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ORIGINAL ARTICLE

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Aquatic connectivity treatments increase fish and macroinvertebrate use of *Typha*-invaded Great Lakes coastal wetlands

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Abstract

1. Coastal wetlands provide critical habitat for aquatic organisms and important ecosystem services for the terrestrial and aquatic landscapes that they bridge, but increasingly common invasive macrophytes disrupt plant communities, food webs, habitat structure and littoral–pelagic linkages. In Laurentian Great Lakes coastal wetlands, invasive cattails (*Typha* × *glauca* and *T. angustifolia*, hereafter *Typha*) homogenise ecosystem structure and reduce nearshore dissolved oxygen, and plant, fish and macroinvertebrate diversity. We hypothesised that management treatments which reduce *Typha* and its abundant litter promote structural heterogeneity and mitigate physicochemical and biodiversity impacts.
2. To test this hypothesis, we implemented a large-scale (2,048 m^2 treatment units), multi-site (four coastal wetlands) experiment in northern Michigan (U.S.A.) to examine how invasive *Typha* mechanical harvesting treatments (biomass harvest, aquatic connectivity channels, *Typha*-dominated control) altered fish, macroinvertebrate, plant, larval amphibian abundance and diversity, and water quality for 2-year post-treatment.
3. Both harvest and channel treatments reduced *Typha* biomass, cover and dominance; harvest increased multi-taxa species richness, fish diversity and abundance; and channels altered plant, fish, and macroinvertebrate community structures. Dissolved oxygen was greater and litter was reduced by both treatments, indicating likely mechanisms for shifts in fish and macroinvertebrate use.
4. Our results suggest that harvesting invasive macrophytes can ameliorate biodiversity impacts and improve habitat quality, and that adding aquatic connectivity channels can increase community complexity.
5. *Typha* management that incorporates both harvesting and aquatic connectivity channels appears to provide the greatest benefit to several taxonomic groups, likely by reducing *Typha* and its litter, increasing dissolved oxygen availability, and increasing the connection between open water and wetland interiors. Increasing

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habitat complexity and aquatic connectivity of invaded wetlands can promote biodiversity and provides a more realistic management goal than the complete elimination of invasive macrophytes.

KEYWORDS
biodiversity, coastal wetlands, Great Lakes, invasive plants, restoration, *Typha*

1 | INTRODUCTION

Lake fringing wetlands exert disproportionate ecological influence on their adjoining aquatic ecosystems (Sierszen et al., 2012; Wetzel, 1992). The coastal wetlands of the Laurentian Great Lakes, in particular, are critical for fish populations as they provide spawning grounds for adults, nursery areas for larvae and juveniles, and food sources for many species (Brazner & Beals, 1997; Jude & Pappas, 1992; Trebitz & Hoffman, 2015). Aquatic macrophytes provide food, spawning, nursery and refuge habitat for fishes, amphibians and macroinvertebrates (Conrow et al., 1990; Hanson et al., 2015; Hecnar, 2004). Many organisms depend on these nearshore, vegetated habitats throughout their lives; for example, vegetation can be a predictor of fish presence in lakes (Brazner & Beals, 1997; Randall et al., 1996). The structural composition of wetland vegetation also is important to aquatic species. For fishes, the presence and configuration of aquatic vegetation growth forms (i.e., emergent, submergent and floating macrophytes) is especially important (Brazner & Beals, 1997; Cvetkovic et al., 2010; Smokorowski & Pratt, 2007). Increased vegetation diversity and structural complexity in wetlands are mirrored by increased diversity and species richness of both larval (Conrow et al., 1990; Höök et al., 2001; Tanner et al., 2004) and adult fish communities (Brazner & Beals, 1997; Leblanc et al., 2014; Tonn & Magnuson, 1982). As structural complexity increases with a mix of floating, emergent and submerged plant types, fish tend to be more abundant and diverse. Macroinvertebrates also benefit from the structural complexity provided by the highly dissected leaves of submerged aquatic plants relative to simple emergent plant stems (Schultz & Dibble, 2012).

Widespread invasion by non-native macrophytes are homogenising species assemblages and reducing structural complexity of freshwater coastal wetlands (McKinney & Lockwood, 1999; Valley & Bremigan, 2002). In the Great Lakes, hybrid (*Typha* × *glauca*) and narrowleaf (*Typha angustifolia*) cattails (hereafter *Typha*) have expanded their ranges, altering environmental conditions (Bansal et al., 2019; Tuchman et al., 2009) and displacing native plant dominated communities (Lishawa et al., 2010; Wilcox et al., 2008). *Typha* alters wetland structure by replacing the heterogeneous conditions typical of complex wetland and aquatic plant communities with a homogenous environment dominated by the emergent plant *Typha* and its tall, dense, difficult-to-penetrate stems and litter (Bansal et al., 2019; Larkin et al., 2012; Lishawa et al., 2017; Tuchman et al., 2009).

Typha invasion results in detrimental effects on fishes and macroinvertebrates (Lawrence et al., 2016; Schrank & Lishawa, 2019) and unknown effects on amphibians. For fishes, densely vegetated habitat structure can reduce foraging efficiency (Gotceitas & Colgan, 1989; Hagerthey et al., 2014) and growth (Crowder & Cooper, 1982). Furthermore, dissolved oxygen (DO) tends to be reduced in *Typha* stands relative to native nearshore vegetation (Bunch et al., 2010; Schrank & Lishawa, 2019), which may prompt fish to move out of these highly productive nearshore zones and reduce available habitat for fishes. *Typha* also fragments wetlands by disconnecting open water from interior marsh and meadow zones important for spawning and rearing of larvae and juvenile fishes (Farrell, 2001; Massa & Farrell, 2020; Neveldine et al., 2019). Because of the density of *Typha* stands, sampling fish within these areas is difficult and studies are lacking. Fish abundance and species richness can be reduced in *Typha* stands relative to native wetland vegetation and fish communities within *Typha* stands can be dominated by hypoxia-tolerant species (Schrank & Lishawa, 2019). *Typha* invasion also is likely to alter aquatic invertebrate communities by reducing habitat complexity (Burton et al., 2002; Schultz & Dibble, 2012) and associated epiphytic heterogeneity (Gosselain et al., 2005; Krecker, 1939), increasing litter accumulation (Farrer & Goldberg, 2009; Vaccaro et al., 2009), and decreasing littoral mixing, resulting in decreased DO (Cardinale, 1996; Croft-White et al., 2021; Schrank & Lishawa, 2019). *Typha*-invaded marshes exhibit reduced macroinvertebrate density and diversity compared to both native marshes (Lawrence et al., 2016) and dredged ponds (Schummer et al., 2012).

Amphibians are key food-web components (Brazner & Beals, 1997; Gibbons et al., 2006), yet they are sensitive to changes in habitat such as those caused by invasive plants (Maerz et al., 2005; Mifsud, 2014; Rittenhouse, 2011). However, the effects of *Typha* invasion on amphibians are unknown. High density stands of *P. australis*, a species similar to *Typha*, extended the larval developmental period of juvenile wood frogs (*Lithobates sylvatica*), a potentially deleterious effect in dry years (Perez et al., 2013). In addition to the reduction of habitat, the high carbon (C):nitrogen (N) and C:phosphorus (P) ratios and the consequent slow decomposition rate of *Typha* litter may negatively affect frog larvae in particular because they rely on periphyton and phytoplankton (Stephens et al., 2013).

The near ubiquity of *Typha* makes eradication an unreasonable goal, whereas managing *Typha* to increase habitat quality and biodiversity may be a viable option. A variety of approaches have been used to control *Typha* and restore wetland habitats and functions, including applying herbicide, controlling water levels,

burning, mowing, grazing and biomass harvesting, and combinations of these techniques (Bansal et al., 2019). Accumulated litter in *Typha* stands is an important driver of plant diversity loss and ecosystem change (Larkin et al., 2012) and management techniques that remove litter have successfully increased plant community recovery (Lishawa et al., 2015, 2017, 2020). Additionally, cutting through channels or dredging ponds within *Typha* stands may increase plant community quality, fish habitat quality (Neveldine et al., 2019), and increase marsh-bird, macroinvertebrate and plant richness (Schummer et al., 2012) by increasing habitat connectivity. However, these approaches have not been adequately or experimentally tested.

