Meneks et al., 2003), suggesting tadpole madtom were selecting against the channelized habitats in French Creek.

Interspecific competition between fishes tolerant of low dissolved oxygen may also contribute to fish assemblage differences between the channelized habitats and spawning pools. The strong chemical defenses of tadpole madtom indicates its potential to defend against predators and competitors (Wright, 2012). However, insufficient information exists to evaluate the magnitude that competitive interactions that may influence fish assemblage structure among the habitat-types in French Creek (Jackson et al., 2001).

The habitat enhancement strategy applied to French Creek incorporated functionally diverse habitat modifications (connectivity channels and spawning pool complexes) that showed marked differences in how the production of YOY of fish responded to novel hydrological events. During years with high ΔWL, CPUE$_{area}$ at spawning pool complexes was limited for largemouth bass and brown bullhead, but low ΔWL years had a positive effect on both taxa in spawning pool complexes. CPUE$_{area}$ at the connectivity channels remained relatively consistent regardless of water level scenario, highlighting the importance of a shallow zonation gradient in maintaining suitable fish habitat impacted by variable water levels (Casselman and Lewis, 1996). Having two types of habitat modifications excavated in French Creek appeared better able to buffer the effects of extreme hydrological variability on the production of some YOY fish than if only spawning pool complexes were used. We interpret our results to indicate that a diversified habitat enhancement strategy (e.g., tandem application of connectivity channels and spawning pool complexes) improved ecological resilience of this drowned river mouth wetland (Peterson

et al., 1998) to extreme hydrological variability on the production of YOY fish (Carlson et al., 2016; Erwin, 2009; Poff, 2018).

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Table 1. List of species caught during emigration survey across 2012, 2013 and 2016-2021. Taxa category assignment shown for the non-YOY (capitalized abbreviations) and YOY (lowercase abbreviations) fish assemblages. Taxa grouped into Other, CYP, yoy cyprinidae, DARTER, Exotics, and large bodied adults (LBA) categories represents groupings of taxa not used as standalone species. Hyphens represents age-class for that species not recorded in French Creek. Untransformed yearly-mean CPUE (SE) for each standalone species presented by age-class. Untransformed yearly-mean CPUE represent capture per net-night per year. When taxa were grouped into a category, yearly-mean CPUE presented for that category. When individual taxa were grouped in a category, a species specific CPUE was not presented (i.e., n.a.).

Common Name	Latin Name	Non-YOY cat.	Mean CPUE (SE)	YOY cat.	Mean CPUE (SE)
Bluegill	*Lepomis macrochirus*	BG	0.8 (0.4)	lepomis	n.a.
Blackchin shiner	*Notropis heterodon*	BLCH	1.6 (1.3)	yoy cyprinidae	n.a.
Bluntnose minnow	*Pimephales notatus*	BLN	2.7 (2.1)	yoy cyprinidae	n.a.
Blacknose shiner	*Notropis heterolepis*	BLNO	0.4 (0.2)	-	n.a.
Brown bullhead	*Ameiurus nebulosus*	BBH	18.9 (11.1)	bbh	19.5 (6.5)
Central mudminnow	*Umbra limi*	CMM	37.8 (13.5)	cmm	9.8 (4.4)
Fathead minnow	*Pimephales promelas*	FATH	2.3 (2.0)	-	n.a.
Golden shiner	*Notemigonus crysoleucas*	GOSH	4.1 (1.8)	yoy cyprinidae	n.a.
Grass pickerel	*Esox americanus vermiculatus*	GP	1.4 (0.5)	gp	2.0 (1.2)
Pumpkinseed	*Lepomis gibbosus*	PS	7.6 (1.4)	lepomis	n.a.
Tadpole madtom	*Noturus gyrinus*	TMAD	13.6 (10.5)	tmad	1.8 (1.0)
Yellow bullhead	*Ameiurus natalis*	YBH	0.2 (0.1)	-	n.a.
Yellow perch	*Perca flavescens*	YP	3.2 (0.6)	yp	0.3 (0.2)
Bowfin	*Amia calva*	LBA	n.a.	bf	269.4 (143.8)
Chain pickerel	*Esox niger*	LBA	n.a.	-	n.a.
Common carp	*Cyprinus carpio*	LBA	n.a.	-	n.a.
Largemouth bass	*Micropterus salmoides*	LBA	n.a.	lmb	756.2 (238.4)
Northern pike	*Esox lucius*	LBA	n.a.	np	19.7 (11.0)
Smallmouth bass	*Micropterus dolomieu*	LBA	n.a.	other	n.a.
Banded killifish	*Fundulus diaphanus*	OTHER	n.a.	other	n.a.
Black crappie	*Pomoxis nigromaculatus*	OTHER	n.a.	other	n.a.
Brook silverside	*Labidesthes sicculus*	OTHER	n.a.	other	n.a.
Rock bass	*Ambloplites rupestris*	OTHER	n.a.	other	n.a.
White sucker	*Catostomus commersonii*	-	n.a.	other	n.a.
Bridle shiner	*Notropis bifrenatus*	CYP	n.a.	-	n.a.
Common shiner	*Luxilus cornutus*	CYP	n.a.	-	n.a.
Creek chub	*Semotilus atromaculatus*	CYP	n.a.	-	n.a.
Eastern silvery minnow	*Hybognathus regius*	CYP	n.a.	-	n.a.
Emerald shiner	*Notropis atherinoides*	CYP	n.a.	yoy cyprinidae	n.a.
Mimic shiner	*Notropis volucellus*	CYP	n.a.	-	n.a.
Pugnose shiner	*Notropis anogenus*	CYP	n.a.	-	n.a.
Spotfin shiner	*Cyprinella spiloptera*	CYP	n.a.	-	n.a.
Spottail shiner	*Notropis hudsonius*	CYP	n.a.	-	n.a.
Iowa darter	*Etheostoma exile*	DARTER	n.a.	-	n.a.
Tessellated darter	*Etheostoma olmstedi*	DARTER	n.a.	other	n.a.
Etheostoma spp		DARTER	n.a.	-	n.a.
Round goby	*Neogobius melanostomus*	EXOTIC	n.a.	other	n.a.
Rudd	*Scardinus erythropthalmus*	EXOTIC	n.a.	-	n.a.
Tubenose goby	*Proterorhinus semilunaris*	EXOTIC	n.a.	-	n.a.

