Aquatic Botany 169 (2021) 103327

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Contrasting trajectories in macrophyte community development after shoreline restoration: water level obscures trends

Paige M. Kleindl *,[1], Alan D. Steinman

Robert B. Annis Water Resources Institute, Grand Valley State University, 740 W. Shoreline Dr, Muskegon, MI, 49441, USA

ARTICLE INFO

Keywords:
Macrophytes
Epiphytic algae
Shoreline restoration
Great Lakes
Coastal wetlands
Muskegon Lake

ABSTRACT

Macrophytes are critical components of biologically productive lake littoral zones. Sensitivity to environmental factors such as sediment content and light availability makes macrophytes potential bioindicators of anthropogenic stress. The industrial past of Muskegon Lake (Michigan, USA) has severely disturbed the system, resulting in shoreline hardening and sediment contamination. Shoreline restoration during 2010 and 2011 presented an opportunity to use macrophytes as indicators of pre-restoration (2009–2010), shorter-term (2011–2012) and longer-term (2018) post-restoration ecosystem status. Macrophytes were sampled along transects perpendicular to the shoreline in two restored and one reference habitat, and predicted to experience post-restoration density and richness increases. Epiphytic algae were surveyed in 2018 only. Restored habitat quality, based on macrophyte species composition, minimally improved during post-restoration and there was no clear pattern in macrophyte richness and density. Water level was the strongest environmental driver of macrophyte community change, especially in 2018, when emergent macrophyte richness declined. Epiphytic algal dry weight was not sufficient to negatively impact macrophytes, as wave exposure lowered algal densities. Post-restoration habitat quality remained greater at the reference transect than at the two restored transects, although the restored habitats exhibited contrasting trajectories due to differences in slope (%), wave exposure, and disturbance.

1. Introduction

Throughout the industrial world, humans have substantially altered lakes to meet their needs for urbanization, recreation, and navigation. Anthropogenic disturbances such as shoreline hardening, lake dredging, and pollution runoff have impaired functional lake habitats, thereby decreasing water quality and ecosystem complexity (Whittier et al., 2002). Development along the shoreline disconnects terrestrial and aquatic habitats, often altering shoreline sediment organic matter content and composition and reducing littoral biodiversity (Brauns et al., 2011; Gabriel and Bodensteiner, 2012; Søndergaard et al., 2007). Industrial degradation is visible throughout the Laurentian Great Lakes region, where three-fourths of coastal habitats have been destroyed by human development, and the remaining river mouth and littoral ecosystems are of poor habitat quality (Larson et al., 2013). In Muskegon, Michigan, historical industrialization around Muskegon Lake, a drowned river mouth lake that connects directly to Lake Michigan, hardened the shoreline with rip-rap and seawalls, and littered shallow waters with slag, slab wood, and other unwanted materials (Steinman et al., 2008).

Increased human awareness and concern for aquatic ecosystem health, as well as an appreciation for the blue economy's impact on community revitalization (Graziano et al., 2019), have driven numerous, large-scale restoration efforts. In Europe, the Water Framework Directive has increased the use of biological indicators to evaluate the health of water bodies, aiding in the development of restoration and conservation management plans (Penning et al., 2008; Søndergaard et al., 2007, 2013). In the U.S., the Environmental Protection Agency designated severely degraded water bodies in the Great Lakes region as Areas of Concern (AOCs), prompting actions to recover and remediate lost ecosystem beneficial uses. Biomonitoring (e.g., fish and macrophytes) has helped assess AOC status and measure coastal wetland

Abbreviations: HertL, Heritage Landing; GrandT, Grand Trunk; NWRef, Northwest Reference; WL, water level; Chl-*a*, chlorophyll-*a*; C-value, Coefficient of Conservatism.

* Corresponding author.
E-mail address: pklei007@fiu.edu (P.M. Kleindl).
[1] Present address: Florida International University OE148, 11200 SW 8th St, Miami, FL, 33199, USA.

https://doi.org/10.1016/j.aquabot.2020.103327
Received 25 March 2020; Received in revised form 29 October 2020; Accepted 3 November 2020
Available online 6 November 2020
0304-3770/

condition (e.g., Ogdahl and Steinman, 2015; Uzarski et al., 2017), as it advances adaptive management strategies, improves restoration techniques, and increases restoration value to investors and the public (Palmer et al., 2007).

Macrophytes respond quickly to environmental changes in shallow aquatic ecosystems, making them valuable aquatic bioindicators. Considered habitat engineers, macrophytes stabilize sediment, determine organic matter accumulation, reduce wave action, and provide habitat refugia (Allen, 1971; Lacoul and Freedman, 2006; Thomaz and Cunha, 2010). Macrophyte fitness and community structure are determined by light (Chambers and Kalff, 1985; Phillips et al., 2016) and nutrients (Hilt et al., 2018), and associated drivers such as shoreline slope (Barko et al., 1991), water depth (Kolada, 2014), precipitation, and organic matter content (Squires and Lesack, 2003). Epiphytic organisms, particularly algae, also can influence macrophyte production by reducing light and altering dissolved gas and nutrient concentrations (Allen, 1971; Sand-Jensen and Søndergaard, 1981; Phillips et al., 1978, 2016). Epiphytic algae are ecologically significant because of their role in nutrient cycling and as the base of aquatic food webs (Allen, 1971; Vadeboncoeur and Steinman, 2002).

In Muskegon Lake, littoral shoreline restoration from 2010 to 2011 made macrophytes useful bioindicators for restoration assessment. Based on macrophyte surveys during pre- (2009–2010) and post-restoration (2011–2012), Ogdahl and Steinman (2015) concluded that distinguishing restoration responses from environmental effects (i.e., water level, sediment organic matter, and wave exposure) would require a longer-term data set due to sediment physical disturbance associated with restoration efforts. Therefore, the study's first objective was to compare macrophyte community composition, richness, density, and cover in 2018 to previous data (2009–2012) and infer if shoreline restoration had improved habitat quality based on Michigan's Coefficient of Conservatism (C-value) for macrophyte taxa. Restored habitats were compared to a Muskegon Lake reference habitat containing a non-industrialized shoreline to separate macrophyte metric changes associated with restoration from changes due to other agents of environmental variation. We hypothesized that metrics of macrophyte community structure would indicate greater improvement in restored habitats compared to reference habitats.

Since interactions with epiphytic algae can influence macrophyte growth, an epiphytic algae survey occurred in 2018 at the restored and reference Muskegon Lake habitats to determine how epiphytic algal community structure was influenced by environmental variables (e.g., wind and wave action, turbidity, and nutrients) among habitats and if epiphytic algae were negatively impacting macrophyte fitness. We hypothesized that epiphytic algal density and chlorophyll-*a* (Chl-*a*) would be greater in more protected habitats (i.e., low wind index), where less water movement may prevent algal sloughing and decrease turbidity. Increased epiphytic algal biomass at protected habitats could thicken the boundary layer between the water column and macrophyte and impede light transmittance; biomass was predicted to surpass defined thresholds, resulting in negative impacts to macrophyte fitness.

