Muskegon Lake Area of Concern Habitat Restoration Project: Macrophyte Assessment

Final Project Report

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Introduction

As part of the Great Lakes coastal wetlands ecosystem, drowned river mouths provide critical ecosystem services within the Great Lakes (Jude and Pappas 1992, Wei et al. 2004, Sierszen et al. 2012). Despite their ecological significance, approximately three-quarters of the coastal wetlands in heavily-developed areas of the Great Lakes have been lost, and the wetlands that remain often suffer from degraded quality (Jude and Pappas 1992). Much of this loss has been the result of activities that have hardened the shoreline and altered the sediments (Albert and Minc 2004).

Muskegon Lake, like many other drowned river mouth systems in the Great Lakes, provides a wide array of ecosystem services but has experienced years of environmental abuse. Since the mid-1800's, the lake has been subjected to intense anthropogenic activities including sawmills, foundries, metal finishing plants, and petrochemical storage facilities (Alexander 2006). As a result of these activities, the lake was declared a Great Lakes Area of Concern (AOC) in 1987.

Approximately 780 acres of nearshore habitat has been filled by past industrial activities along the Muskegon Lake shoreline (MLWPHC 2008) and approximately 65% of the shoreline has been hardened with seawalls and concrete or rock riprap (Steinman et al. 2008). Additionally, broken concrete, foundry slag, sheet metal, slab wood, saw dust and other materials in shallow water areas pose hazards to recreation and degrade habitat. This translates to substantial loss and fragmentation of habitat, and threatens fish and wildlife populations.

The Muskegon Lake Habitat Restoration Project was initiated by our project partners, the West Michigan Shoreline Regional Development Commission (WMSRDC) and the Great Lakes Commission (GLC), to "soften" hardened shoreline areas, create or restore emergent and open-water wetlands, and remove unnatural fill in targeted areas along the south shore of Muskegon Lake. This project is a major step toward fulfilling the restoration criteria for delisting Muskegon Lake as a Great Lakes Area of Concern (AOC).

The hardened shoreline and areas of fill along Muskegon Lake's south shore have dramatically altered the environment for macrophyte (rooted and floating aquatic plants) growth. Macrophyte surveys conducted in 1995 and 2005 revealed that the south shore had very little aquatic vegetation compared to the north shore of the lake, where the shoreline is mostly natural and unaltered (AWRI unpublished data). Human-altered near-shore geomorphology, including steep drop-offs and unsuitable substrate, creates unfavorable conditions for plant growth and, consequently, degraded habitat quality along the south shore of the lake.

Macrophytes can be used as indicators of the ecological health of Great Lakes coastal wetlands (Albert and Minc 2004, Cvetkovic et al. 2010, Grabas et al. 2012), as their abundance and community composition reflect the quality of both physical and chemical habitat conditions (Lougheed et al. 2001, Madsen et al. 2001, Cvetkovic et al. 2010, Grabas et al. 2012). Because macrophyte growth is affected, in part, by sediment quality (Barko and Smart 1986, Barko et al. 1991, Squires and Lesack 2003) and nearshore gradient (Duarte and Kalff 1986, Barko et al. 1991, Partanen et al. 2002), macrophytes may also prove to be valuable indicators of shoreline restoration efforts (Grabas et al. 2012).

In an effort to assess the ecological benefits of the Muskegon Lake restoration project, we surveyed macrophyte beds in Muskegon Lake over a 4-year period. Surveys conducted during 2009 and 2010 represent pre-restoration conditions. Post-restoration sampling occurred in 2011, only a few months after restoration was complete, and again in 2012. These data give an indication of short-term effects of restoration on the macrophyte community, and provide important baseline information for future assessments of restoration efficacy.

Methods

Site description – Muskegon Lake is a ~17 km^2 drowned river mouth lake that serves as the receiving water body for the Muskegon River watershed. Muskegon Lake also connects directly to Lake Michigan through a navigation channel, and helps to modulate the influence of the watershed on Lake Michigan.

Macrophyte surveys were conducted at 5 restoration locations along the south shore of the lake (Figure 1). Restoration sites were selected in each of 4 restoration focus areas, as identified by WMSRDC and GLC, and included Grand Trunk, Kirksey, Heritage Landing, South Branch (sampled only in 2009), and Amoco (not sampled in 2009) (Table 1, Figure 1). Two reference sites were located along the north shore of the lake to represent the macrophyte community associated with more natural habitat conditions. The north shore was divided into two reference zones, and one reference site was randomly selected within each zone: Northwest Reference and Northeast Reference (Table 1, Figure 1). At each site, macrophytes were surveyed along a transect extending perpendicular from shore to the greatest extent of plant growth (details below).