Invasive *Typha* clearly modifies wetland structural complexity and water chemistry, resulting in reductions in the biodiversity and abundance of aquatic organisms. What remains unclear is whether management treatments designed to reduce litter and enhance aquatic connectivity will restore wetland biodiversity. Experimental tests of wetland restoration techniques are typically small in scale, limiting their utility to management-relevant scales (Wagner et al., 2008). Here, we conducted a uniquely large-scale, multi-site and multi-taxa experiment to investigate the biodiversity response to treatments and the physiochemical mechanisms behind any such response. Specifically we tested the effectiveness of mechanically harvesting invasive *Typha* and installing aquatic connectivity channels using large experimental plots (32 × 64 m) replicated across four invaded Great Lakes coastal wetland complexes to examine how treatments altered aquatic macroinvertebrate, fish, larval amphibian, and native plant diversity and abundance. We hypothesised that channel additions would increase the abundance and diversity of mobile aquatic organisms (fish, macroinvertebrates and larval amphibians) and shift plant communities away from emergent species toward submergent aquatic species, and that harvesting would increase native plant diversity and abundance.

2 | METHODS

2.1 | Study sites

We selected four Great Lakes coastal wetland complexes in northern Michigan (U.S.A.) for our study, one in the northern Lower Peninsula and three in the eastern Upper Peninsula. Two of the wetlands (Cheboygan Marsh and St. Ignace Marsh) are in the Straits of Mackinac, near the confluence of Lakes Michigan and Huron, and two (Munuscong Marsh and Sand Island Marsh) are in the St. Marys River, the connecting channel between Lakes Superior and Huron (Figure 1). All wetlands shared similar connectivity to the open lake, but hydrogeomorphic type varied among the wetlands; Cheboygan Marsh and St. Ignace Marsh are lacustrine open embayment types, Munuscong Marsh is a connecting channel river delta, and Sand Island is a connecting channel protected embayment (Albert et al., 2005).

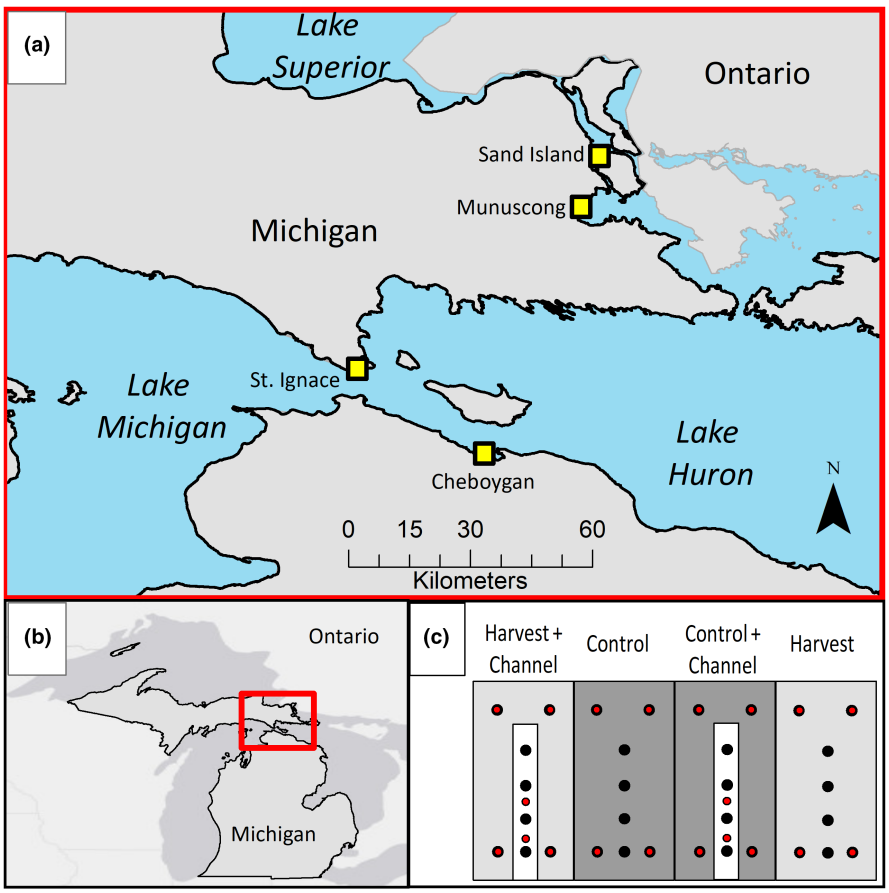


FIGURE 1 Map of experimental treatment wetland locations in northern Michigan, U.S.A. (a); study area within the Great Lakes region (b); diagram of block (64 × 128 m), plot (32 × 64 m), and subplot layout that was repeated at all sites (c); black markers indicate plant sampling locations (1 × 1 m quadrats); red markers indicate fish, larval amphibian, macroinvertebrate and water-quality sampling points (plot corner sampling points overlapped for all taxa).

2.2 | Study design

We conducted our study within invasive *Typha*-dominated portions of the four wetland complexes. Owing to the abundance of advanced generation hybrids in upper Midwest *Typha* populations and the high frequency of disagreement between morphological traits and molecular identification (Geddes et al., 2021), we did not attempt to differentiate between hybrid cattail (*Typha* × *glauca*) and narrow-leaved cattail (*T. angustifolia*), but clumped invasive cattails into one taxon for this study. Invasive cattails have been widespread in all study wetlands for over a decade (Lawrence et al., 2016; Lishawa et al., 2010) and for more than 50 years in Cheboygan Marsh (Lishawa et al., 2013), and were the dominant emergent plant taxon (>50% relative dominance) of >25 ha in each focal wetland.

In order to test biodiversity responses to invasive *Typha* harvest and aquatic connectivity channel treatments, we used a block design with four, 32 × 64 m plots nested within each block. Each treatment block consisted of four randomly assigned treatments: harvest, harvest-channel (a channel nested within a harvested plot), control-channel (a channel nested within an unharvested plot) and control (unmanipulated *Typha*-dominated plot). We created one block in each wetland except St. Ignace, which had two blocks (Figures 1c and 2).

In July and August 2016, we randomly assigned treatments, delineated all blocks and plots, and implemented treatments. Plots were orientated with their length (64 m) perpendicular to the shoreline, so that they crossed the primary water level gradient at each site. Each plot was 32 m wide. We harvested and removed all biomass (i.e., standing litter and living vegetation) at 20 cm above the water level from the harvest and harvest-channel plots using a low ground-pressure Softrak wetland plant harvester (Loglogic). Within the harvest-channel and control-channel plots, we manually cut and removed all biomass at the sediment surface using aquatic weed whackers (RedMax) from 3-m-wide by 50-m-long channels, which bisected the centre of each plot along the water depth gradient (Figure 2). The aquatic weed whackers have flat reciprocating cutting blades, which slide along the surface of the sediment, allowing us to cut stems approximately 2 cm above the surface with minimal substrate disturbance.

2.3 | Field data collection

We collected water quality and biodiversity data (plant, fish, macroinvertebrate and larval amphibian) for 2 years following treatment implementation, in summer (June–August) 2017 and 2018 from subplots within each plot; treatments were implemented at the plot level. Subplot distribution and density differed among the taxa sampled (see below).

2.3.1 | Plant sampling

Within each plot we established eight, 1 × 1-m subplots for plant community data collection. Four subplots were located in plot corners equidistant from the plot margins (8 m) and four subplots were located 12 m apart along the plot's meridian to align with the channels (Figure 1c). In mid-July to mid-August of each study year (2017 and 2018), we estimated the percentage cover for every species and *Typha* stem density and height from each subplot. Invasive cattail height data were used to calculate biomass, using a height-to-biomass allometric equation (Lishawa et al., 2015).