2. Methods

2.1. Habitat description

Muskegon Lake is a ~17 km^2 drowned river mouth lake in central West Michigan, which receives inflow from the 7060 km^2 Muskegon River watershed (Fig. 1). The direct connection between Muskegon Lake and Lake Michigan causes water depths of Muskegon Lake to fluctuate synchronously with Lake Michigan. Muskegon Lake degradation began in the 1850′s when the lumber industry developed along the shoreline and peaked in operation with 47 active sawmills. Foundries and factories replaced the lumber industry in the early 20th century and were concentrated around the south shoreline (i.e., metal finishing plants, a paper mill, and petrochemical storage facilities), discarding unwanted

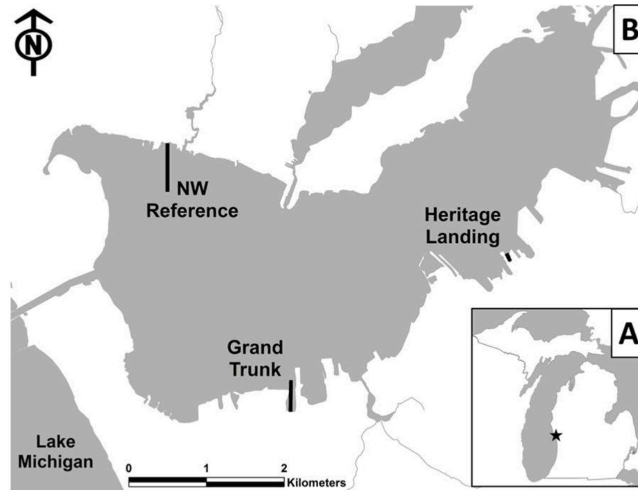

Fig. 1. Muskegon Lake Survey Transects. (A) The state of Michigan, with the location of Muskegon Lake indicated by a black star. (B) A map of Muskegon Lake with the three macrophyte survey transects indicated by black lines showing the length of each transect. The restored transects, Heritage Landing (43.23311396, −86.26211299) and Grand Trunk (43.21582996, −86.29739558), are perpendicular to the southern shoreline and the reference transect, Northwest Reference (43.24735221, −86.31625598), is perpendicular to the northern shoreline.

materials into the lake. Industrial development hardened 65 % (33 km) of the shoreline with seawalls, concrete, and rip-rap. A disproportionately higher amount of disturbance occurred along the south shoreline (78 %) compared to the north shoreline (45 %), which has more residential and natural areas than the south (Steinman et al., 2008).

In response to habitat degradation and the listing of Muskegon Lake as a Great Lakes AOC in 1987, south shoreline restoration took place in 2010 and 2011 to renaturalize 4.2 km through: (1) the removal of unwanted fill debris at (shoreline) or below (underwater) the ordinary high water mark, (2) shoreline vegetation planting using native trees, plugs, and seed mixes, and (3) "living shoreline" restoration techniques such as coconut fibre wave diffusors and large woody debris (Ogdahl and Steinman, 2015). Macrophyte surveys were conducted at two restored habitats along the south shoreline in 2009–2012 and 2018: Heritage Landing and Grand Trunk (Fig. 1, Ogdahl and Steinman, 2015). Restoration occurred along the surveyed portion of Heritage Landing in April 2011 and adjacent to the surveyed habitat at Grand Trunk in June 2010. One reference habitat, Northwest Reference, along the north shoreline also was surveyed to represent macrophyte communities associated with more natural conditions unimpacted by 20th century industrial development and restoration (Fig. 1, Ogdahl and Steinman, 2015). In addition, epiphytic algal communities on the macrophyte species *Vallisneria americana* were sampled at all three habitats in 2018.

2.2. Field protocols

A full description of the macrophyte survey methodology is included in Ogdahl and Steinman (2015). Briefly, surveys took place in August during 2009–2012 and from July 16th-23rd in 2018. Sampling in 2018 occurred ~one month earlier than previous events, but was still within the period of optimal macrophyte growth. At the three survey habitats (hereafter referred to as transects), a transect was established perpendicular to the shoreline and separated into standard distance categories for sampling. Transect ends were defined as the farthest site from the transect origin containing macrophytes before: (1) two consecutive sites with no macrophytes, or (2) the absence of macrophytes at a site greater than 4.5 m deep (Ogdahl and Steinman, 2015). One site beyond the 4.5 m depth was always sampled to confirm macrophyte absence. Transect length was considered the distance between the transect origin and end, and the transect end depth was recorded as the "minimum vegetation limit". Macrophyte cover rank was determined at each transect site using a modified Braun-Blanquet ranking system: 0 = Bare; 1 = 1–25 %; 2 = 26–50 %; 3 = 51–75 %; or 4 = 76–100 % (Poore, 1955; Ogdahl and Steinman, 2015). Macrophyte taxa relative abundance (0–100 %), species richness, and water depth also were determined.

Macrophyte biomass for density calculations and sediment organic matter (OM) were determined at one randomly chosen site within each distance category: 0−20 m from shore, 20−50 m, 50−100 m, 200−300 m, 300−400 m, 400−500 m, etc. (Ogdahl and Steinman, 2015). Transect sites in 2009 were recorded using a GPS. The same general locations were sampled each year, as transect origins were adjusted to begin at the present waterline, which subsequently shifted all other site locations. The same field personnel conducted surveys in 2009–2012 to exclude interpersonal variation; however, 2018 surveys were conducted by new personnel due to staff changes.

Epiphytic algae were collected only during the 2018 macrophyte survey and, due to resource constraints, from one native macrophyte species, *V. americana*. The subdominant and ubiquitous *V. americana* in Muskegon Lake has long, simple leaf blades, which were preferred for ensuring epiphytic algal removal instead of the dominant *Ceratophyllum demersum* with morphologically complex and brittle leaflets. Our research does not represent Muskegon Lake's entire epiphytic algal community but comparisons using a single host taxon provided a consistent substrate surface, which was present at all transects. One site with a 1 m depth was sampled at each transect, where *V. americana* leaf blades almost reached the water's surface. Ten *V. americana* plants were randomly sampled from a 10 m-diameter area, approximately 5 m in any direction of the boat. The top 20 cm of each *V. americana* was removed, secured in a plastic bag, and placed on ice for transport to the lab. Due to slope variation among transects, sampling sites were different distances from the shoreline to maintain the 1 m water depth.

Physical and chemical variables also were measured at each epiphytic algal collection site. Water quality variables (dissolved oxygen [DO], turbidity, pH, water temperature [T], specific conductance [SC], and redox potential [ORP]) were measured with a YSI 6600 sonde. Mean turbidity (NTU) was determined using turbidity values measured at all sites along each transect. A 1 L water sample was collected for analysis of water column soluble reactive phosphorus (SRP), total phosphorus (TP), total Kjeldahl nitrogen (TKN), and nitrate (NO_3^-). Light intensity of photosynthetically active radiation (PAR) was measured using a Li-Cor quantum sensor and used to quantify the light extinction coefficient.

2.3. Laboratory processing

Macrophyte, water, and sediment samples were refrigerated until processing, within 60 days. Macrophyte biomass was cleaned of sediment and *Dreissena* spp. mussels, and then dried at 85 °C for 96 h to determine plant dry weight. Sediments were ashed at 550 °C for 4 h to determine OM concentrations (%), as the difference between pre- and post-combustion sediment weights (Ogdahl and Steinman, 2015).

For the epiphytic algae survey, SRP, TKN, and NO_3^- subsamples were filtered through 0.45 μm acid washed filters. TP underwent an acidic digestion using ammonium persulfate with +5 N sulfuric acid and was stored at 4 °C. SRP, TP, and TKN were analyzed using a SEAL AQ2 discrete automated analyzer (APHA, 1998) and NO_3^-/NO_2^- was analyzed with ion chromatography using a Dionex ICS-2100 (APHA, 1998). Toothbrushes were used to remove epiphytic algae from both sides of *V. americana* blades; blades and toothbrushes were rinsed with distilled water. Separate toothbrushes were used for each *V. americana* to eliminate epiphytic algal contamination among samples. ImageJ software was used to determine macrophyte surface area for epiphytic algal density calculations (Schneider et al., 2012).

An aliquot of toothbrush-removed algae was used to determine Chl-*a* by filtering the sample through a 0.7 μm GF/F filter (Whatman®) and freezing at −18 °C. Within 30 days of freezing, filters were ground and steeped in 90 % buffered acetone for 24 h in the dark. After centrifuging, Chl-*a* (μg/cm^2) was analyzed using a Shimadzu UV-1601 spectrophotometer (Steinman et al., 2017). A 50 mL subsample of epiphytic algae was preserved with 1 % Lugols solution and used for non-diatom algae identification in a Palmer-Maloney nanoplankton counting chamber. Permanent slides were created for diatom identification. All algae were identified to genus using a Nikon H550L Eclipse 80i light microscope.