Non-YOY OTHER	**0.5 (0.2)**	n.a.
LBA	**11.1 (6.5)**	n.a.
CYP	**4.4 (3.8)**	n.a.
DARTER	**0.3 (0.3)**	n.a.
EXOTIC	**0.09 (0.03)**	n.a.
yoy lepomis	n.a.	**6.9 (3.2)**
yoy cyprinidae	n.a.	**39.2 (22.0)**
yoy other	n.a.	**0.13 (0.07)**

Table 2. AIC model selection results from linear mixed-effect modeling on fish CPUE$_{area}$ and species richness for the non-YOY and YOY fish assemblages. Top ranked models (within 2 units of the lowest AIC score) are presented relative to the null model. Top ranked models did not differ statistically, and the model with the fewest terms was selected to describe the response (bolded ranked model). Variables separated by a colon in a column header indicate an interaction between the terms. Variables not part of an interaction were treated as an additive main-effect.

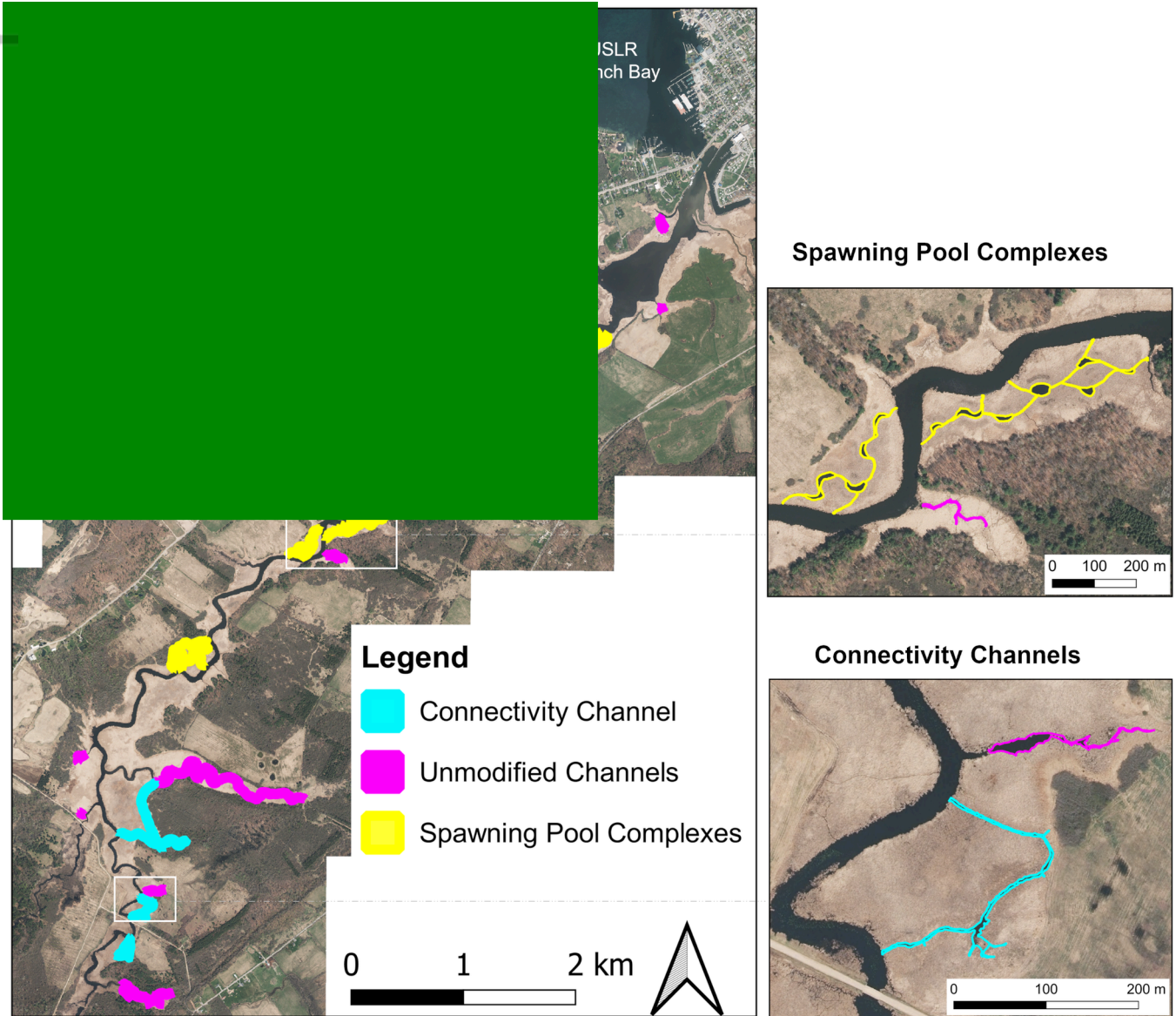| Response	Age-Class	Model Rank	Habitat	DeltaWL	WLSpring	DO	TEMP	Distance	WLSpring : DeltaWL	Habitat : DeltaWL	Habitat : WLSpring	Habitat : DeltaWL : WLSpring	AIC SCORE
DENSITY	NON-YOY	1	•	•	•					•			171.70
		2	•	•	•				•	•	•	•	171.96
		3	•	•						•			**172.09**
		4	•	•	•	•				•			173.68
		Null											190.63
	YOY	**1**	•	•	•				•				**222.5**
		2	•	•	•	•			•				224.20
		Null											253.56
SPECIES RICHNESS	NON-YOY	**1**	•	•	•				•				**492.94**
		2	•	•	•				•	•	•	•	494.74
		3	•	•	•			•	•				494.87
		Null											513.71
	YOY	1	•	•	•				•	•	•	•	360.08
		2	•	•	•	•	•		•				360.55
		3	•	•	•	•			•				**360.78**
		Null											392.60