2.3.2 | Fish and larval amphibian sampling

We established either four or six subplots for fish sampling within each plot: four plots within the harvest and control treatment plots, which corresponded with the corner vegetation subplots (i.e., 8 m from each plot margin), and two additional subplots located 15 and 30 m into the channels within the harvest-channel and control-channel plots (Figure 1c). We sampled fishes three times throughout the growing season (June, July and August) in each year (2017 and 2018) from each subplot using three Gee minnow traps (mesh size 0.64 cm) set over one to three nights. We used minnow traps in lieu of fyke nets or electrofishing because minnow traps are effective at sampling small-bodied fishes in dense vegetation (Henning et al., 2014; Jacobus & Webb, 2005; Webb, 2008) and vegetation density in most subplots precluded efficient sampling by these other methods. Minnow traps were set 5 m apart, baited with dry dog food, and were checked every 24 h. Fishes were identified to species-level (or lowest taxonomic group possible) in the field and enumerated. Any adults of difficult-to-identify species (e.g., shiner species) were euthanised with 250 mg/L tricaine methanesulfonate (MS-222), fixed in 10% formalin, and transferred to 70% ethanol after 24 h for later identification in the laboratory. Fish abundance was quantified for each subplot as catch-per-unit-effort (CPUE) as the number of fishes captured in the set of three minnow traps in each subplot in 24 h. We did not include fish data from the Munuscong Marsh treatment block in our analysis because fish abundance across all plots and treatments was extremely low, indicating that minnow trap sampling at this site was ineffective. Larval amphibians were collected in minnow traps during fish sampling and were enumerated and released in the field (Skelly & Richardson, 2010). For each subplot the CPUE for larval amphibians was defined as the number of larvae captured in the set of three minnow traps in a 24 h period.

2.3.3 | Macroinvertebrate sampling

We collected macroinvertebrate samples in late July to early August in 2017, to correspond with the period when emergent plants typically reach maximum annual biomass and late instars of most aquatic insects are present and easy to identify (Kashian & Burton, 2000). We collected at least three replicate samples per subplot, each replicate consisting of 1-m dip net (0.5-mm mesh) sweeps at the water surface, mid-depth and substrate surface. In the field, we emptied nets into white pans and picked macroinvertebrates

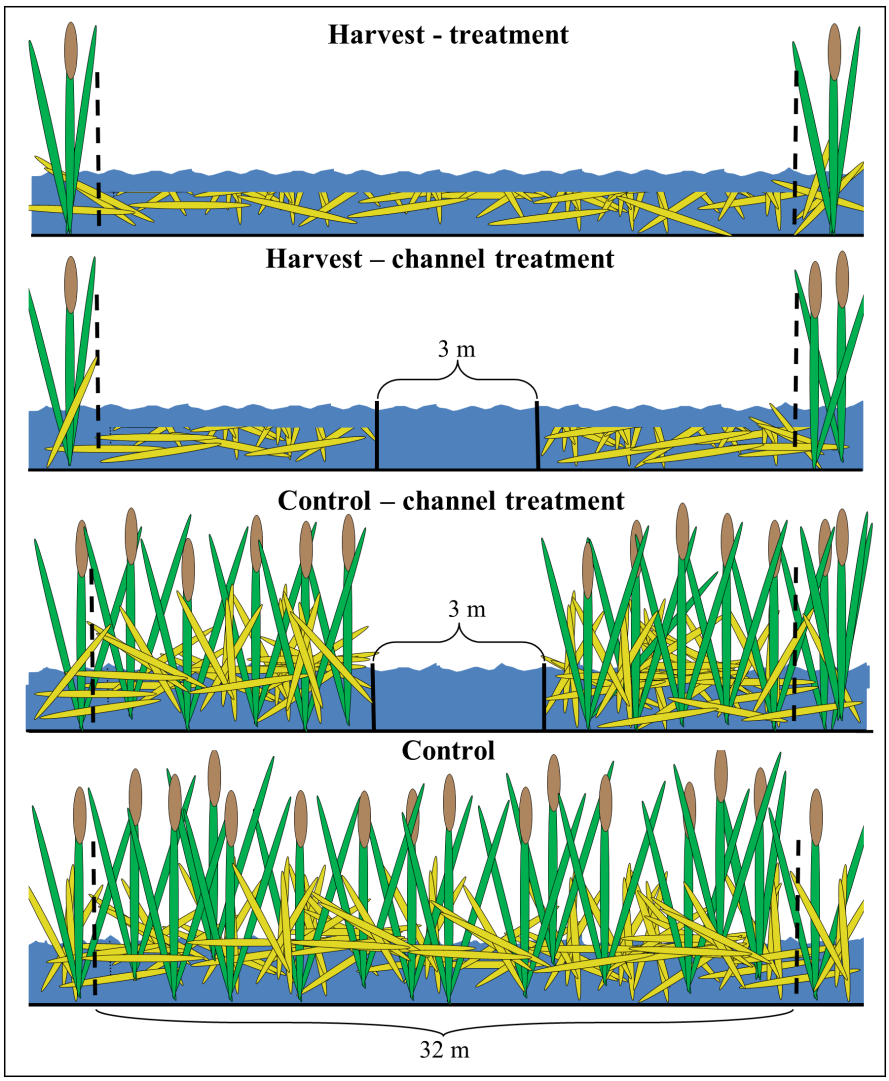


FIGURE 2 Invasive cattail management treatments: harvest, biomass cut and collected at 20-cm above the sediment; harvest channel, biomass harvest treatment plus a 3-m-wide channel in which biomass was cut and removed at the sediment surface; control-channel, a sediment surface-harvest channel within an untreated matrix; and control, no manipulation. Reproduced with permission from Lishawa et al. (2020).

(Uzarski et al., 2004). In the laboratory, organisms were sorted to the finest taxonomic group possible, and richness and abundance metrics were estimated. Crayfish were sampled using the same method as fishes. In the field, we observed dramatically different patterns of invertebrate abundance by treatment within the Munuscong block, where large numbers of Asellidae were present in the control and harvest treatments. Therefore, we statistically evaluated this metric (invertebrate abundance [number/m^2]) as a full model (all blocks), with Munuscong block excluded, and with the Munuscong block alone.

2.3.4 | Water-quality sampling

We measured standard water-quality parameters to relate taxonomic data with abiotic conditions. These parameters included water depth, temperature, DO, turbidity, pH, specific conductivity (determined *in situ*), total N, total P and chlorophyll-*a* (chl-a, determined in the lab). *In situ* water-quality parameters were measured at each subplot and sampling date using a YSI Professional Plus Multiparameter Instrument (Xylem Inc.) and a Hach 2100Q Portable Turbidimeter. Nutrients (total N and P) were collected during fish sampling and analysed using standard methods on a SEAL Autoanalyser 3 spectrophotometer (SEAL Analytical). Chloride, fluoride and sulfur also were collected during fish sampling, laboratory-filtered through a MF-Millipore 0.45-μm MCE membrane filter, and analysed on a Dionex Integrion High-Performance Ion Chromatography system (Thermo Fisher Scientific Inc.). Chlorophyll-*a* samples were collected by filtering a known volume of water through a 45-μm filter in the field. Filters were stored on ice and chll-*a* was analysed using a Turner Designs TD-700 Fluorometer. All analyses were completed at the University of Michigan Biological Station, in Pellston, Michigan, USA.

2.4 | Data analyses

Preliminary data analysis indicated no statistical differences between channels, whether they were nested within a harvest matrix (i.e., harvest-channel) or within an unharvested matrix (i.e., control-channel). Likewise we found no statistical differences between the

harvested treatment matrix and the harvest plots (Figure 2). Thus, subsequent analyses involved collapsing the data into one of three treatments for statistical analyses: harvest, channel and control (where harvest included both harvest and harvest matrix plots; channel included channel plots nested within a harvested matrix or nested within a control matrix; and control included control and control matrix plots). We evaluated the relative quality of full (harvest, harvest + channel, control, control + channel) and simplified models (harvest, channel or control) by assessing delta Akaike information criterion (AIC) values (Burnham & Anderson, 2004). For the preponderance of response variables, model quality did not differ substantially (ΔAIC <2; 15 cases) or the simple model was better (ΔAIC >2; 20 cases), further supporting the decision to analyse more parsimonious models (Table S1). We tested treatment effects (channel, harvest, control) on plant, fish, macroinvertebrate and larval amphibian community and diversity metrics (richness, Shannon diversity [H′] and abundance) using linear mixed-effects (LME) models with block and year as sources of random error. We assessed model fit by evaluating the conditional and marginal R^2 values, which represent the variance explained by the fixed effect (i.e., treatment) and the variance explained by the full model (i.e., fixed effects and random effects), respectively. We assessed differences among treatments using the least squares means approach and Tukey's honestly significant difference *post hoc* (HSD) tests. Response variable data were log- or square root-transformed, when necessary, to meet LME model assumptions of normality and homoscedasticity of residuals. We evaluated multivariate community distribution using nonmetric multidimensional scaling (NMDS) ordination with Bray–Curtis dissimilarity calculations and assessed community differences by site and treatment using permutational multivariate analysis of variance (PERMANOVA). We used indicator species analyses to determine whether taxonomic groups were associated with treatments, where the indicator statistic represents the fidelity (i.e., the proportion of perfect indication) of a species to one or more treatment. We analysed data in R 4.1.1 (R Core Team, 2021), using the *nlme* package for lme (Pinheiro et al., 2017), the *vegan* package for diversity calculations, NMDS, PERMANOVA and Betadispersion tests (Oksanen et al., 2020), and the *indicspecies* package for indicator species analysis (Dufrêne & Legendre, 1997). Significance for all statistical tests was $\alpha < 0.05$.