Table 1. Location information for the origin of each sampling transect and restoration details.

Site	**Latitude (N)**	**Longitude (W)**	**Scheduled Date of Restoration**	**Actual Date of Restoration**	**Restoration Type**
Northwest Reference	43˚ 14' 50.09"	86˚ 18' 56.67"	N/A	N/A	N/A
Northeast Reference	43˚ 14' 47.96"	86˚ 16' 51.41"	N/A	N/A	N/A
South Branch	43˚ 14' 52.61"	86˚ 14' 49.41"	July 2009	June 2010	None at our location*
Heritage Landing	43˚ 13' 58.33"	86˚ 15' 42.49"	August 2009	April 2011	Shoreline and underwater fill removal**
Kirksey	43˚ 13' 57.58"	86˚ 16' 36.02"	August 2009	October 2010	Shoreline fill removal** and vegetation planting
Amoco	43˚ 13' 18.57"	86˚ 17' 04.25"	September 2009	April 2011	Shoreline and underwater fill removal**
Grand Trunk	43˚ 12' 57.44"	86˚ 17' 49.19"	July 2009	June 2010	Shoreline wetland restoration and underwater fill removal**

N/A = not applicable

*Restoration at South Branch occurred along Muskegon River, rather than in the lake where our transect was located due to the withdrawal of a landowner from the project.

**Fill removal refers to the removal of unnatural fill (i.e., sawmill waste; industrial and/or commercial demolition material, such as broken concrete) at (shoreline) or below (underwater) the ordinary high water mark.