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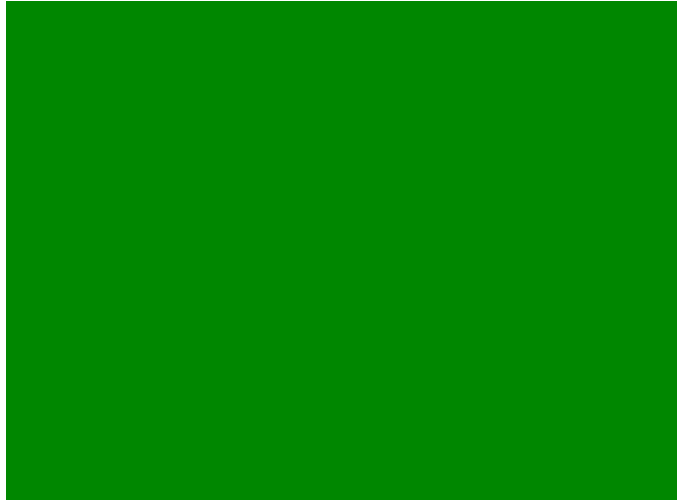
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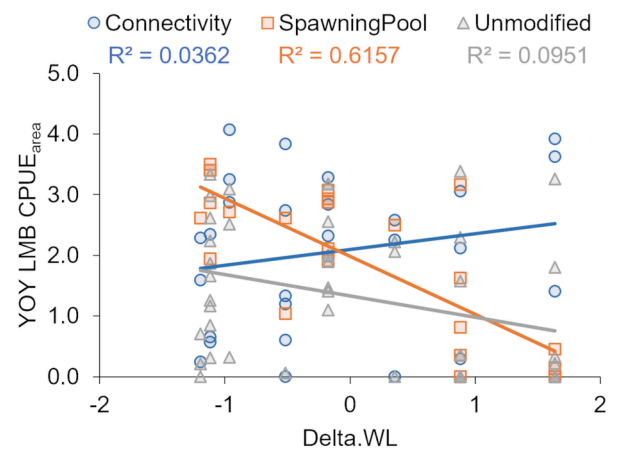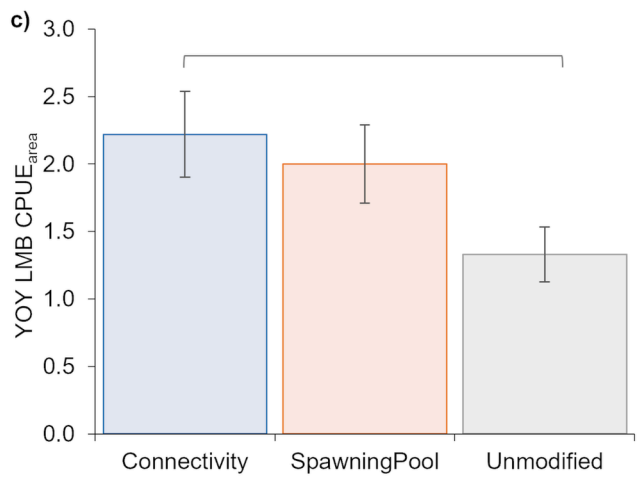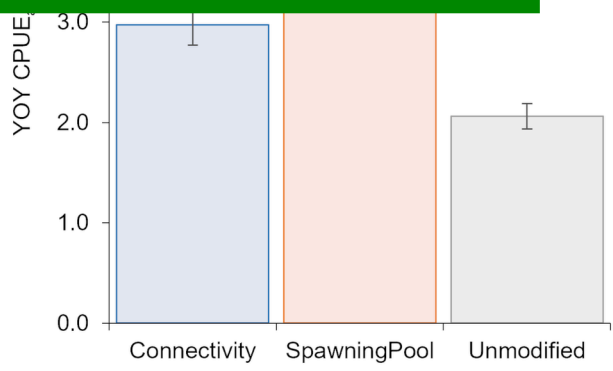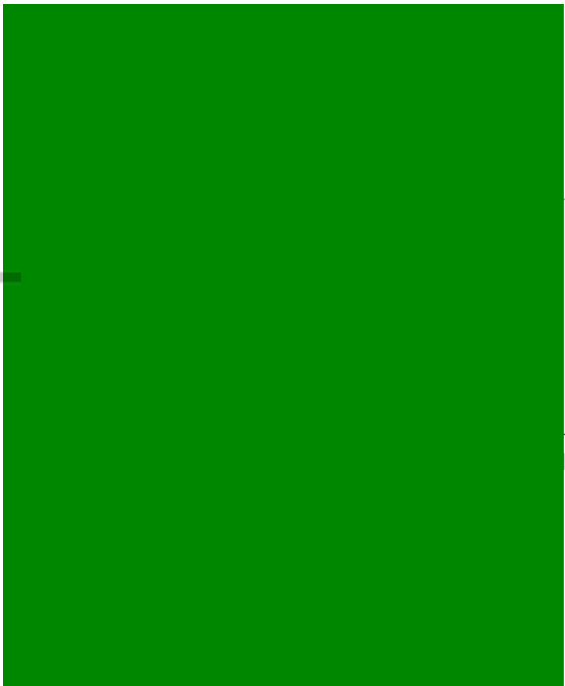
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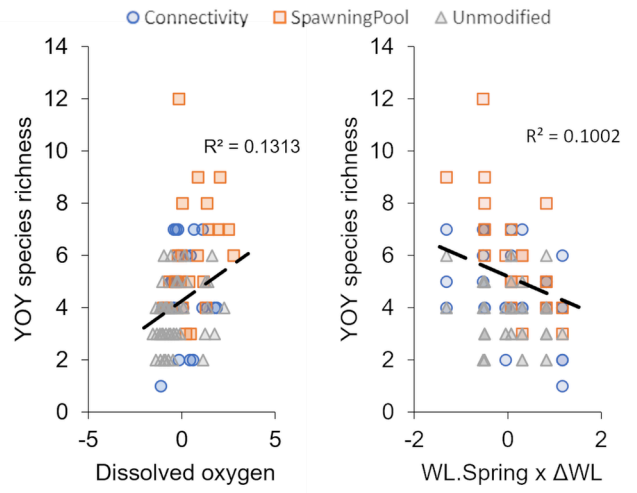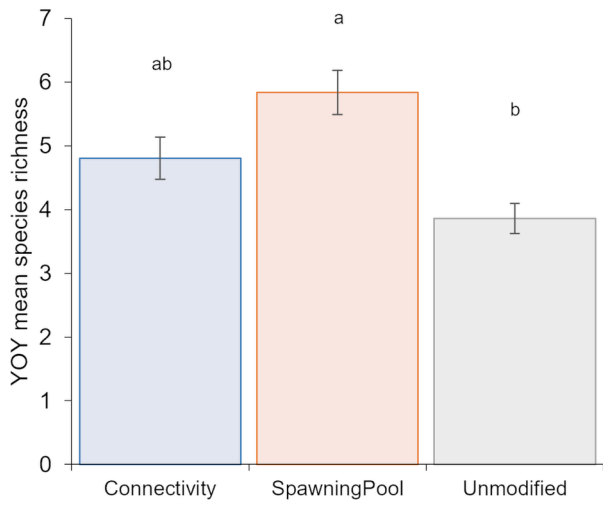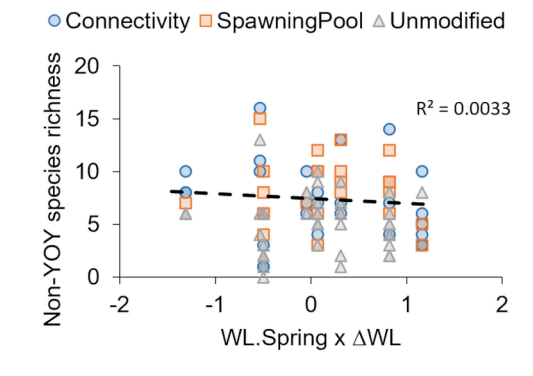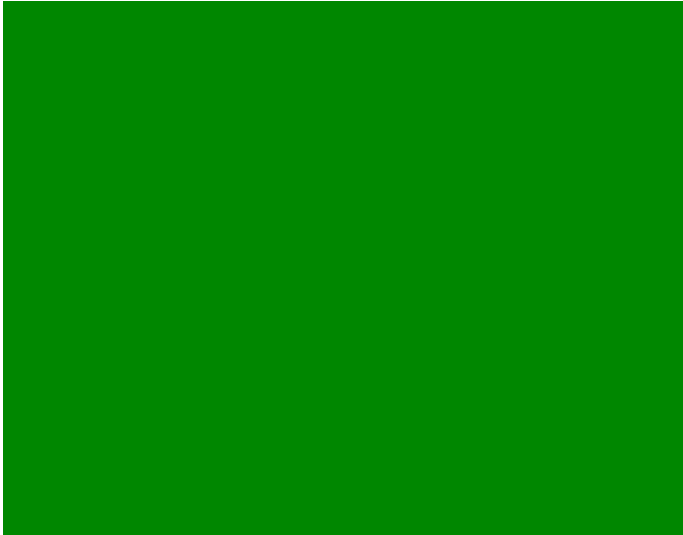
Figure8.revised.tif