2.4. Data analyses

Macrophyte mean cover rank, total and mean species richness were calculated for each transect and survey year. Species richness excluded grass and tree species but included filamentous green algae and *Chara* spp., as they were included in density calculations during the previous survey; filamentous green algae were treated as one species. Total macrophyte density (g/m^2) per transect for all survey years was calculated by summing the mass (g) of dry plant material collected along a transect and dividing by the area sampled (Ogdahl and Steinman, 2015). The State of Michigan's Coefficient of Conservatism (C-value) was applied to each taxon; a range from 0 to 10 represented the probability a species would occur within an undisturbed habitat. Taxa with a C-value = 0 were either invasive or more likely to be found in highly degraded habitat, while a C-value = 10 indicated taxa that were more likely to be found in an ecologically healthy habitat, similar to pre-European settlement conditions (Bourdaghs et al., 2006). Mean C-values were determined for each transect per survey year and for each restoration state: reference, pre-restoration, and post-restoration (see below for explanation).

In addition to the macrophyte density, richness, and cover rank variables measured previously (Ogdahl and Steinman, 2015), taxon relative abundance was included in this study. To calculate a taxon's weighted relative abundance along a transect, its relative abundance (0–100 %) at a certain site was multiplied by its corresponding cover rank (0–4). The sum of all site-weighted relative abundance was then divided by the sum of all cover ranks along the transect.

Exposure to wind and wave action, defined as bathymetric slope (%) and wind index, was calculated for each transect and survey year. Transect slope was calculated by dividing the difference between transect end and origin water depths by the transect length and multiplying the result by 100 (Ogdahl and Steinman, 2015). Site slopes along a transect also were determined by dividing the difference between two adjacent sites' water depths by the distance between the two sites and multiplying the result by 100; mean site slope also was calculated. Wind index was determined (Keddy, 1982) first by measuring fetch along the four cardinal and four ordinal directions at transect origin and ends. The percentage of time (% frequency) wind speed exceeded 19.3 km/h for each direction, a previously assigned threshold (Ogdahl and Steinman, 2015), was multiplied by the corresponding fetch value and the results were summed. Mean transect WI, the average between transect origin and end WI, was determined for all survey years. Low WI values indicated protection from wind and wave action.

Total precipitation and mean air temperature during the growing season (April-August) were determined for all survey years (NCEI, 2019). Change in Lake Michigan water level (WL) compared to the long-term Lake Michigan mean (1917–2018) was determined for each survey year (CO-OPS, 2019). Annual mean Secchi disk depth and surface phytoplankton chlorophyll-*a* were determined using values collected at six locations in Muskegon Lake during May, July, and September of each year, as a part of the Muskegon Lake Long-Term Monitoring Program (Steinman et al., 2008). Additional environmental variables were calculated for each transect and survey year: mean percent OM, transect length, mean water depth, and the minimum vegetation limit (Middelboe and Markager, 1997).

Ogdahl and Steinman (2015) analyzed differences in physical variables (mean WI, transect slope, and mean percent OM) among transects using one-way ANOVAs. In this study, restoration state was added as a categorical variable, transect was treated as a 'repeated' measure, and 2018 data were added to the ANOVA analyses. Differences in physical parameters among transects and restoration states (mean WI, mean site slope, and mean percent OM) were therefore tested using two-way repeated measures ANOVAs with the aov() function, a part of the *UsingR* package in R (Verzani, 2018). When significance was detected, a pairwise *t*-test with Bonferroni correction was used. Restoration states were defined as: (1) reference, which included Northwest Reference data from 2009 to 2012 and 2018, (2) pre-restoration, which included restored transect data from 2009 to 2010, and (3) post-restoration, which included restored transect data from 2011, 2012, and 2018. Differences in biological variables among transects and restoration states (total density, mean richness, and mean cover rank) also were tested using two-way repeated measures ANOVAs and post-hoc pairwise *t*-tests. Normality was tested using Shapiro-Wilk, variance was tested using Levene's Test of equal variance, and all data were square-root transformed.

A redundancy analysis (RDA) was performed to evaluate how well macrophyte biological data (total density, total richness, and mean cover rank) were explained by measured environmental variables (mean slope, mean WI, mean OM, mean air temperature, total precipitation, transect length, water level, mean Secchi depth and phytoplankton Chl-*a*) among transects, survey years, and restoration states. Linear models were used to determine if trends in macrophyte biological variables among survey years remained after removing the effect of water level; models included survey year, transect, and restoration state as covariates and excluded phytoplankton Chl-*a* and Secchi depth. Two models were created for each biological variable: (1) water level was included as a variable and (2) water level was excluded. Transects were treated as a random factor in all models using the lmer() function, a part of the *lmerTest* package in R (Kuznetsova et al., 2017).

Epiphytic algal cell density (cells/μm^2) was determined using the surface area of *V. americana* leaf blades. Chl-*a* concentrations and cell density differences among transects were tested using Kruskal–Wallis and a post-hoc Wilcoxon test with Bonferroni correction. Normality was tested using Shapiro-Wilk, variance was tested using Levene's Test of equal variance, and all data were square-root transformed. Relationships between biological (Chl-*a* and density) and environmental data (DO, ORP, pH, T, turbidity, PAR, light extinction, mean WI, SC, water depth, TP, SRP, NO_3^-, and TKN) were evaluated using regression analysis. Mean WI values used in the epiphytic algal analyses were the same values used in the 2018 macrophyte survey analyses. All statistical analyses were performed using R version 3.5.2 (R Core Team, 2017).

3. Results

3.1. Macrophytes

3.1.1. Environmental variables

Northwest Reference's transect length was shortest in 2018 compared to 2009–2012, while restored transect lengths remained the same from 2012 to 2018 (Table 1). Water depth at all transects increased in 2018 and minimum vegetation limit was greatest at Heritage Landing in 2018 compared to previous years, while limits at Grand Trunk and Northwest Reference fell within the previous ranges (Fig. 2A). Throughout the survey, minimum vegetation limit usually increased as mean water depth increased at all transects, with both values decreasing in 2012 at all transects. Heritage Landing was the deepest transect among survey years and displayed a different minimum vegetation limit trajectory over time.

Mean site slope was steeper at Northwest Reference and Heritage Landing in 2018 compared to previous years, with Grand Trunk's 2018 slope falling within the previous range (Table 1). Regardless of year, Heritage Landing had a significantly steeper slope than Northwest Reference and Grand Trunk; restoration state and interaction were not significant ($p_{Transect} < 0.001$, $F = 57.4$; $p_{Restoration} = 0.97$, $F = 0.002$; $p_{Interaction} = 0.011$, $F = 0.23$; $df = 1$, 2-way RM ANOVA). Wind index declined at all transects from 2012 to 2018, with Northwest Reference experiencing its lowest WI compared to previous years and the restored transects experiencing intermediate WI (Table 1). Among survey years, WI was greatest at Northwest Reference (i.e., greatest wind and wave exposure) and lowest at Heritage Landing, with a non-significant restoration state and interaction ($p_{Transect} < 0.001$, $F = 252.8$; $p_{Restoration} = 0.98$, $F = 0.0$; $p_{Interaction} = 0.98$, $F = 0.0$; $df = 1$, 2-way RM ANOVA). Percent OM was greatest for Heritage Landing and Grand Trunk and lowest for Northwest Reference in 2018 compared to previous years (Table 1). Percent OM did vary among transects but was not statistically significant ($p_{Transect} = 0.82$, $F = 0.2$; $p_{Restoration} = 0.3$,

Table 1
Transect length (m), mean ± 1 standard error (SE) bathymetric slope (%), mean ± 1 SE WI (wind index), mean ± 1 SE OM (%), and mean ± 1 SE cover rank for the three Muskegon Lake transects over the five survey years. Total precipitation (cm), mean ± 1 SE air temperature (°C), and change in Lake Michigan water level (m) relative to the long-term Lake Michigan mean for all five survey years. Mean ± 1 SE Secchi disk depth (m) and mean ± 1 SE phytoplankton chlorophyll-*a* (μg/L) for all five survey years. Subscripts on transect or variable names indicate sample size per transect or per all survey years, respectively. Superscripts on transect names indicate significant similarities or differences among transects based on two-way repeated measures ANOVAs and post-hoc pairwise *t*-tests with Bonferroni correction.