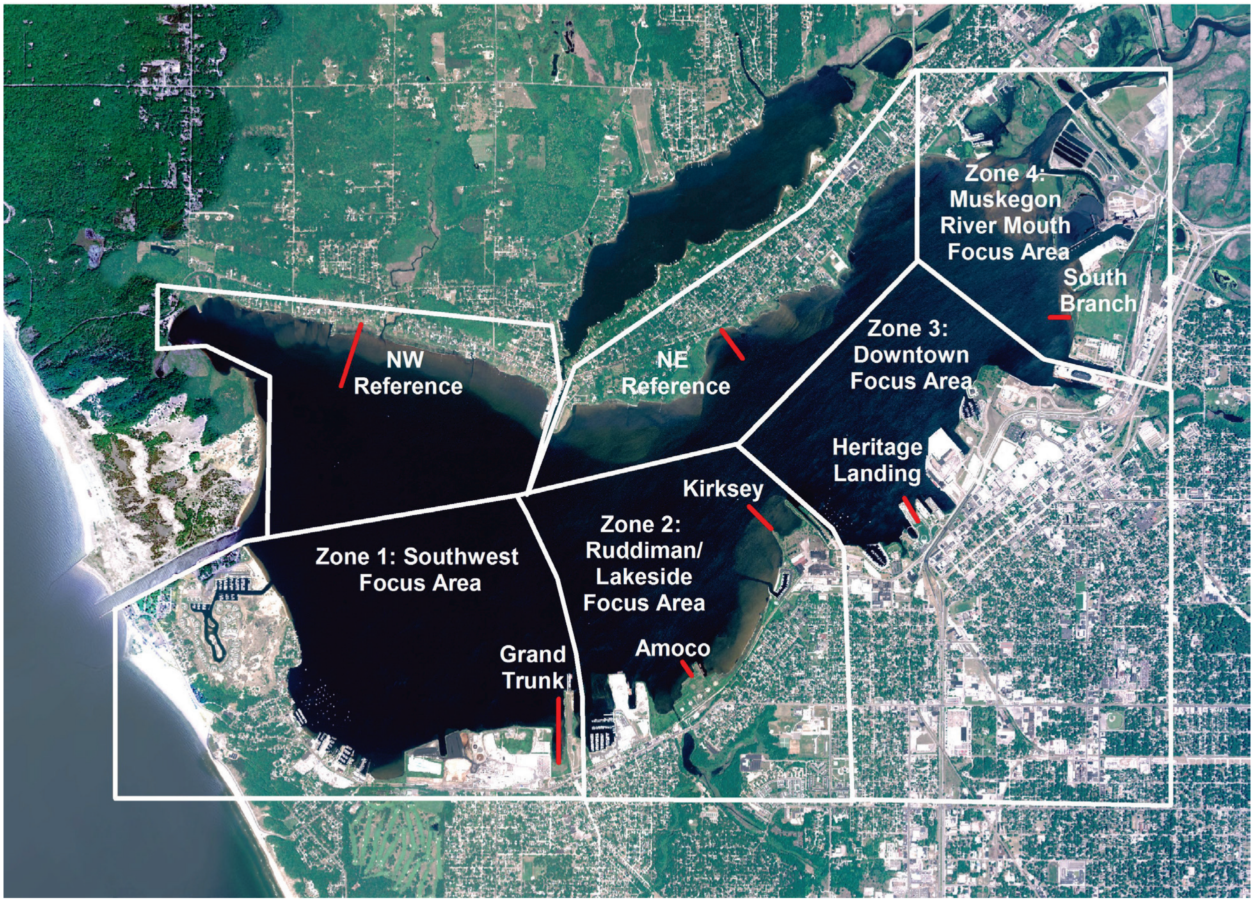

Figure 1. Transect locations and lengths (red lines) for macrophyte assessment in Muskegon Lake. See text for sampling details.

Field protocols – Macrophyte surveys took place August 24-26, 2009, August 10-19, 2010, August 8-11, 2011, and August 13-23, 2012. Transects were established perpendicular to shore, with transect points located every 5 m from 0-10 m from shore, every 10 m from 10-100 m from shore, every 25 m from 100-300 m from shore, and every 50 m from 300+ m from shore. A handheld GPS unit was used to locate the transect origin on shore. Transects extended to the farthest point of macrophyte growth, as determined by 1) 2 consecutive sites with no growth, or 2) the absence of macrophytes at a site greater than 4.5 m deep, indicating the drop-off beyond which macrophytes can grow had been reached (see Figure 2). Double-headed rake tosses upon approach to the transect allowed us to determine the approximate extent of plant growth and helped us discern between extensive bare patches and the actual farthest extent of growth. A transect width of 10 m was chosen to reflect our ability to visually assess the macrophyte community within approximately 5 m of the boat in any direction. Water depth was measured at each site.

At each point along the transect, overall plant cover was assigned one of the following ranks: 0 = Bare; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; or 4 = 76–100%. In addition, all plants within ~ 5 m radius of each sampling point were identified to species, and species percent abundance (0-100%) was estimated. When plants were too deep to be easily distinguished from the water surface, a double-headed weighted rake was tossed three times to aid in identifying species, assigning cover rank, and estimating relative abundance. Voucher specimens for plants that could not be identified were brought back to the lab for identification.

Plant biomass and sediment organic matter were sampled at one randomly-selected transect point in each of the following distance-from-shore categories: 0-20 m, 20-50 m, 50-100 m, 200-300 m, 300-400 m, 400-500 m, etc. Plant biomass was harvested using two garden rakes attached to each other at a pivot point near the middle of each rake's handle. The teeth of the rakes faced each other in order to cut and secure the plants when the handles were pulled together. A chain connected to the rakes fixed the sampling area at 0.6 m^2. A total area of 1.8 m^2 (3 scoops) was sampled at each point along the transect; where biomass was very high, only 0.6 or 1.2 m^2 (1 or 2 scoops) was sampled. One sediment core was collected (4-cm diameter, 10 cm deep) using a hand-held gravity corer (Davis and Steinman 1998).

Laboratory processing – Plant biomass and sediment samples were kept refrigerated until laboratory processing. Plant biomass samples were cleaned of sediment, *Dreissena* mussels, and filamentous green algae. Samples were sorted by species, dried at 85˚C for 96 hours, and weighed. Sediment samples were homogenized by hand and three 5-g subsamples were taken. Sediment subsamples were dried for 24 hr at 105˚C, weighed, ashed at 550˚C for 4 hr, and re-weighed. Sediment organic matter was calculated as the difference between pre- and post-combustion weights, expressed as a percentage of sediment dry weight. Values for each of the three subsamples were averaged for each sampling point.

Data analysis – Biomass density within each transect was calculated by summing the dry mass (g) of all plants collected along a transect and dividing that value by the area sampled (area sampled = total number of scoops x 0.6 m^2). Total biomass was calculated by multiplying biomass density by the total area of each transect (total area = transect length x 10 m transect width).