Figure9.revised.tif

Legend:
- Lost spawning pool area after 2017 flood
- Remaining spawning pool area after 2017 flood
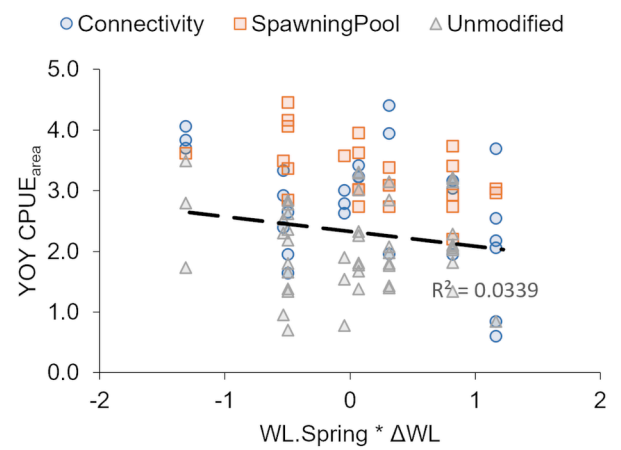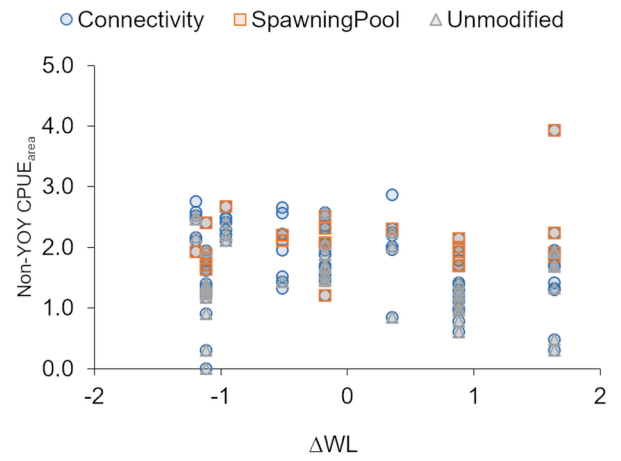- Dislodged Typha Mat

0   25   50 m

Figure 2.tif

b) YOY

Figure 4.revised.tif

a)

Adult

Legend:
- EXOTICS
- DARTERS
- BLACKCHIN SHINER
- BLACKNOSE SHINER
- GRASS PICKEREL
- BLUEGILL
- YELLOW BULLHEAD
- OTHER CYP.
- FATHEAD MINNOW
- OTHER
- BLUNTNOSE MINNOW
- GOLDEN SHINER
- LARGE BODIED ADULTS
- YELLOW PERCH
- BROWN BULLHEAD
- PUMPKINSEED
- TADPOLE MADTOM
- CENTRAL MUDMINNOW

Connectivity · Unmodified · SpawningPool

b) **All YOY**

Connectivity · Unmodified · SpawningPool

Legend:
- largemouth bass
- brown bullhead
- bowfin
- cyp.
- northern pike
- lepomis
- tadpole madtom
- central mudminnow
- grass pickerel
- other

c) **YOY lmb Excluded**

Connectivity · Unmodified · SpawningPool

Figure 5.tif

Figure 6.tif

Figure Captions

Figure 1. Map of the location of French Creek within the Laurentian Great Lakes (insets) with the location of the habitat-type complexes along the mainstem of French Creek. Examples of delineated spawning pool complexes, connectivity channel complexes and unmodified habitats shown in outsets.

Figure 2. Example of a dislodged *Typha* x *glauca* mat that exposed spawning pools to the mainstem of French Creek. Imagery taken in 2020, with digitized open-water area remaining (solid white) and lost (white dots) of the spawning pool complex.

Figure 3. Untransformed mean spring water levels (WLSpring) and ΔWL for each survey year. Spring water level (primary y-axis) measured in meter above International Great Lakes Datum (mIGLD) represents mean water levels between 15-March and 15-April of each year. ΔWL (secondary y-axis) represents the rate of change in water levels (m) from mean spring water levels to the emigration survey (mean-June water levels).

Figure 4. Rarefaction curves of species diversity on the cumulative abundance of non-YOY (**a**) and YOY (**b**) fish assemblages. Shadding represents 95% confidence intervals for each habitat-type.