3 | RESULTS

3.1 | Total biodiversity

Harvesting *Typha* biomass at 20 cm above the water surface increased multi-taxa species richness in both years following treatment (year-1: fish, plants, macroinvertebrates and larval amphibians; year-2: fish, plants and larval amphibians) with an average fixed-effect of 3.00 additional species per m^2 compared to control plots in year-1 ($p = 0.01$) and an additional 1.33 species per m^2 in year-2 ($p = 0.018$; year-2 data did not include macroinvertebrates). Likewise, Shannon diversity differed by treatment in both years; harvesting increased diversity compared to channel treatments in year-1 and promoted greater diversity than channel or control treatments in year-2 (fixed effect, 0.27; $p = 0.008$; Figure 3; Table 1). Creating channels reduced multi-taxa species richness compared to harvest or control treatments in both years following treatment (Figure 3; Table 1).

3.2 | Fish response

All calculated metrics of fish diversity (richness, Shannon diversity [H′] and abundance [CPUE]), were affected by treatment (all metrics $p < 0.01$) and each metric was significantly greater in harvest than in control; channels were intermediate between the control and harvest treatments (Table 1). Indicator species analyses revealed that several fish families were significantly associated with each treatment: yellow perch (family: Percidae) corresponded with channel treatments, true minnows (family: Leuciscidae) were associated with harvest treatments, whereas sunfishes (family: Centrarchidae) were indicators of both channel and harvest treatments (Table 2). At the family level, Centrarchidae were over three-fold more abundant in channel than harvest or control treatments; Leuciscidae were >10-fold more abundant in the harvest than channel or control treatments; and mudminnows (family: Umbridae) were half as abundant in channel than in harvest or control treatments (Table 3). Fish composition diverged by treatment type (PERMANOVA: $F = 3.99$; $R^2 = 0.06$; $p < 0.01$) with channel plots exhibiting significantly greater multivariate dispersion than harvest or control plots (Beta dispersion by group $p < 0.01$; Figure 4). A total of 15 fish species were found in the control treatment, 14 in the harvest and 16 in the channel treatments (Table S2).

3.3 | Plant response

Channel treatments nearly eliminated *Typha* from the plant community, and significantly reduced all measures of *Typha* vigour including biomass, cover, relative dominance (RD; % of total vegetative cover), average height and density (stems/m^2; Table 3). However, harvest and control treatments did not differ significantly from each other except in *Typha* RD, where the control treatment had greater dominance than the harvest treatment (61.21 ± 2.22 and 55.08 ± 2.38, respectively). Treatments altered plant diversity and RD metrics, with lower richness, H′, *Typha* RD, *Carex* spp. RD, grass RD and emergent spp. in channel than control and harvest treatments (all $p < 0.001$; Table 1). Aquatic channel creation also shifted plant functional group dominance, with channels having nearly three-fold greater relative dominance of submergent species than either harvest or control treatments ($p < 0.001$; Table 3). Of total plant species, 56 were found in harvested treatments, 38 in controls and 28 in channels (Table S3). Indicator species analysis highlighted plant community shifts by treatment, with no species associated with control plots; four species of submergent plants and an aquatic moss associated with the channel treatments; a grass, a sedge, a forb and a horsetail associated with harvest treatments; and

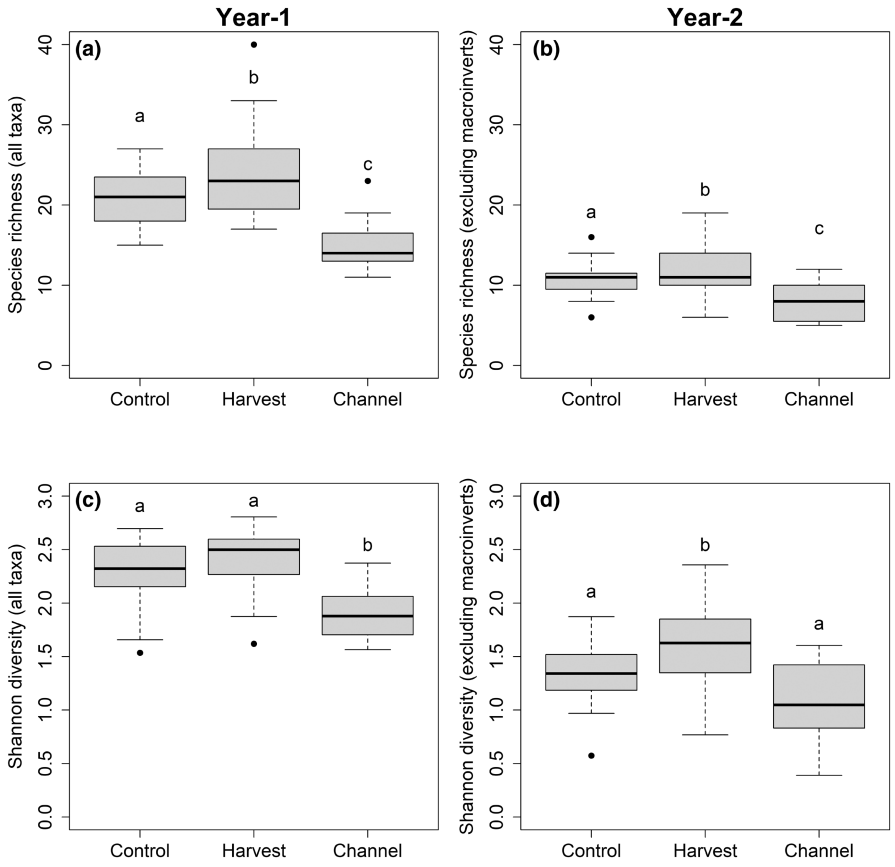


FIGURE 3 Multi-taxa species richness in year-1 (a) and year-2 (b); Shannon diversity in year-1 (c) and year-2 (d) by treatment. Year-1 taxonomic groups sampled included fish, macroinvertebrates, plants and larval amphibians; Year-2 taxonomic groups sampled included fish, plants and larval amphibians (macroinvertebrates were not sampled in Year-2). Statistical differences between treatments, determined by the least-squares means method, are indicated by non-overlapping superscript letters.

one species of submergent plant associated with harvest and channel treatments (Table 4). Multivariate plant community composition varied significantly by treatment (PERMANOVA: $F = 26.83$; $R^2 = 0.15$; $p < 0.001$). The channel treatment plots diverged in NMDS species space from control and harvest plots and were significantly and positively correlated with submergent plant cover, water depth and total vegetation cover vectors (Figure 4).