		Pre-restoration		Post-restoration		
Variable	Transect	2009	2010	2011	2012	2018
	NWRef$_5$	650	800	750	650	600
Transect Length (m)	**HertL$_5$**	100	125	125	125	125
	GrandT$_5$	400	400	450	400	400
	NWRef$_{139}$ *a*	0.5 ± 0.1	0.6 ± 0.2	0.6 ± 0.1	0.4 ± 0.1	0.8 ± 0.3
Mean Slope (%)	**HertL$_{64}$*b***	3.7 ± 2.3	3.1 ± 2.1	3.7 ± 2.3	3.3 ± 2.2	4.7 ± 3.5
	GrandT$_{111}$*a*	0.7 ± 0.3	0.7 ± 0.3	0.8 ± 0.3	0.5 ± 0.2	0.6 ± 0.5
	NWRef$_{10}$ *a*	367.0 ± 11.4	386.7 ± 13.0	331.2 ± 25.2	389.9 ± 8.8	317.2 ± 31.0
Mean WI	**HertL$_{10}$ *b***	57.5 ± 15.0	41.1 ± 13.3	43.8 ± 16.7	65.7 ± 12.0	44.6 ± 19.5
	GrandT$_{10}$ *c*	136.0 ± 92.7	112.4 ± 86.7	104.2 ± 79.2	154.9 ± 105.3	117.0 ± 93.8
	NWRef$_{28}$	1.2 ± 0.4	1.2 ± 0.4	2.2 ± 1.4	0.9 ± 0.1	0.6 ± 0.1
Mean OM (%)	**HertL$_{15}$**	5.3 ± 2.1	7.7 ± 1.6	8.4 ± 1.7	6.8 ± 1.4	9.4 ± 1.0
	GrandT$_{24}$	22.0 ± 3.9	25.4 ± 5.4	15.9 ± 4.1	25.4 ± 6.4	25.5 ± 6.4
	NWRef$_{139}$	2.7 ± 0.4	2.4 ± 0.3	2.3 ± 0.2	2.9 ± 0.3	3.5 ± 0.2
Mean Cover Rank	**HertL$_{64}$**	3.6 ± 0.4	3.2 ± 0.4	2.8 ± 0.4	3.0 ± 0.4	2.5 ± 0.3
	GrandT$_{111}$	2.8 ± 0.3	3.6 ± 0.2	3.6 ± 0.2	3.3 ± 0.2	3.6 ± 0.3
Total Precipitation (cm)$_{3648}$		36.5	38.2	53.5	30.2	47.2
Mean Air Temperature (°C)$_{3648}$		16.0 ± 0.1	19.1 ± 0.1	17.8 ± 0.1	18.8 ± 0.1	17.6 ± 0.1
Lake Michigan Water Level Change (m)$_{152}$		−0.1	−0.3	−0.3	−0.4	0.5
Mean Secchi Disk Depth (m)$_{54}$		2.0 ± 0.1	2.5 ± 0.1	2.4 ± 0.1	2.5 ± 0.2	2.3 ± 0.1
Mean Phytoplankton Chlorophyll-*a* (μg/L)$_{54}$		6.7 ± 0.9	7.8 ± 1.2	10.6 ± 3.5	4.0 ± 0.7	10.9 ± 1.4

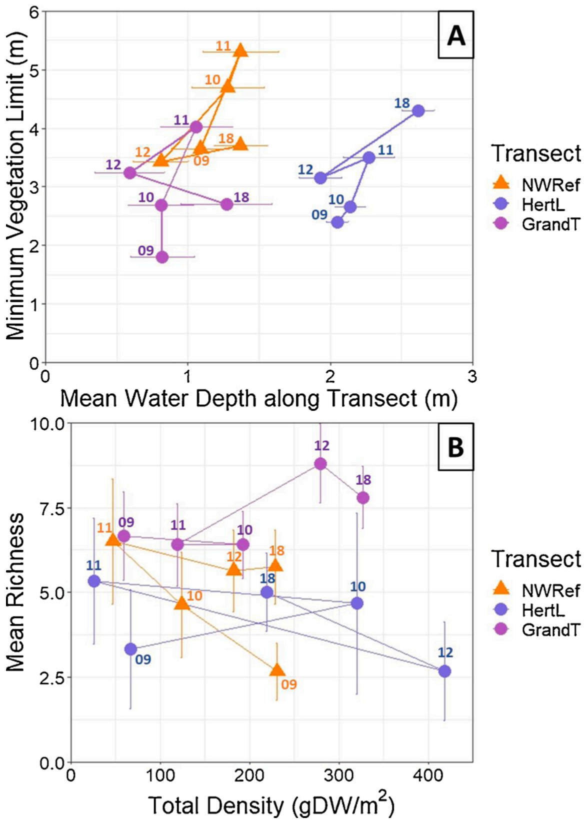

Fig. 2. Environmental and Biological Scatterplots. An environmental and biological scatterplot, with colors representing transects (NWRef, HertL, and GrandT), shapes representing restored (HertL and GrandT) and reference transects (NWRef), and numbers representing the last two digits of each survey year. A) The minimum vegetation limit (m, i.e., end of transect water depth, $n_{NWRef} = 5$, $n_{HertL} = 5$, $n_{GrandT} = 5$) against mean ± 1 SE water depth (m, $n_{NWRef} = 139$, $n_{HertL} = 64$, $n_{GrandT} = 111$). B) Mean ± 1 SE macrophyte species richness ($n_{NWRef} = 40$, $n_{HertL} = 15$, $n_{GrandT} = 25$) against total macrophyte density (g DW/m^2, $n_{NWRef} = 40$, $n_{HertL} = 15$, $n_{GrandT} = 25$).

$F = 1.1$; $p_{Interaction} = 0.43$, $F = 0.64$; $df = 1$, 2-way RM ANOVA).

In 2018, mean temperature fell within the previous range and precipitation accumulation was the second highest recorded over the five years (Table 1). Mean water level in 2009 was below the long-term mean and continued declining through 2012; however, the 2018 mean water level (+0.5 m) was much higher than the long-term mean (Table 1). Mean Secchi disk depth decreased from 2012 to 2018 and mean whole-lake phytoplankton Chl-*a* was the greatest in 2018 (10.9 μg/L) compared to previous years (Table 1).

3.1.2. Biological factors and community composition

Mean macrophyte richness ($p_{Transect} = 0.87$, $F = 0.13$; $p_{Restoration} = 0.40$, $F = 0.72$; $p_{Interaction} = 0.80$, $F = 0.06$; $df = 1$, 2-way RM ANOVA) and total macrophyte density ($p_{Transect} = 0.07$, $F = 2.71$; $p_{Restoration} = 0.54$, $F = 0.39$; $p_{Interaction} = 0.14$, $F = 2.25$; $df = 1$, 2-way RM ANOVA) were not significantly different among transects, restoration state, or interaction. Mean macrophyte density did not show any consistent increase or decrease over time at any transect (Fig. 2B). However, from 2012 to 2018, macrophyte total density increased at Grand Trunk and Northwest Reference and decreased at Heritage Landing (Fig. 2B). No consistent trends over time were found for mean richness among transects (Fig. 2B). A minimal richness increase was observed at Northwest Reference from 2012 to 2018, while richness decreased at both restored transects. Mean cover rank also increased in 2018 at Northwest Reference and Grand Trunk, whereas Heritage Landing's cover rank decreased (Table 1); cover was not significant ($p_{Transect} = 0.59$, $F = 0.54$; $p_{Restoration} = 0.88$, $F = 0.02$; $p_{Interaction} = 0.67$, $F = 0.18$; $df = 1$, 2-way RM ANOVA).