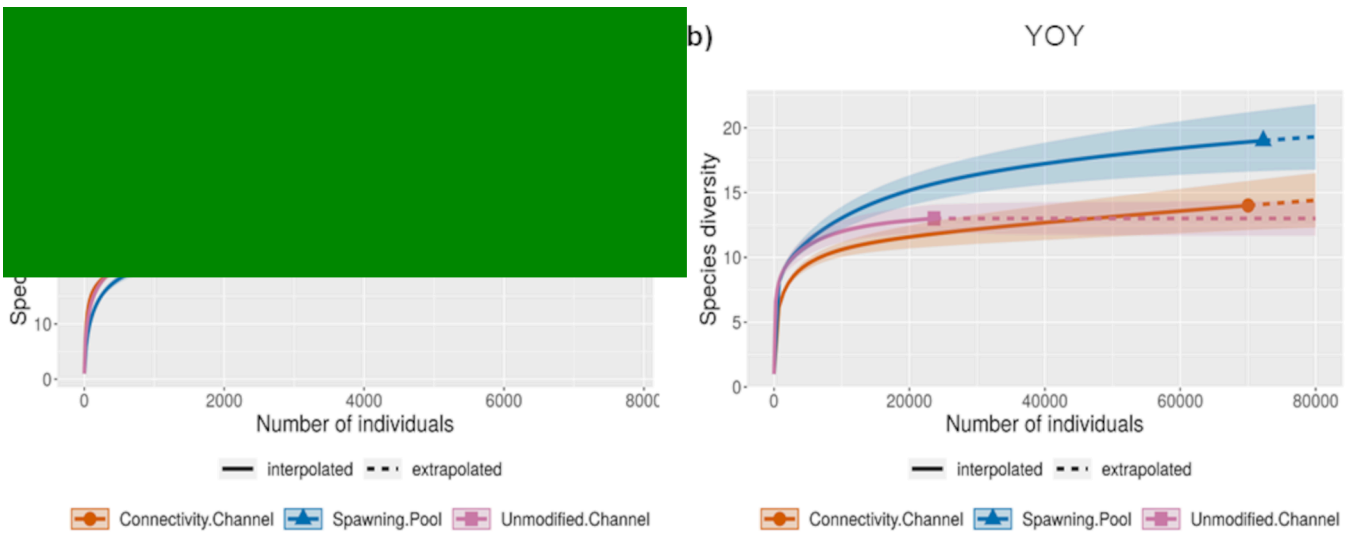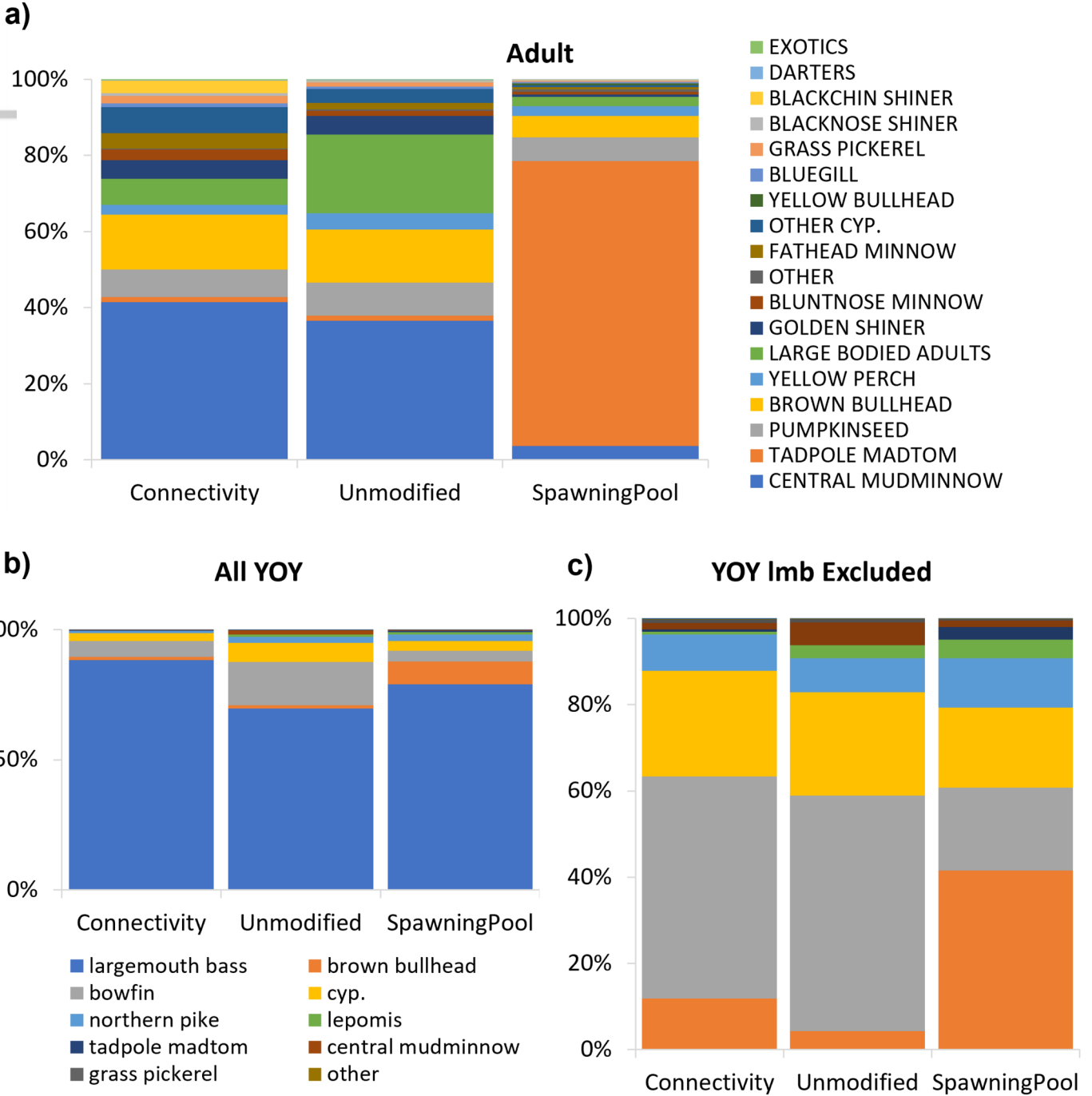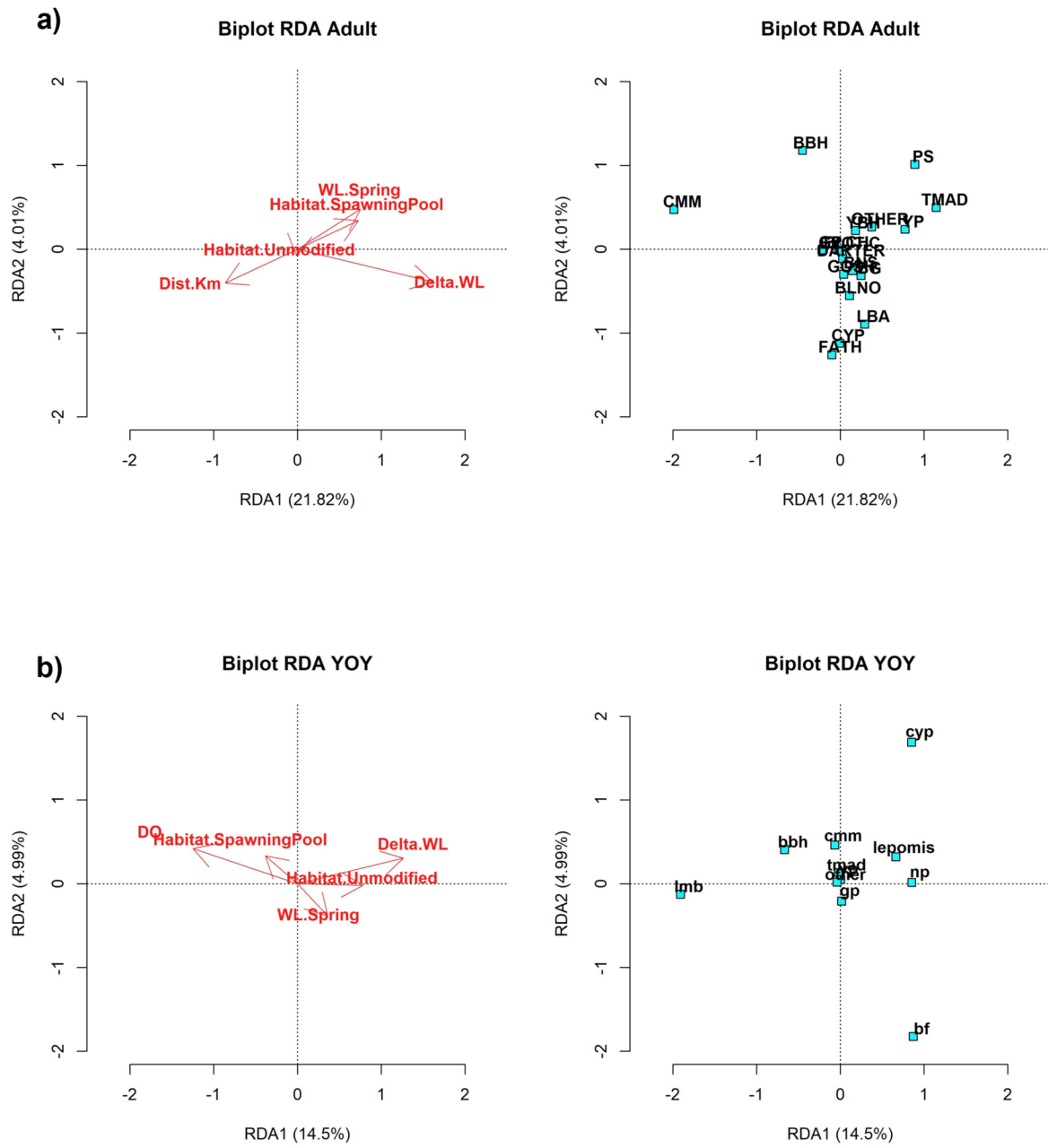**Figure 5.** Cumulative proportional abundance of the adult (non-YOY) (**a**) and YOY (**b**) fish assemblages captured at connectivity channels, unmodified channels and spawning pool complexes in French Creek across years (2012, 2013, 2016-2021). Because YOY largemouth bass (lmb) dominated the YOY fish assemblage, relative abundance of the remaining taxa after excluding YOY lmb was explored (**c**). Taxa presented in the figure and legend correspond and are ordered from bottom to top. More common taxa were represented at the bottom of the figure, whereas less common taxa were grouped towards the top of the figure.