3.4 | Macroinvertebrate response

Macroinvertebrate abundance differed among treatments (all blocks $p = 0.04$; Munuscong excluded $p = 0.03$; Munuscong only $p = 0.004$; Table 1). When Munuscong was included in analyses, abundance was higher in control and harvest compared to channel treatments ($p = 0.04$; Table 1). When Munuscong was excluded from analyses, abundance was higher in harvest treatments compared to controls ($p < 0.05$; Table 1). Munuscong had a different community of macroinvertebrates compared to other sites, with isopods in the family Asellidae comprising between 79% and 97% of the invertebrate community in the harvest and control treatments. Consequently, the pattern in Munuscong, with more macroinvertebrates in control and harvest compared to channel treatments ($p < 0.05$), had a strong effect on the overall analysis. Treatment did not affect macroinvertebrate diversity but did affect richness; pairwise comparisons showed that invertebrate richness was lower in the channel compared to the control and harvest treatments ($p < 0.05$; Table 1). Indicator species analysis showed that several families were associated with treatments (Table 5). The family Mesoveliidae (water treaders) were associated with controls. Cambaridae (crayfish) were associated with channels and more abundant in the channel and harvest treatments compared to the controls. Gomphidae (club-tailed dragonflies) were associated with harvest treatments and more abundant in harvest than control or channel treatments (Tables 1 and 3). Likewise, Lestidae (spread-winged damselflies) and Polycentropodidae (trumpet net and tube-making caddis flies) were associated with control and harvest treatments. Lestids were similar in abundance in control and harvest treatments, but never found in channels. Polycentropodidae were more abundant in the control treatments compared to the harvest and channel treatments and more abundant in the harvest treatment compared to the channels (Tables 1 and 3). Macroinvertebrate communities (aggregated at the plot-level) diverged by treatment type in multivariate space (PERMANOVA: $F = 1.96$; $R^2 = 0.05$; $p < 0.001$; Figure 4c), with the channel communities differing from the control and harvest communities. *Typha* biomass, detritus, conductivity, pH and water depth were significant explanatory variables that corresponded with variability in community composition. Table S4 includes the full list of macroinvertebrate taxa identified by treatment.

3.5 | Larval amphibian response

We collected 1993 larval amphibians across both years. Treatment affected the quantity of larval amphibians ($p = 0.047$) and the mean

TABLE 1 Summary statistics and results of linear mixed effects models of biodiversity variables by treatment with block treated as a random factor for single year models (e.g., variable ~ Treatment, random = Block) and block, year, plot, and subplot treated as nested random factors for repeated measures models (e.g., variable ~ Treatment, random = Year/Block/Plot/Subplot).

	Model fit		ANOVA	Treatment		
Variable	Marginal R^2	Conditional R^2	Treatment (p)	Control $\overline{X} \pm SE$	Harvest $\overline{X} \pm SE$	Channel $\overline{X} \pm SE$
Species richness all taxa (2017)*	0.33	0.52	<0.001	20.75 ± 0.45^{a}	23.75 ± 0.70^{b}	15.00 ± 0.57^{c}
Species richness all taxa (2018)†	0.21	0.67	<0.001	10.71 ± 0.29^{a}	12.04 ± 0.40^{b}	8.00 ± 0.39^{c}
Shannon diversity H′ (2017)*	0.29	0.60	<0.001	2.28 ± 0.04^{a}	2.40 ± 0.04^{a}	1.89 ± 0.04^{b}
Shannon diversity H′ (2018)†	0.26	0.26	<0.001	1.34 ± 0.04^{a}	1.61 ± 0.05^{b}	1.08 ± 0.06^{a}
Fish richness	0.02	0.72	<0.01	3.63 ± 0.14^{a}	4.44 ± 0.19^{b}	3.75 ± 0.29^{ab}
Fish H′	0.04	0.71	<0.001	0.70 ± 0.04^{a}	0.94 ± 0.04^{b}	0.81 ± 0.07^{ab}
Fish abundance (CPUE)	0.06	0.85	<0.01	4.09 ± 0.37^{a}	6.36 ± 0.65^{b}	5.41 ± 1.04^{c}
Plant richness	0.27	0.61	<0.001	5.77 ± 0.19^{a}	6.03 ± 0.23^{a}	3.47 ± 0.32^{b}
Plant H′	0.19	0.99	<0.001	1.09 ± 0.03^{a}	1.15 ± 0.03^{a}	0.83 ± 0.04^{b}
Larval amphibian abundance (CPUE)	0.01	0.99	0.047	0.92 ± 0.13	1.66 ± 0.27	2.44 ± 0.71
Invertebrate richness†	0.18	0.32	<0.001	11.31 ± 0.38^{a}	11.81 ± 0.28^{a}	8.50 ± 0.46^{b}
Invertebrate H′†	<0.01	0.84	0.47	1.50 ± 0.10	1.56 ± 0.09	1.45 ± 0.09
Invertebrate abundance (number/m^2)†	0.03	0.64	0.04	149.38 ± 15.94^{a}	135.34 ± 10.67^{a}	77.31 ± 3.34^{b}
Invertebrate abundance (number/m^2) (without Munuscong)†	0.09	0.24	0.03	62.21 ± 2.89^{a}	82.50 ± 3.09^{b}	78.58 ± 4.34^{ab}
Invertebrate abundance (number/m^2) (Munuscong only)†	0.45	0.50	0.004	410.88 ± 34.20^{a}	293.88 ± 28.30^{a}	73.50 ± 0.45^{b}

Note: The marginal R^2 (i.e., variance explained by the fixed effect of treatment), Conditional R^2 (i.e., variance explained by the full model fixed and random effects), analysis of variance (ANOVA) p-values for fixed effects, treatment means and *post hoc* test results determined with least-squares means method, where non-overlapping superscript letters indicate significant differences ($p < 0.05$) between treatments, are presented for each model.

*Species richness data include total plant, fish, larval amphibian and macroinvertebrate species per subplot.

†Macroinvertebrate data were not collected in 2018; 2018 species richness data include plant, fish and larval amphibians, invertebrate data are from 2017 only.

TABLE 2 Results of indicator species analysis of 2017 and 2018 fish data collapsed to families by treatment type (Control, Channel, Harvest) where indicator value represents the proportion of perfect indication within a treatment or combination of treatments.

Treatment	Fish family	Indicator statistic	p-value
Control	None	NA	NA
Channel	Percidae	0.311	0.04
	Centrarchidae[a]	0.844	<0.01
Harvest	Leuciscidae	0.494	0.03
	Centrarchidae[a]	0.844	<0.01

[a]Centrarchidae were indicative of both channel treatments and harvest treatments.

number of amphibians collected per plot was highest in the channel. However, *post hoc* comparisons by treatment did not result in significant pairwise differences by treatment (Table 1).

3.6 | Environmental conditions

After controlling for the random effect of block, a suite of measured environmental conditions varied by treatment (Table 6). Both harvest and channel treatments reduced plant litter cover compared to controls, and channel treatments had lower surface litter than harvest treatments. Total vegetation cover (including submergent vegetation) was greatest in the channel treatments. Harvest treatment increased average DO ($p < 0.001$), water temperature ($p < 0.001$) and conductivity ($p = 0.002$), and decreased water depth ($p < 0.001$) compared to controls and channel treatments. The relationship between DO and time of day differed by treatment, where the slope for controls was significantly lower than the slope of both channel and harvest treatments ($p < 0.01$; Figure 5). Water depth was greatest in channel treatments (66.0 ± 2.1 cm), moderate in controls (63.1 ± 1.8) and lowest in harvest treatments

TABLE 3 Response variables ($\overline{X} \pm SE$) grouped across years.