Macrophyte taxonomic composition was more similar between the restored transects than with the reference transect, and compared to 2009–2012 observations, Northwest Reference experienced a greater composition change in 2018 than either restored transect (Fig. 3). *Typha* spp. (*T. augustifolia*, *T.* x *glauca*, and *T. latifolia*), *V. americana*, and *Phragmites australis* were abundant at Northwest Reference from 2009 to 2012, but were rare or absent in 2018, when floating *Wolffia* spp. increased in abundance. In contrast, *Ceratophyllum demersum* was the most abundant macrophyte at both restored transects for all survey years, with Heritage Landing containing a greater relative abundance of *Elodea* spp. and Grand Trunk containing a greater relative abundance of *V. americana*.

C-values for all three transects increased from 2012 to 2018 (Table A.1). By 2018, Grand Trunk's C-value (4.2) reached Northwest Reference quality standards (4.2); however, Heritage Landing's C-value (3.6) was lower than reference standards (Table A.1). For restoration states, reference (4.1) had a C-value greater than pre- (3.7) and post-restoration (3.7, Table A.1).

3.1.3. Biological community response to environmental drivers

RD axis 1 explained 51.3 % and RD axis 2 explained 7.5 % of the dataset's variation in the RDA, with density, wind index, transect length, and slope having the greatest explanatory power (Fig. 4). Transect clusters overlapped along the RD1 axis, with transect slope, length, wind index, and total macrophyte richness having strong effects. Survey years 2009, 2011, and 2018 were associated with greater precipitation and phytoplankton Chl-*a*, high water level, and low temperature and Secchi depth. Sampling years 2010 and 2012 were associated with high macrophyte density, high temperature and Secchi depth, and low precipitation, phytoplankton Chl-*a*, and water level. Data did not separate into restoration state clusters.

When water level was included as a predictor in the macrophyte mean richness model, no environmental variables were significant (Table A.2); however, when water level was removed, mean richness was significantly greater when wind index was higher ($b = 0.69$, $t = 2.83$, $p = 0.05$, Table A.2), precipitation was greater ($b = 0.98$, $t = 3.19$, $p = 0.03$, Table A.2), and mean temperature was higher ($b = 1.86$, $t = 2.73$, $p = 0.05$, Table A.2). In the macrophyte total density and mean cover rank models, no environmental variables were significant when water level was included or removed as a predictor (Table A.2).

3.2. Epiphytic algae: environmental and biological variables

During the July 2018 sampling period, both mean epiphytic algal density (Chi-squared = 18.0, $p < 0.001$, $df = 2$, Kruskal Wallis, Fig. 5A) and Chl-*a* (Chi-squared = 23.48, $p < 0.001$, $df = 2$, Kruskal Wallis, Fig. 5B) on *V. americana* were highest at Heritage Landing followed by Grand Trunk and Northwest Reference. Of the three transects, Heritage Landing had the lowest mean turbidity and greatest light availability (high PAR and low light-extinction) while Grand Trunk had the greatest NO_3^- and TKN concentrations (Table A.3). When comparing biological and environmental variables, epiphytic algal Chl-*a* and density were both significantly negatively correlated with WI and light extinction and positively correlated with PAR (Table A.4).

4. Discussion

4.1. Macrophyte responses to restoration

We originally assumed that restored macrophyte habitat quality (i.e., C-value), richness, cover, and density would increase during post-restoration (Fig. 6A). Instead, physical habitat differences and restoration disturbance, as noted in Ogdahl and Steinman (2015), as well as

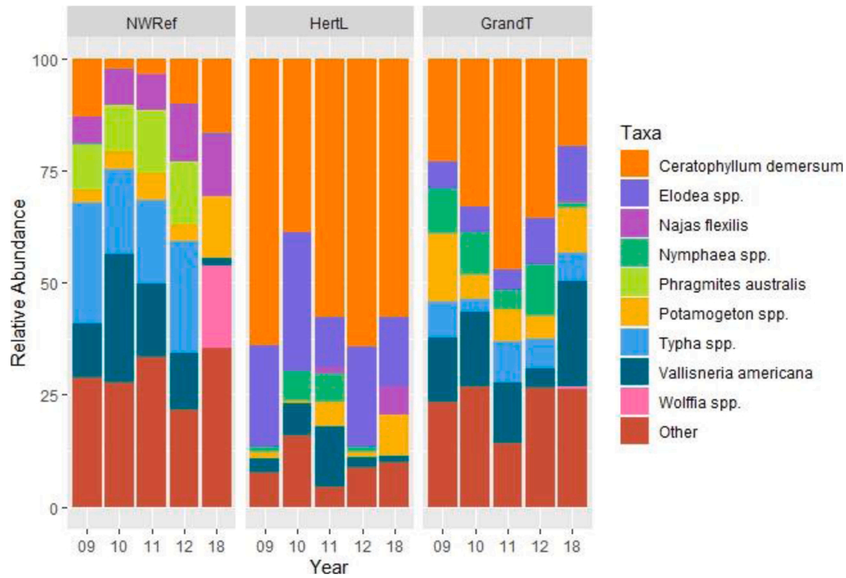

Fig. 3. Macrophyte Weighted Relative Abundance Stacked Barplot. A stacked barplot of macrophyte taxa weighted relative abundance changes within the five-year survey among all three transects. Each stacked bar represents the average relative abundance of represented macrophyte taxa at a transect per survey year ($n_{NWRef} = 140$, $n_{HertL} = 64$, $n_{GrandT} = 111$).

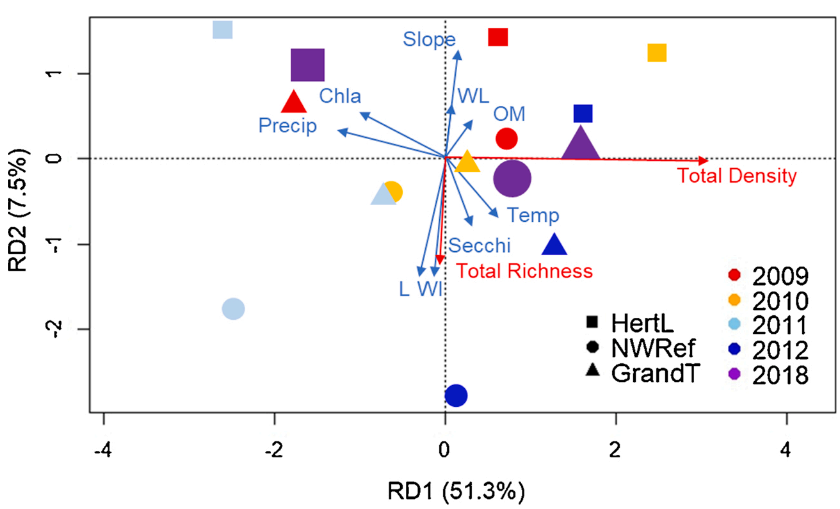

Fig. 4. Macrophyte RDA. A Macrophyte RDA, with symbols representing one transect per survey year, symbol shapes representing transects (NWRef, HertL, and GrandT), and colors representing survey years (2009–2012 and 2018). 2018 symbols (purple) were intentionally increased in size to differentiate from other years. Blue vectors represent environmental variables and red vectors represent macrophyte biological variables. Vector length is associated with a variable's explanatory power.

increased water level altered the expected restoration sequence (Fig. 6B). As of 2018, restored habitat quality had improved; however, improvement was neither strong nor consistent and did not surpass reference conditions. Water level rise was the main determinant of macrophyte community change, and deviated restoration trajectories in 2018 by decreasing macrophyte density and richness. At Grand Trunk and Northwest Reference, multiple emergent macrophyte taxa disappeared and the shoreward expansion of remaining emergent taxa was slowed, with newly inundated habitat instead being colonized by floating *Wolffia* spp. The lack of restoration effect suggested water level was a dominant driver of macrophyte change, while water transparency, reflected in minimum vegetation limit, Secchi depth, and precipitation, likely influenced macrophytes but was masked by the degree of water level increase.