Figure 6. RDA biplots for the environmental vectors (left panels) and species scores (right panels) of the non-YOY (adult) (**a**) and YOY (**b**) fish assemblages. Species names are acronyms defined in Table 1. Non-YOY taxa identified by capitalized acronyms and YOY taxa by lowercase acronyms.

Figure 7. Main-effect of habitat-type (left panels) and interaction terms (right panels) on $\log_{10}$ (n+1) transformed non-YOY (**a**) and YOY (**b**) fish $CPUE_{area}$. Habitat-types (left panels) covered by the same line are statistically equivalent based on Tukey post-hoc pairwise comparisons ($p >$

0.05). CUE$_{area}$ of the most abundant fish caught, YOY largemouth bass (LMB), showed a significant habitat-type by ΔWL interaction (**c**). CPUE$_{area}$ of YOY LMB increased at connectivity channels and decreased at spawning pool complexes with rising ΔWL.

Figure 8. Non-YOY (**a**) and YOY (**b**) yearly species richness. Left panels show differences in yearly species richness among habitat-types. Habitat-types that share the same letter do not differ statistically based on Tukey pairwise comparisons ($p > 0.05$). Right panel for non-YOY species richness (**a**) and YOY species richness (**b**) visualizes the WLSpring by ΔWL interaction, and the middle panel for (**b**) depicts the significant main-effect of dissolved oxygen on YOY species richness.

Figure 9. Patterns in temperature (**a**) and dissolved oxygen (**b**) among habitat-types (left panels). Habitat-types that share the same letter did not differ statistically based on Tukey pairwise comparisons ($p > 0.05$). Middle and right panel for temperature (**a**) show the habitat-type by ΔWL interaction and main-effect (black dashed line) of WLSpring on temperature, respectively. Right panel for dissolved oxygen (**b**) shows the main-effect (black dashed line) of ΔWL on dissolved oxygen.

Table 1. List of species caught during emigration survey across 2012, 2013 and 2016-2021. Taxa category assignment shown for the non-YOY (capitalized abbreviations) and YOY (lowercase abbreviations) fish assemblages. Taxa grouped into Other, CYP, yoy cyprinidae, DARTER, Exotics, and large bodied adults (LBA) categories represents groupings of taxa not used as standalone species. Hyphens represents age-class for that species not recorded in French Creek. Untransformed yearly-mean CPUE (SE) for each standalone species presented by age-class. Untransformed yearly-mean CPUE represent capture per net-night per year. When taxa were grouped into a category, yearly-mean CPUE presented for that category. When individual taxa were grouped in a category, a species specific CPUE was not presented (i.e., n.a.).