Variable	Model fit		Treatment		
Plant metrics	Marginal R^2	Conditional R^2	Control $\overline{X} \pm SE$	Harvest $\overline{X} \pm SE$	Channel $\overline{X} \pm SE$
Typha biomass (g/m^2)	0.31	0.39	979.00 ± 70.98^a	705.58 ± 46.72^b	3.82 ± 1.51^c
Typha cover (%)	0.49	0.90	15.40 ± 0.67^a	12.57 ± 0.59^b	0.18 ± 0.06^c
Typha relative dominance (% of total cover)	0.47	0.95	61.20 ± 2.22^a	55.08 ± 2.38^b	2.63 ± 1.39^c
Typha height (m)	0.63	0.70	2.14 ± 0.06^a	2.01 ± 0.05^a	0.28 ± 0.08^b
Typha density (stems/m^2)	0.45	0.68	27.22 ± 1.22^a	31.05 ± 1.44^b	0.44 ± 0.14^c
Submergent spp. (% of total cover)	0.31	0.93	24.55 ± 2.19^a	28.34 ± 1.76^a	73.63 ± 4.19^b
Forb spp. (% of total)	0.05	0.20	1.77 ± 0.43^a	2.34 ± 0.55^a	9.89 ± 3.07^b
Fish families (CPUE)					
Centrarchidae	0.02	0.48	0.30 ± 0.05^a	0.88 ± 0.10^b	3.37 ± 0.93^b
Gasterosteidae	<0.01	0.48	1.25 ± 0.33	1.51 ± 0.34	0.51 ± 0.11
Ictaluridae	0.16	0.16	0.18 ± 0.02^a	0.85 ± 0.18^b	0.18 ± 0.29^a
Leuciscidae	0.01	1.00	0.05 ± 0.02^a	0.69 ± 0.16^b	0.02 ± 0.01^{ab}
Percidae	0.02	1.00	0.01 ± 0.00	0.00 ± 0.00	0.03 ± 0.01
Umbridae	0.16	0.77	2.21 ± 0.11^a	2.43 ± 0.12^a	1.18 ± 0.10^b
Invertebrate families (number/m^2)					
Cambaridae	0.02	0.75	0.03 ± 0.02^a	0.06 ± 0.02^b	0.88 ± 0.16^b
Gomphidae	0.14	0.33	0.34 ± 0.07^a	0.94 ± 0.11^b	0.13 ± 0.06^a
Lestidae	0.26	0.30	1.81 ± 0.20^a	1.19 ± 0.13^a	0.00 ± 0.00^b
Physidae	0.26	0.30	4.19 ± 0.52^a	3.06 ± 0.37^a	2.81 ± 0.55^b
Polycentropodidae	0.09	0.29	0.91 ± 0.11^a	0.56 ± 0.10^{ab}	0.06 ± 0.03^b

Note: For each model, the marginal R^2 (i.e., variance explained by the fixed effect of treatment) and Conditional R^2 (i.e., variance explained by the full model fixed and random effects) are presented, and statistical differences between treatments, determined by the least-squares means method, are indicated by non-overlapping superscript letters.

(59.0 ± 1.9; Table 6). pH was slightly, but significantly lower in the channel treatments (7.40 ± 0.02) than in the harvest (7.44 ± 0.01) and controls (7.43 ± 0.01). Total N, P, chloride, and fluoride did not differ by treatments, whereas sulfur concentrations were greatest in channel treatments (Table 6).

4 | DISCUSSION

We evaluated biodiversity responses to a large-scale, multi-site, invasive macrophyte management experiment, designed to address and potentially reverse structural changes associated with plant invasion. Both treatments that we tested (harvesting biomass above the water and creating aquatic connectivity channels) effectively reduced biomass and dominance of *Typha* and its litter, with channel creation almost completely eliminating *Typha*. Elimination of the *Typha* canopy released submerged aquatic species in created channels, with greater total vegetative cover than either harvest or control treatments. So, while treatments reduced the cover of *Typha* and its litter, a structurally complex mix of native plant species including high relative dominance of submergent plants filled the void created by removing the invasive plants. Furthermore, DO in treated areas rebounded more quickly during the day compared to controls. Fish and macroinvertebrate abundance and fish diversity were significantly higher in harvest than controls; we infer that these responses resulted from increased DO and the reduction of *Typha* litter in harvest relative to unmanaged *Typha* stands. While channel treatments did not increase the diversity (richness or H′) of any taxonomic group (fish, plants, macoinvertebrates or amphibians), taxa associated with more open-water conditions were more abundant in this treatment. Our results suggest that mechanical harvesting of *Typha* can benefit not only plant biodiversity, but also higher trophic levels (Figure 6).

4.1 | Environmental drivers

Typha treatments employed in this study altered DO, an important driver of aquatic community change. As expected, we observed increased DO with time of day across treatments, which is likely to have been associated with photosynthesis. However, DO in control treatments did not rebound as quickly throughout the day compared to both the harvest and channel treatments. This is likely to have occurred because more abundant *Typha* biomass and litter in control treatments physically prohibited lateral mixing of oxygen-rich water from pelagic regions into regions dominated by *Typha*, with

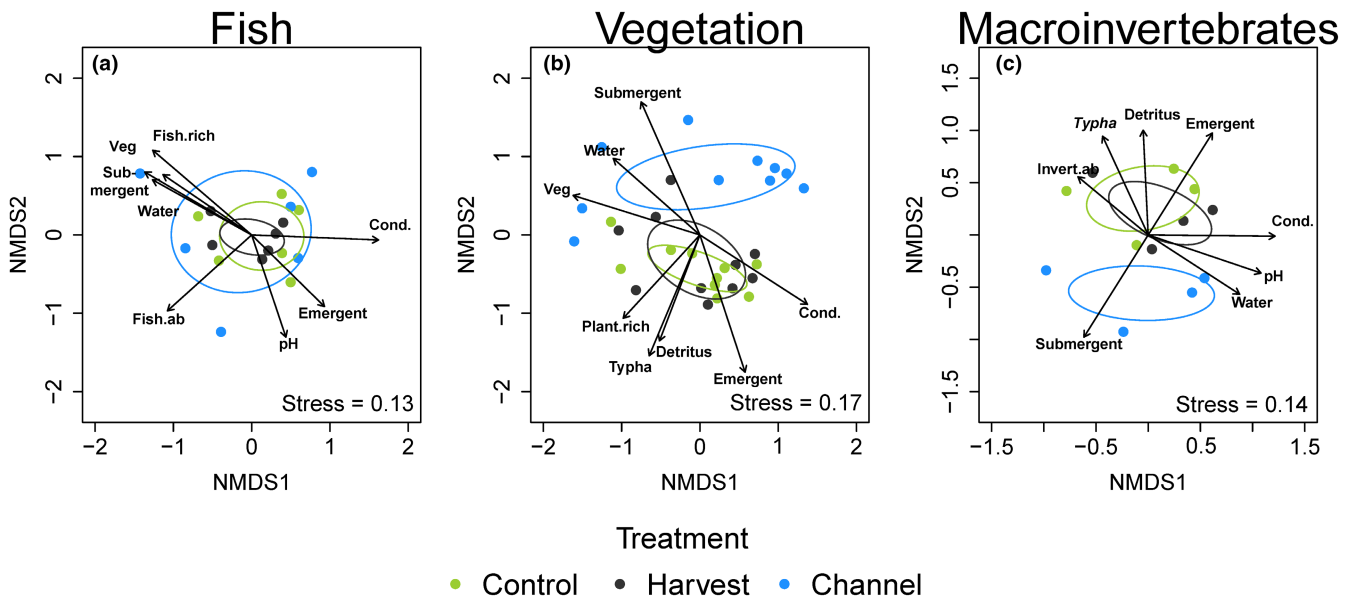


FIGURE 4 Nonmetric multidimensional scaling ordination of the plot-level fish (a), vegetation (b), and macroinvertebrate (c) community composition within treatment plots. Fish and vegetation data were collected in both years of the study, whereas macroinvertebrate data were only collected 1-year post treatment. Dissimilarity was based on Bray–Curtis distances and plots were constructed using two dimensions. Fitted vector arrows are significant ($p < 0.05$, by permutation procedure) and their length is proportional to their explanatory strength. Explanatory variables were: total vegetation cover (Veg); fish abundance per net (Fish.ab); conductivity (Cond.); emergent species relative dominance (Emergent); submergent species relative dominance (Submergent); water depth (Water); plant species richness (Plant. rich); below-water detritus (Detritus); *Typha* biomass (Typha).

TABLE 4 Results of indicator species analysis of plant data by treatment type (Control, Channel, Harvest) where indicator statistic represents the proportion of perfect indication within a treatment or combination of treatments.

Treatment	Plant species	Indicator statistic	*p*-value
Control	None	NA	NA
Channel	*Potamogeton* spp.	0.306	<0.01
	Elodea canadensis	0.301	0.01
	Potamogeton gramineus	0.280	0.02
	Vallisneria americana	0.201	0.03
	Aquatic moss	0.201	<0.01
	Potamogeton zosteriformis[a]	0.266	0.03
Harvest	*Phalaris arundinacea*	0.304	0.02
	Carex stricta	0.218	0.02
	Campanula aparinoides	0.207	0.03
	Equisetum fluviatile	0.201	0.04
	Potamogeton zosteriformis[a]	0.266	0.03

[a]*P. zosteriformis* was indicative of both channel treatments and harvest treatments.