Although Muskegon Lake-restored habitats had not reached reference standards almost 10 years post-restoration, macrophyte response time was not uncommon. In lakes suffering from different anthropogenic stresses such as acidification and eutrophication, macrophytes generally responded slowly to restoration and varied in response time from a few years to over 20 years (Hilt et al., 2018; Jeppesen et al., 2005; Søndergaard et al., 2007). Adequate light availability was required for macrophyte recovery, and positive community improvement was often delayed by water level increase (Roelofs et al., 2002), as seen in Muskegon Lake, and by light limitation from reduced water clarity (Jeppesen et al., 2005; Søndergaard et al., 2007; Verhofstad et al., 2017).

4.2. Contrasting restored trajectories

Differences in physical habitat and restoration effort influenced macrophyte responses in the two restored habitats to 2018 water level increase and the contrast between restoration trajectories. Heritage Landing's steep slope, and low wind and wave exposure, contrasted the gentle slopes and high exposure at Grand Trunk and Northwest Reference. Reduced seed bank and benthic organic matter at Heritage Landing due to sediment removal during restoration, which may take multiple years to recover, and steep slope, which limited macrophyte habitat and light availability, likely accounted for the frequent post-restoration richness and density declines, especially when water level increased. Less disruptive restoration adjacent to Grand Trunk's transect and a gentle slope accounted for the steady post-restoration macrophyte

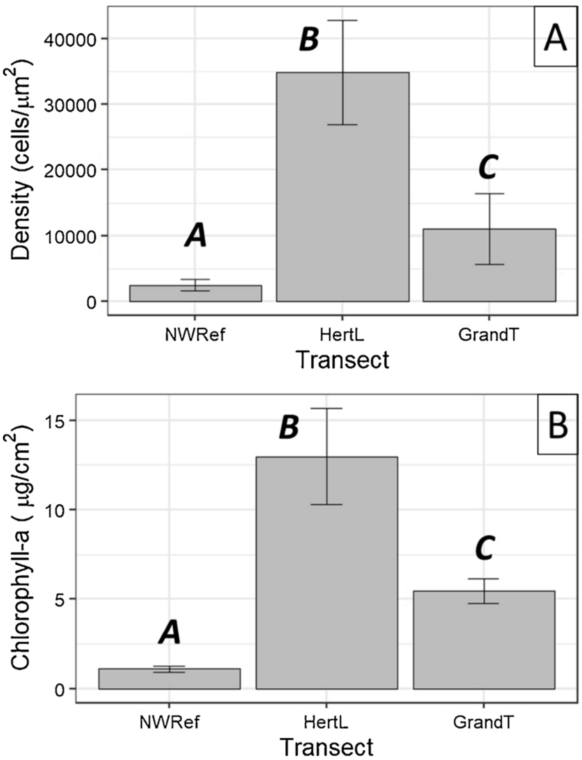

Fig. 5. Epiphytic Algae Barplots. Mean + 1 SE of epiphytic algal biological variables at each of the three transects in 2018. Letters represent statistically significant differences among transects ($p < 0.001$, Kruskal Wallis). (A) Mean epiphytic algal density (cells/μm^2, $n_{NWRef} = 10$, $n_{HertL} = 10$, $n_{GrandT} = 10$). (B) Mean epiphytic algal chlorophyll-*a* concentrations (μg/cm^2, $n_{NWRef} = 10$, $n_{HertL} = 10$, $n_{GrandT} = 10$).

density and richness increase, which followed the reference trajectory, and the mitigation of the 2018 water level increase. Restored habitat characteristics therefore determined each transect's ability to reach reference standards and its degree of resiliency to unanticipated environmental change.

4.3. Epiphytic algal shading

Epiphytic algal shading can become detrimental to *V. americana* (Chambers and Kalff, 1987) or other similarly shaped macrophytes when algal dry mass (DM) surpasses 1500 μg/cm^2 (Köhler et al., 2010) or 6000 μg/cm^2 (Guan et al., 2020), respectively. Assuming that Chl-*a* is 1 % of periphytic algal dry mass (Moulton et al., 2009), mean epiphytic algal dry mass on *V. americana* at the three transects (HertL = 1300 μg/cm^2 DM; GrandT = 500 μg/cm^2 DM; NWRef = 100 μg/cm^2 DM) did not meet these defined thresholds and therefore, were not adversely affecting *V. americana*. Greater wind and wave action could have dislodged weakly-attached algae from macrophytes at Grand Trunk and Northwest Reference, decreasing epiphytic algal biomass at these transects (Strand and Weisner, 1996). The dominant, adnate-attached diatom *Cocconeis* at Northwest Reference, which can withstand disturbance-driven environments, supported wave action as a main driver of epiphytic algal community structure; *Cocconeis* abundance was lowest at Heritage Landing where the colonial diatom *Fragliaria* and filamentous green alga *Bulbochaete* dominated, both of which favor low-disturbance regimes (Berthon et al., 2011).

4.4. Conclusion

Long-term data of macrophytes in Muskegon Lake following shoreline restoration revealed that restored transects have not yet achieved the same habitat quality as a reference location. Physical habitat differences among sites, as well as differences in restoration design, influenced the pace and nature of restoration recovery. Environmental factors, specifically water level and water transparency, strongly impacted the macrophyte community, conflating the restoration assessment. Although dense epiphytic algal cover may increase macrophyte competition for light and nutrients, this was not a major problem in Muskegon Lake possibly because of wave action. Identification of habitat restoration locations should take environmental factors,

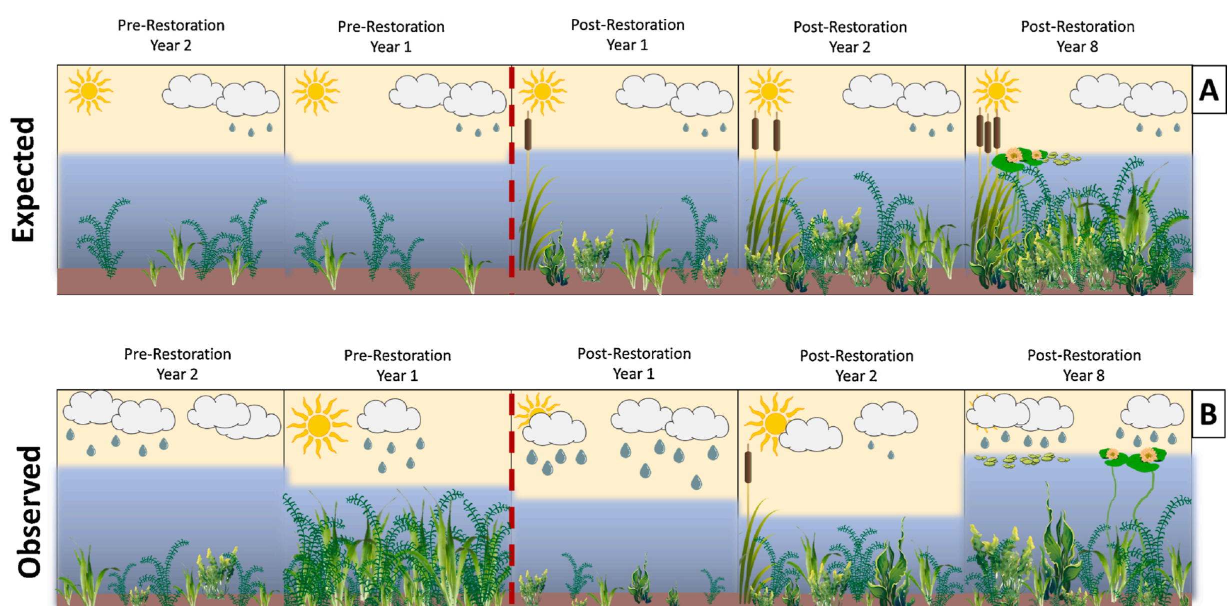

Fig. 6. Muskegon Lake Expected vs. Observed Restoration Trajectory. A conceptual diagram of Muskegon Lake's macrophyte community trajectory; the red dashed line separates pre-restoration (left of line) and post-restoration (right of line) conditions. The sun represents warmer air temperatures and clouds represent cooler air temperatures. Raindrop size and number indicates precipitation accumulation during the growing season. Water level is shown in blue. Macrophyte total density is represented by macrophyte size and number and total richness is represented by the number of different macrophyte types. A) Expected Muskegon Lake restoration trajectory. B) Observed Muskegon Lake restoration trajectory.

especially slope, exposure, and sediment composition, into consideration to optimize restoration success. Restoration in the Great Lakes region should additionally account for future water level change.