Common Name	Latin Name	Non-YOY cat.	Mean CPUE (SE)	YOY cat.	Mean CPUE (SE)
Bluegill	*Lepomis macrochirus*	BG	0.8 (0.4)	lepomis	n.a.
Blackchin shiner	*Notropis heterodon*	BLCH	1.6 (1.3)	yoy cyprinidae	n.a.
Bluntnose minnow	*Pimephales notatus*	BLN	2.7 (2.1)	yoy cyprinidae	n.a.
Blacknose shiner	*Notropis heterolepis*	BLNO	0.4 (0.2)	-	n.a.
Brown bullhead	*Ameiurus nebulosus*	BBH	18.9 (11.1)	bbh	19.5 (6.5)
Central mudminnow	*Umbra limi*	CMM	37.8 (13.5)	cmm	9.8 (4.4)
Fathead minnow	*Pimephales promelas*	FATH	2.3 (2.0)	-	n.a.
Golden shiner	*Notemigonus crysoleucas*	GOSH	4.1 (1.8)	yoy cyprinidae	n.a.
Grass pickerel	*Esox americanus vermiculatus*	GP	1.4 (0.5)	gp	2.0 (1.2)
Pumpkinseed	*Lepomis gibbosus*	PS	7.6 (1.4)	lepomis	n.a.
Tadpole madtom	*Noturus gyrinus*	TMAD	13.6 (10.5)	tmad	1.8 (1.0)
Yellow bullhead	*Ameiurus natalis*	YBH	0.2 (0.1)	-	n.a.
Yellow perch	*Perca flavescens*	YP	3.2 (0.6)	yp	0.3 (0.2)
Bowfin	*Amia calva*	LBA	n.a.	bf	269.4 (143.8)
Chain pickerel	*Esox niger*	LBA	n.a.	-	n.a.
Common carp	*Cyprinus carpio*	LBA	n.a.	-	n.a.
Largemouth bass	*Micropterus salmoides*	LBA	n.a.	lmb	756.2 (238.4)
Northern pike	*Esox lucius*	LBA	n.a.	np	19.7 (11.0)
Smallmouth bass	*Micropterus dolomieu*	LBA	n.a.	other	n.a.
Banded killifish	*Fundulus diaphanus*	OTHER	n.a.	other	n.a.
Black crappie	*Pomoxis nigromaculatus*	OTHER	n.a.	other	n.a.
Brook silverside	*Labidesthes sicculus*	OTHER	n.a.	other	n.a.
Rock bass	*Ambloplites rupestris*	OTHER	n.a.	other	n.a.
White sucker	*Catostomus commersonii*	-	n.a.	other	n.a.
Bridle shiner	*Notropis bifrenatus*	CYP	n.a.	-	n.a.
Common shiner	*Luxilus cornutus*	CYP	n.a.	-	n.a.
Creek chub	*Semotilus atromaculatus*	CYP	n.a.	-	n.a.
Eastern silvery minnow	*Hybognathus regius*	CYP	n.a.	-	n.a.
Emerald shiner	*Notropis atherinoides*	CYP	n.a.	yoy cyprinidae	n.a.
Mimic shiner	*Notropis volucellus*	CYP	n.a.	-	n.a.
Pugnose shiner	*Notropis anogenus*	CYP	n.a.	-	n.a.
Spotfin shiner	*Cyprinella spiloptera*	CYP	n.a.	-	n.a.
Spottail shiner	*Notropis hudsonius*	CYP	n.a.	-	n.a.
Iowa darter	*Etheostoma exile*	DARTER	n.a.	-	n.a.
Tessellated darter	*Etheostoma olmstedi*	DARTER	n.a.	other	n.a.
Etheostoma spp		DARTER	n.a.	-	n.a.
Round goby	*Neogobius melanostomus*	EXOTIC	n.a.	other	n.a.
Rudd	*Scardinus erythropthalmus*	EXOTIC	n.a.	-	n.a.
Tubenose goby	*Proterorhinus semilunaris*	EXOTIC	n.a.	-	n.a.
Non-YOY OTHER			**0.5 (0.2)**		n.a.
LBA			**11.1 (6.5)**		n.a.
CYP			**4.4 (3.8)**		n.a.
DARTER			**0.3 (0.3)**		n.a.
EXOTIC			**0.09 (0.03)**		n.a.
yoy lepomis			n.a.		**6.9 (3.2)**
yoy cyprinidae			n.a.		**39.2 (22.0)**
yoy other			n.a.		**0.13 (0.07)**

Table 2. AIC model selection results from linear mixed-effect modeling on fish CPUE$_{area}$ and species richness for the non-YOY and YOY fish assemblages. Top ranked models (within 2 units of the lowest AIC score) are presented relative to the null model. Top ranked models did not differ statistically, and the model with the fewest terms was selected to describe the response (bolded ranked model). Variables separated by a colon in a column header indicate an interaction between the terms. Variables not part of an interaction were treated as an additive main-effect.

Response	Age-Class	Model Rank	Habitat	DeltaWL	WLSpring	DO	TEMP	Distance	WLSpring : DeltaWL	Habitat : DeltaWL	Habitat : WLSpring	Habitat : DeltaWL : WLSpring	AIC SCORE
DENSITY	NON-YOY	1	•	•	•					•			171.70
		2	•	•	•				•	•	•	•	171.96
		3	•	•						•			**172.09**
		4	•	•	•	•				•			173.68
		Null											190.63
	YOY	**1**	•	•	•				•				**222.5**
		2	•	•	•	•			•				224.20
		Null											253.56
SPECIES RICHNESS	NON-YOY	**1**	•	•	•				•				**492.94**
		2	•	•	•				•	•	•	•	494.74
		3	•	•	•			•	•				494.87
		Null											513.71
	YOY	1	•	•	•				•	•	•	•	360.08
		2	•	•	•	•	•		•				360.55
		3	•	•	•	•			•				**360.78**
		Null											392.60