TABLE 5 Results of indicator species analysis of invertebrate families by treatment type (Control, Channel, Harvest) where indicator value represents the proportion of perfect indication within a treatment or combination of treatments.

Treatment	Invertebrate family	Indicator statistic	*p*-value
Control	Mesoveliidae	0.361	0.03
	Lestidae[a]	0.820	<0.01
	Polycentropodidae[a]	0.587	<0.05
Channel	Cambaridae	0.531	<0.01
Harvest	Gomphidae	0.595	<0.05
	Lestidae[a]	0.820	<0.01
	Polycentropodidae[a]	0.587	<0.05

[a]Lestidae and Polycentropodidae were indicative of both control treatments and harvest treatments.

respiration rates in litter-dense controls likely to be greater than in treated areas with reduced litter. Additionally, replacement of invasive *Typha* with submergent plant species and subsequent increases in light penetration may result in increased photosynthesis underwater, increasing DO (Rose & Crumpton, 1996). Likewise, DO was lower in a *Typha*-invaded than a native plant-dominated coastal wetland (Schrank & Lishawa, 2019). Changes in littoral pelagic mixing with distance from open water edge to wetland interior influence both environmental conditions and community structure in coastal wetlands (Burton et al., 2002; Cardinale et al., 1997, 1998; Trebitz et al., 2005).

Water temperature in both harvest and channel treatments was higher than in *Typha*-dominated controls; shading by tall live and standing dead *Typha* reduces water temperature 1–2°C relative to

TABLE 6 Summary statistics of environmental variables ($\overline{X} \pm SE$), linear mixed effects models of environmental variables by treatment with block treated as random factors (e.g., variable ~ Treatment, random = Block).

	Model fit		ANOVA	Treatment		
Variable	Marginal R^2	Conditional R^2	p	Control $\overline{X} \pm SE$	Harvest $\overline{X} \pm SE$	Channel $\overline{X} \pm SE$
Total vegetation cover (% cover)*	0.03	0.98	0.002	24.28 ± 1.12^{a}	25.56 ± 1.69^{a}	27.00 ± 3.51^{b}
Litter above water (% cover)*	0.50	0.99	<0.001	12.22 ± 0.77^{a}	5.95 ± 0.54^{b}	0.40 ± 0.07^{c}
Typha + litter (% cover)*	0.50	0.61	<0.001	27.64 ± 1.08^{a}	18.55 ± 1.84^{b}	0.50 ± 1.30^{c}
Litter below water (% cover)*	0.31	0.57	<0.001	90.68 ± 1.43^{a}	81.43 ± 2.29^{b}	49.97 ± 4.05^{c}
Dissolved oxygen (mg/L)*	<0.01	0.71	<0.001	2.02 ± 0.06^{a}	2.47 ± 0.08^{b}	2.16 ± 0.10^{a}
Water temperature (°C)*	0.16	0.34	<0.001	20.80 ± 0.06^{a}	21.50 ± 0.06^{b}	21.43 ± 0.08^{c}
Water depth (cm)*	0.02	0.82	<0.001	63.06 ± 1.77^{a}	59.00 ± 1.90^{b}	66.00 ± 2.06^{c}
Specific conductivity (μS/cm)*	<0.01	0.71	0.002	394.16 ± 11.97^{a}	414.41 ± 11.81^{b}	378.85 ± 15.03^{ab}
pH*	0.01	0.89	0.036	7.43 ± 0.01^{ab}	7.44 ± 0.01^{a}	7.40 ± 0.02^{b}
Total nitrogen (μg/L)†	0.02	0.13	0.539	514.84 ± 60.56	488.08 ± 40.30	438.44 ± 32.99
Total phosphorus (μg/L)†	<0.01	0.07	0.167	23.24 ± 4.48	20.51 ± 3.69	20.74 ± 3.79
Chloride (mg/L)†	0.00	0.00	0.994	24.25 ± 4.86	24.19 ± 4.97	23.80 ± 4.95
Chlorophyll-*a* (μg/L)†	0.02	0.22	0.479	67.32 ± 12.38	59.55 ± 8.37	35.38 ± 6.53
Sulfur (mg/L)†	0.01	0.46	0.031	2.61 ± 0.64^{a}	3.06 ± 0.84^{ab}	3.38 ± 0.89^{b}
Fluoride (mg/L)†	0.02	0.02	0.322	0.04 ± 0.00	0.05 ± 0.00	0.05 ± 0.00

Note: The marginal R^2 (i.e., variance explained by the fixed effect of treatment), conditional R^2 (i.e., variance explained by the full model fixed and random effects), analysis of variance (ANOVA) p-values for fixed effects, treatment means and *post hoc* test results determined with least-squares means method, where non-overlapping superscript letters indicate significant differences ($p < 0.05$) between treatments, are presented for each model.

*Data averaged across years.

†Data from 2017 only.

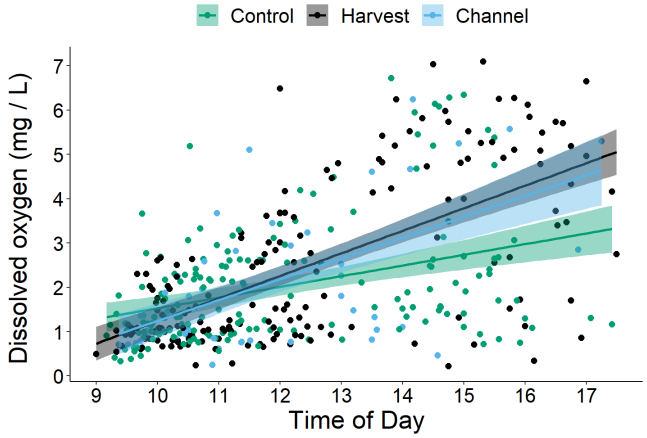


FIGURE 5 Dissolved oxygen was significantly higher in harvest plot on average (2.47 ± 0.08 mg/L) compared to control or channel plots (2.02 ± 0.06 and 2.16 ± 0.10 mg/L) and control plot DO had a significantly lower slope than channel and harvest plots throughout the day (ANCOVA: $F_{2, 416} = 8.8$, $p < 0.001$). The shading shows the 95% confidence interval around the regression line.

more sparsely vegetated areas (Lawrence et al., 2016; Schrank & Lishawa, 2019). Water temperature is likely to have an indirect effect on both fish and macroinvertebrate communities as reduced water temperature can reduce growth, especially for larval and juvenile fishes (Hill & Magnuson, 1990), and the feeding rates and metabolism of a variety of species (Wotton, 1995). Shading also could affect algal communities, the food source of both macroinvertebrates and larval amphibians, but more studies are needed to determine these effects (Lawrence et al., 2016).

Several environmental factors varied statistically among treatments, but the quantity of mean differences was unlikely biologically significant. Water depth, for instance, was an average of 7 cm greater in the channel plots compared to the harvest plots with controls intermediate. These minor but statistically significant differences can be explained by the physical removal of biomass and litter from the channels and the mechanical harvester's flattening of some litter onto the sediment surface. Likewise, specific conductivity and pH varied by treatment but the differences were very minor (Table 6).