Funding

This work was supported by the National Oceanic and Atmospheric Association [grant number NOAA-NMFS-HCPO-2017-2005105]; the Michigan Chapter of the North American Lake Management Society, East Lansing, MI; the West Michigan Chapter of the Air and Waste Management Society, Grand Rapids, MI; the Michigan Lakes and Streams Association, Kalamazoo, MI; and Grand Valley State University, Allendale, MI. The funding sources were not involved in the research study design, data collection, data analysis and interpretation, report writing, or in the decision to submit the article for publication.

CRediT authorship contribution statement

Paige M. Kleindl: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition. **Alan D. Steinman:** Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

Funding for this research project was provided by the National Oceanic and Atmospheric Association's Habitat Focus Area grant awarded to the West Michigan Shoreline Regional Development Commission (WMSRDC) with a subcontract to the Annis Water Resources Institute. Additional funding was provided by the Lake Research Student Grant from the Michigan Chapter of the North American Lake Management Society (McNALMS), the Presidential Research Grant from Grand Valley State University, the Graduate Megan E. Cook Scholarship from the Michigan Lake and Stream Association (MLSA), and the Environmental Scholarship from the West Michigan Air and Waste Management Association (WMAWMA). The authors gratefully acknowledge the support of our project partners: WMSRDC, Muskegon Lake Watershed Partnership, Muskegon River Watershed Assembly, and the Great Lakes Commission. We thank Maggie Oudsema, Rachel Orzechowski, Emily Kindervater, and Mike Hassett for field work, laboratory, and data analysis assistance. We thank Brian Scull for his help with nutrient analysis and Dr. Sarah Hamsher with voucher algae identification. Previous sampling efforts for Muskegon Lake macrophytes were completed by Maggie Oudsema, Mary Ogdahl, Brian Hanson, Eric Tidquist, and James Smit. Maggie Oudsema, Whitney Nelson, Kelli Johnson, and Sara Damm assisted with previous plant and sediment processing. We thank Dr. Mark Luttenton for voucher macrophyte identification and manuscript comments. We also thank Dr. Erica Young, Dr. Evelyn Gaiser, Sarah Lamar, Emily Kindervater, as well as Prof. Jan Vermaat and two anonymous reviewers for manuscript comments.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aquabot.2020.103327.

References

Allen, H.L., 1971. Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. Ecol. Monographs 41, 97–127. https://doi.org/10.2307/1942387.

APHA, A., 1998. Wef. Standard Methods for the Examination of Water and Wastewater., 21, p. 1378.

Barko, J.W., Gunnison, D., Carpenter, S.R., 1991. Sediment interactions with submersed macrophyte growth and community dynamics. Aquat. Bot. 41, 41–65. https://doi.org/10.1016/0304-3770(91)90038-7.

Berthon, V., Bouchez, A., Rimet, F., 2011. Using diatom life-forms and ecological guilds to assess organic pollution and trophic level in rivers: a case study of rivers in south-eastern France. Hydrobiologia 673, 259–271. https://doi.org/10.1007/s10750-011-0786-1.

Bourdaghs, M., Johnston, C.A., Regal, R.R., 2006. Properties and performance of the floristic quality index in Great Lakes coastal wetlands. Wetlands 23, 718–735. https://doi.org/10.1672/0277-5212(2006)26[718:papotf]2.0.co;2.

Brauns, M., Gücker, B., Wagner, C., Garcia, X.F., Walz, N., Pusch, M.T., 2011. Human lakeshore development alters the structure and trophic basis of littoral food webs. J. Appl. Ecol. 48, 916–925. https://doi.org/10.1111/j.1365-2664.2011.02007.x.

Chambers, P.A., Kalff, J., 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42, 701–709. https://doi.org/10.1139/f85-090.

Chambers, P.A., Kalff, J., 1987. Light and nutrients in the control of aquatic plant community structure. I. In situ experiments. J. Ecol. 611–619. https://doi.org/10.2307/2260193.

CO-OPS (Center for Operational Oceanographic Products and Services), 2019. Tides and Currents. National Oceanographic and Atmospheric Administration (NOAA), Center for Operational Oceanographic Products and Services, p. 2019 (accessed 04.29.19. http://www.co-ops.nos.noaa.gov/waterlevels.

Gabriel, A.O., Bodensteiner, L.R., 2012. Impacts of riprap on wetland shorelines, Upper Winnebago pool lakes, Wisconsin. Wetlands 32, 105–117. https://doi.org/10.1007/s13157-011-0251-y.

Graziano, M., Alexander, K.A., Liesch, M., Lema, E., Torres, J.A., 2019. Understanding an emerging economic discourse through regional analysis: blue economy clusters in the US Great Lakes basin. Appl. Geogr. 105, 111–123. https://doi.org/10.1016/j.apgeog.2019.02.013.

Guan, J., Jacoby, C.A., Frazer, T.K., 2020. Light attenuation by periphyton on Vallisneria americana. Ecol. Indic. 116, 106498. https://doi.org/10.1016/j.ecolind.2020.106498.

Hilt, S., Alirangues Nuñez, M.M., Bakker, E.S., Blindow, I., Davidson, T.A., Gillefalk, M., Hansson, L., Janse, J.H., Janssen, A.B.G., Jeppesen, E., Kabus, T., Kelly, A., Köhler, J., Lauridsen, T.L., Mooij, W.M., Noordhuis, R., Phillips, G., Rücker, J., Schuster, H., Søndergaard, M., Teurlincx, S., van de Weyer, K., van Donk, E., Waterstraat, A., Willby, N., Sayer, C.D., 2018. Response of submerged macrophyte communities to external and internal restoration measures in north temperate shallow lakes. Front. Plant Sci. 9, 194. https://doi.org/10.3389/fpls.2018.00194.

Jeppesen, E., Søndergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Rainer, D., Dokulil, M.T., Foy, B., Gerdeaux, D., Hampton, S.E., Hilt, S., Kangur, K., Köhler, J., Lammens, E.H.H.R., Lauridsen, T.L., Manca, M., Miracle, M.R., Moss, B., Nõges, P., Persson, G., Phillips, G., Portielje, R., Romo, S., Schelske, C.L., Straile, D., Tatri, I., Willén, E., Winder, M., 2005. Lake responses to reduced nutrient loading–an analysis of contemporary long-term data from 35 case studies. Freshw. Biol. 50, 1747–1771. https://doi.org/10.1111/j.1365-2427.2005.01415.x.

Keddy, P.A., 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquat. Bot. 14, 41–58. https://doi.org/10.1016/0304-3770(82)90085-7.

Köhler, J., Hachol, J., Hilt, S., 2010. Regulation of submerged macrophyte biomass in a temperate lowland river: interactions between shading by bank vegetation, epiphyton, and water turbidity. Aquat. Bot. 92, 129–136. https://doi.org/10.1016/j.aquabot.2009.10.018.