4.2 | Structural complexity

Submergent species are typically reduced or absent from dense invasive *Typha* stands (Lawrence et al., 2016). We found that submergent plant abundance was three-fold greater in channels than in *Typha*-dominated controls, with four species of submergent plants indicative of channel treatments. This rapid submergent plant response to below-water removal of *Typha* reflects a pattern in a St. Marys River wetland (Lishawa et al., 2017). Submergent plants

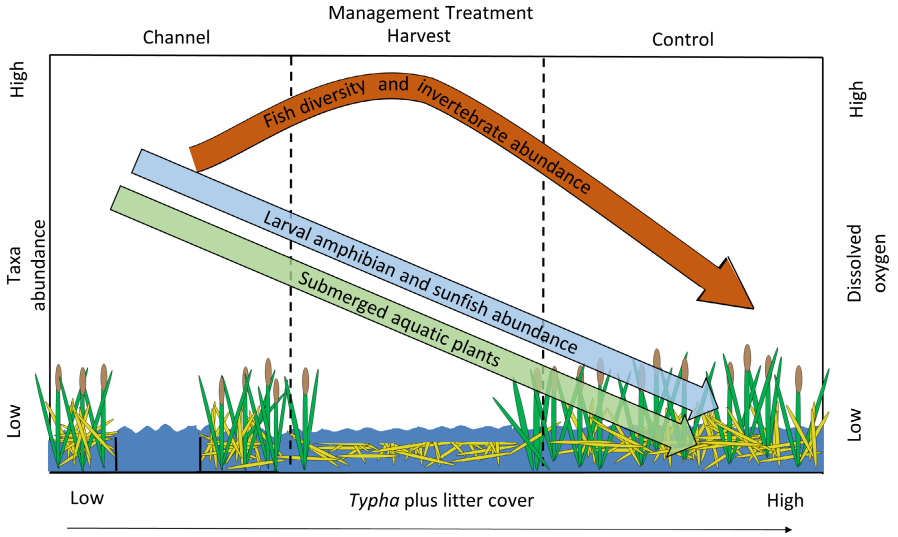


FIGURE 6 Conceptual diagram summarising the patterns of response of fishes, macroinvertebrates, aquatic plants and larval amphibians to harvest and aquatic connectivity (channel) management treatments. The relationships of these abundance and biodiversity responses to *Typha* and its litter and DO levels also are shown.

are likely to have responded to increased available space, increased light penetration and increased plant-available nutrients in channel plots; a shorter-term (1-year) parallel study (Johnson et al., 2019) found that light transmission was approximately four-fold greater throughout the water column and plant-available P and potassium within the sediment was 70% greater in channels than in control or harvest treatments.

Lower macroinvertebrate abundance within *Typha*-dominated control treatments was likely to have been related to structural homogeneity and the associated low abundance of submerged aquatic plants. Although macroinvertebrate density can increase as vegetation structural complexity increases (Thomaz et al., 2008), submerged aquatic vegetation can be more important for macroinvertebrates than emergent aquatic vegetation (Jolley et al., 2013; Paukert & Willis, 2003) and structural differences between individual emergent species may be of less importance to macroinvertebrates (Stahr & Kaemingk, 2017). Macroinvertebrates benefit from the highly dissected leaves of many submerged aquatic plants, which increase habitat complexity (Schultz & Dibble, 2012). Similar to our results, Lawrence et al. (2016) found that macroinvertebrate abundance was higher in native nearshore zones, where abundance of submerged aquatic plants was higher, compared to *Typha*-invaded zones. Among macroinvertebrate groups, crayfish are important components of the aquatic food web as a source of food for fishes and birds, and a key link in nearshore food webs (Peters et al., 2014), yet the effects of *Typha* invasion on crayfish abundance was unknown before our study. We identified crayfish as indicator species of created channels and that their abundance was higher in channels than control and harvest plots, suggesting that *Typha* negatively affects crayfish as it does other macroinvertebrate species. Within insect groups, gomphid dragonflies were an indicator of the harvest treatment suggesting that harvested *Typha* provides suitable habitat for this group.

Habitat complexity also influences fish communities (Harrel & Dibble, 2001; Henning et al., 2014; Lopes et al., 2015), and the abundance of dense *Typha* and its litter in the control treatments is likely to be the primary cause of reduced fish abundance relative to harvest and channel treatments, and reduced diversity and richness relative to harvest treatments. Even among families that prefer relatively dense vegetation such as Centrarchidae (Harrel & Dibble, 2001), individuals were more frequent in harvest or channel treatments, suggesting that the high density of *Typha* and its litter and reduced DO levels made *Typha*-dominated controls inhospitable. Only mudminnows and brook sticklebacks, species noted for their ability to survive and thrive in low oxygen conditions (Klinger et al., 1982), were found in both harvest and control treatments with similar frequency.

Channels did not increase total diversity, yet they were an important habitat type for a variety of taxonomic groups. Surprisingly, juvenile centrarchids, a group known to use vegetated areas for cover (Harrel & Dibble, 2001; Stahr & Kaemingk, 2017) and relatively tolerant of low oxygen (Killgore & Hoover, 2001), were more abundant in channels than controls. We suspect that this is because fish may be moving in and out of the harvested areas into the channel to feed or for cover. Likewise, channels excavated through *Typha* stands increased use of these features by juvenile northern pike (*Esox lucius*) (Neveldine et al., 2019). We also found that larval amphibians tended to be most abundant in channels. Tadpoles feed primarily on algae and detritus (Montaña et al., 2019) and because of elevated light levels in channels relative to other treatments (Johnson et al., 2019), these more open areas may be important for tadpole feeding.

4.3 | Study limitations and future research recommendations

Several limitations to our study warrant discussion and illuminate directions for future research. Firstly, fish data collected at Munuscong Marsh differed substantially from the other sites in this study; effectively zero fish were collected from Munuscong Marsh. We cannot eliminate the possibility that the absence of trapped fish was not to the consequence of an actual paucity of fish, but rather a limitation of the collection methods (i.e., minnow traps). In future studies

researchers could better account for the full fish community composition while further limiting sampling gear bias by employing a combination of minnow traps, which are effective in dense vegetation, and fyke nets or electrofishing in channels. Secondly, we collected substantially greater quantity of macroinvertebrates at Munuscong resulting from a single family of aquatic isopods (Asellidae). We attempted to reconcile these site-specific differences in fish and macroinvertebrates by excluding Munuscong data from the fish analyses entirely and analysing Munuscong invertebrate abundance data separately from the other blocks. Furthermore, our study did not quantify macroinvertebrate biomass, which would better predict food-web effects than abundance and diversity measures. Finally, the short-term nature of this study (2-year) did not allow us to evaluate the length of time that treatments would remain effective or the appropriate periodicity of repeated harvesting to maintain improved habitat quality. Longer-term studies are critical to evaluate the persistence of treatment effects on vegetation and aquatic organisms and to inform management actions.

4.4 | Management implications

Increasing habitat complexity and aquatic connectivity of invaded wetlands can promote biodiversity and provides a more realistic management goal than the complete elimination of invasive macrophytes. Invasive *Typha* has become the dominant plant taxa in more than 28,000 ha (c.13% of total area) of coastal wetlands across the Laurentian Great Lakes (Carson et al., 2018), reducing habitat quality for a range of wildlife and plant species. As such, *Typha* management should be a conservation and restoration priority in the region. Cutting *Typha* below-water is an effective method for killing the plant (Lishawa et al., 2017; Sale & Wetzel, 1983) as it severs the pressurised air-ventilation system that allows *Typha* to thrive in anoxic conditions by actively transporting oxygen to its rhizomes and roots (Bendix et al., 1994; McKee et al., 1989). Furthermore, mechanical treatments may avoid the potential negative effects of herbicide treatment, which include increasing post-treatment nutrient availability (Lawrence et al., 2016) and reducing macrophyte diversity (Mudge & Houlahan, 2019). Although we did not observe secondary invasion associated with this study, consideration should be taken to post-treatment invasion by other aquatic invasive plant species, such as *Hydrocharis morsus-ranae* and *Lythrum salicaria*, which commonly invade following *Typha* and *Phragmites australis* treatment (Frieswyk & Zedler, 2006; Robichaud & Rooney, 2021). Importantly, the potential impacts of using heavy machinery in natural systems on herptiles and other resident organisms, and strictly avoiding vegetation manipulation during secretive marsh-bird breeding season is of critical importance. Our channel treatments, which involved cutting *Typha* below-water, were highly effective at nearly eliminating *Typha* for two years following treatment. Our results suggest that *Typha* management that incorporates both harvesting and the inclusion of aquatic connectivity channels would provide increased benefit to all taxonomic groups, likely by reducing *Typha* and its litter, increasing oxygen availability, and increasing the connection between open water and wetland interior. A combination of channel and harvest treatments allows oxygen-rich water to flow into more interior regions and allow the movement of organisms into harvested areas which are less physically dense than *Typha* stands. Incorporating biomass harvest and channel treatments into expansive *Typha* stands will increase wetland-scale structural complexity and biodiversity.

AUTHOR CONTRIBUTIONS

Conceptualisation: SL, AS, BL and DA. Developing methods: SL, BL, AS and DA. Data analysis: SL, AS. Preparation of figures and tables: SL, AS. Conducting the research, data interpretation, writing: SL, AS, BL, DM, DA.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data are available at the Dryad Digital Repository.

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