Kolada, A., 2014. The effect of lake morphology on aquatic vegetation development and changes under the influence of eutrophication. Ecol. Indic. 38, 282–293. https://doi.org/10.1016/j.ecolind.2013.11.015.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Soft. 82 (13), 1–26. https://doi.org/10.18637/jss.v082.i13.

Lacoul, P., Freedman, B., 2006. Environmental influences on aquatic plants in freshwater ecosystems. Environ. Rev. 14, 89–136. https://doi.org/10.1139/a06-001.

Larson, J.H., Trebitz, A.S., Steinman, A.D., Wiley, M.J., Mazur, M.C., Pebbles, V., Braun, H.A., Seelbach, P.W., 2013. Great Lakes rivermouth ecosystems: scientific synthesis and management implications. J. Great Lakes Res. 39, 513–524. https://doi.org/10.1016/j.jglr.2013.06.002.

Middelboe, A.L., Markager, S., 1997. Depth limits and minimum light requirements of freshwater macrophytes. Freshw. Biol. 37, 553–568. https://doi.org/10.1046/j.1365-2427.1997.00183.x.

Moulton, T.P., Souza, M.L., Walter, T.L., Krsulović, F.A., 2009. Patterns of periphyton chlorophyll and dry mass in a neotropical stream: a cheap and rapid analysis using a hand-held fluorometer. Mar. Freshw. Res. 60, 224–233. https://doi.org/10.1071/MF08081.

NCEI (National Centers for Environmental Information), 2019. Climate Data Online. National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information, p. 2019 (accessed 04.29.19. http://www.ncdc.noaa.gov/cdo-web/.

Ogdahl, M.E., Steinman, A.D., 2015. Factors influencing macrophyte growth and recovery following shoreline restoration activity. Aquat. Bot. 120, 363–370. https://doi.org/10.1016/j.aquabot.2014.10.006.

Palmer, M., Allan, J.D., Meyer, J., Bernhardt, E.S., 2007. River restoration in the twenty-first century: data and essential future efforts. Restor. Ecol. 15, 472–481. https://doi.org/10.1111/j.1526-100X.2007.00243.x.

Penning, W.E., Dudley, B., Mjelde, M., Hellsten, S., Hanganu, J., Kolada, A., van den Berg, M., Poikane Phillips, G., Willby, N., Ecke, F., 2008. Using aquatic macrophyte community indices to define the ecological status of European lakes. Aquat. Microb. Ecol. 42, 253–264. https://doi.org/10.1007/s10452-008-9183-x.

Phillips, G.L., Eminson, D., Moss, B., 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. Aquat. Bot. 4, 103–126. https://doi.org/10.1016/0304-3770(78)90012-8.

Phillips, G., Willby, N., Moss, B., 2016. Submerged macrophyte decline in shallow lakes: what have we learnt in the last forty years? Aquat. Bot. 135, 37–45. https://doi.org/10.1016/j.aquabot.2016.04.004.

Poore, M.E.D., 1955. The use of phytosociological methods in ecological investigations: I. The Braun-Blanquet system. J. Ecol. 43, 226–244.

R Core Team, 2017. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Roelofs, J.G.M., Brouwer, E., Bobbink, R., 2002. Restoration of aquatic macrophyte vegetation in acidified and eutrophicated shallow soft water wetlands in the Netherlands. Ecological Restoration of Aquatic and Semi-Aquatic Ecosystems in the Netherlands (NW Europe). Springer, Dordrecht, pp. 171–180.

Sand-Jensen, K., Søndergaard, M., 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. Int. Rev. Der Gesamten Hydrobiol. Und Hydrogr. 66, 529–552. https://doi.org/10.1002/iroh.19810660406.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671.

Søndergaard, M., Jeppesen, E., Lauridsen, T.L., Skov, C., Van Nes, E.H., Roijackers, R., Lammens, E., Portielje, R.O.B., 2007. Lake restoration: successes, failures and long-term effects. J. Appl. Ecol. 44, 1095–1105. https://doi.org/10.1111/j.1365-2664.2007.01363.x.

Søndergaard, M., Phillips, G., Hellsten, S., Kolada, A., Ecke, F., Mäemets, H., Mjelde, M., Azzella, M.M., Oggioni, A., 2013. Maximum growing depth of submerged macrophytes in European lakes. Hydrobiologia 704, 165–177. https://doi.org/10.1007/s10750-012-1389-1.

Squires, M.M., Lesack, L.F., 2003. The relation between sediment nutrient content and macrophyte biomass and community structure along a water transparency gradient among lakes of the Mackenzie Delta. Can. J. Fish. Aquat. Sci. 60, 333–343. https://doi.org/10.1139/f03-027.

Steinman, A.D., Ogdahl, M., Rediske, R., Ruetz, C.R., Biddanda, B.A., Nemeth, L., 2008. Current status and trends in Muskegon Lake, Michigan. J. Great Lakes Res. 34, 169–188. https://doi.org/10.3394/0380-1330(2008)34[169:CSATIM]2.0.CO;2.

Steinman, A.D., Lamberti, G.A., Leavitt, P.R., Uzarski, D.G., 2017. Biomass and pigments of benthic algae. In: Hauer, R.F., Lamberti, G.A. (Eds.), Methods in Stream Ecology, Vol. 1. Academic Press, Massachusetts, pp. 223–241.

Strand, J.A., Weisner, S.E., 1996. Wave exposure related growth of epiphyton: implications for the distribution of submerged macrophytes in eutrophic lakes. Hydrobiologia 325, 113–119. https://doi.org/10.1007/BF00028271.

Thomaz, S.M., Cunha, E.R.D., 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. Acta Limnol. Bras. 22, 218–236. https://doi.org/10.4322/actalb.02202011.

Uzarski, D.G., Brady, V.J., Cooper, M.J., Wilcox, D.A., Albert, D.A., Axler, R.P., Bostwick, P., Brown, T.N., Ciborowski, J.J.H., Danz, N.P., Gathman, J.P., Gehring, T. M., Grabas, G.P., Garwood, A., Howe, R.W., Johnson, L.B., Lamberti, G.A., Moerke, A.H., Murry, B.A., Miemi, G.J., Normaent, C.J., Ruetz, C.S., Steinman, A.D., Tozer, D.C., Wheeler, R., O'Donnell, T.K., Schneider, J.P., 2017. Standardized measures of coastal wetland condition: implementation at a Laurentian Great Lakes basin-wide scale. Wetlands 37, 15–32. https://doi.org/10.1007/s13157-016-0835-7.

Vadeboncoeur, Y., Steinman, A.D., 2002. Periphyton function in lake ecosystems. Scientific World J. 2, 1449–1468. https://doi.org/10.1100/tsw.2002.294.

Verhofstad, M.J.J.M., Núñez, M.A., Reichman, E.P., van Donk, E., Lamers, L.P.M., Bakker, E.S., 2017. Mass development of monospecific submerged macrophyte vegetation after the restoration of shallow lakes: roles of light, sediment nutrient levels, and propagule density. Aquat. Bot. 141, 29–38. https://doi.org/10.1016/j.aquabot.2017.04.004Get.

Verzani, J., 2018. UsingR: Data Sets, Etc. for the Text "Using R for Introductory Statistics". R package version 2.0-6, second edition. https://CRAN.R-project.org/package=UsingR.

Whittier, T.R., Paulsen, S.G., Larsen, D.P., Peterson, S.A., Herlihy, A.T., Kaufmann, P.R., 2002. Indicators of ecological stress and their extent in the population of northeastern lakes: a regional-scale assessment: although stressors such as nonnative fish introductions, mercury contamination, and shoreline alteration are not generally considered subjects for environmental management, they are as widespread as eutrophication, and more extensive than acidification, in the lakes of the northeastern states. BioScience 52, 235–247. https://doi.org/10.1641/0006-3568(2002)052[0235:IOESAT]2.0.CO;2.