Taxon relative abundance was calculated for each transect using a weighted mean. This approach was chosen as a way to incorporate both percent abundance and cover rank in describing the importance of individual taxa within a transect. In this calculation, the percent abundance of a taxon at a given sampling location was weighted by its cover rank at that location. As a result, taxa with higher cover ranks contribute more to the overall mean relative abundance than those with lower cover ranks. The calculation involved 1) multiplying the percent abundance of the taxon (0-100%) at each sampling location by its cover rank (1-4) at that location, to give a weighted relative abundance, 2) calculating the sum of weighted relative abundance values for that taxon along the transect, and 3) dividing by the sum of cover values for the transect:

$$\overline{\mathrm{A}}_w = \frac{\sum \mathrm{AC}}{\sum \mathrm{C}};$$

where w stands for weighted, A= taxon relative abundance, and C=cover rank. Table 2 shows an example that illustrates the difference between calculating un-weighted vs. weighted mean relative abundance (Table 2).

Table 2. Hypothetical data from a macrophyte sampling transect. Mean percent abundance (un-weighted) is calculated for each species and compared to weighted mean relative abundance, which accounts for cover rank. Cover ranks: 0 = Bare; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; or 4 = 76–100%.

Distance from shore	**Cover Rank**	**Species 1**	**% Abundance**	**Species 2**	**% Abundance**
5 m	1	*Vallisneria americana*	100	*Najas flexilis*	0
10 m	1	*Vallisneria americana*	100	*Najas flexilis*	0
20 m	3	*Vallisneria americana*	20	*Najas flexilis*	80
30 m	4	*Vallisneria americana*	5	*Najas flexilis*	95
40 m	2	*Vallisneria americana*	0	*Najas flexilis*	100
Mean			45		55
vs.					
Weighted mean			25		75

V. americana = ((100*1)+(100*1)+(20*3)+(5*4)+(0*2))/(1+1+3+4+2) = 25
N. flexilis = ((0*1)+(0*1)+(80*3)+(95*4)+(100*2))/(1+1+3+4+2) = 75

We applied the State of Michigan's Coefficient of Conservatism (C) to each macrophyte species we identified. These C-values range from 0-10 and represent the probability that a species will occur within an undisturbed landscape. Therefore, a species with a C-value of 0 can be found in highly degraded areas and a species with a C-value of 10 is usually found in high quality areas (Herman et al. 2001). All non-native species were assigned a C-value of 0 (Bourdaghs et al. 2006). A mean C-value was calculated for each transect.

Differences in macrophyte cover, sediment organic matter, and biomass among sites and years were tested using a Kruskal-Wallis One Way ANOVA on Ranks and multiple pairwise comparisons were tested using Dunn's Method. Normality was tested using the Kolmogorov-Smirnov test. All statistical analyses were conducted using SigmaPlot (version 12.3; Systat).

Results

Water Depth

All of the macrophyte transects were characterized by relatively shallow (<3 m) and consistent water depth followed by a steep drop-off, with the exception of the Northwest Reference site (Figure 2). This site had a much more gradual decline in slope (i.e., gradual increase in water depth) over the length of the transect, which was also substantially longer (650-800 m) than the other sites (100-400 m) (Figure 2). The maximum depth at which macrophyte growth was found was also much greater at the Northwest Reference site (3.65-5.30 m) than at the other sites (1.43-2.68 m) (Figure 2). Mean depth was deepest at Heritage Landing and shallowest at South Branch and Grand Trunk (Table 3). Mean water depth in 2012 was 20-50 cm lower than the grand mean from 2009-2011, reflecting an overall decline in Great Lakes water levels during 2012 (USACE 2012).

Table 3. Mean water depth for transects in Muskegon Lake. South Branch was sampled only in 2009; Amoco was not sampled 2009.

	Mean Depth			
Site	**2009**	**2010**	**2011**	**2012**
NW Reference	1.09	1.38	1.28	0.93
NE Reference	1.22	1.28	1.21	1.01
South Branch	0.76	--	--	--
Heritage	2.05	2.14	2.27	1.93
Kirksey	1.07	1.03	1.23	0.77
Amoco	--	1.25	1.27	0.76
Grand Trunk	0.82	0.81	1.06	0.59

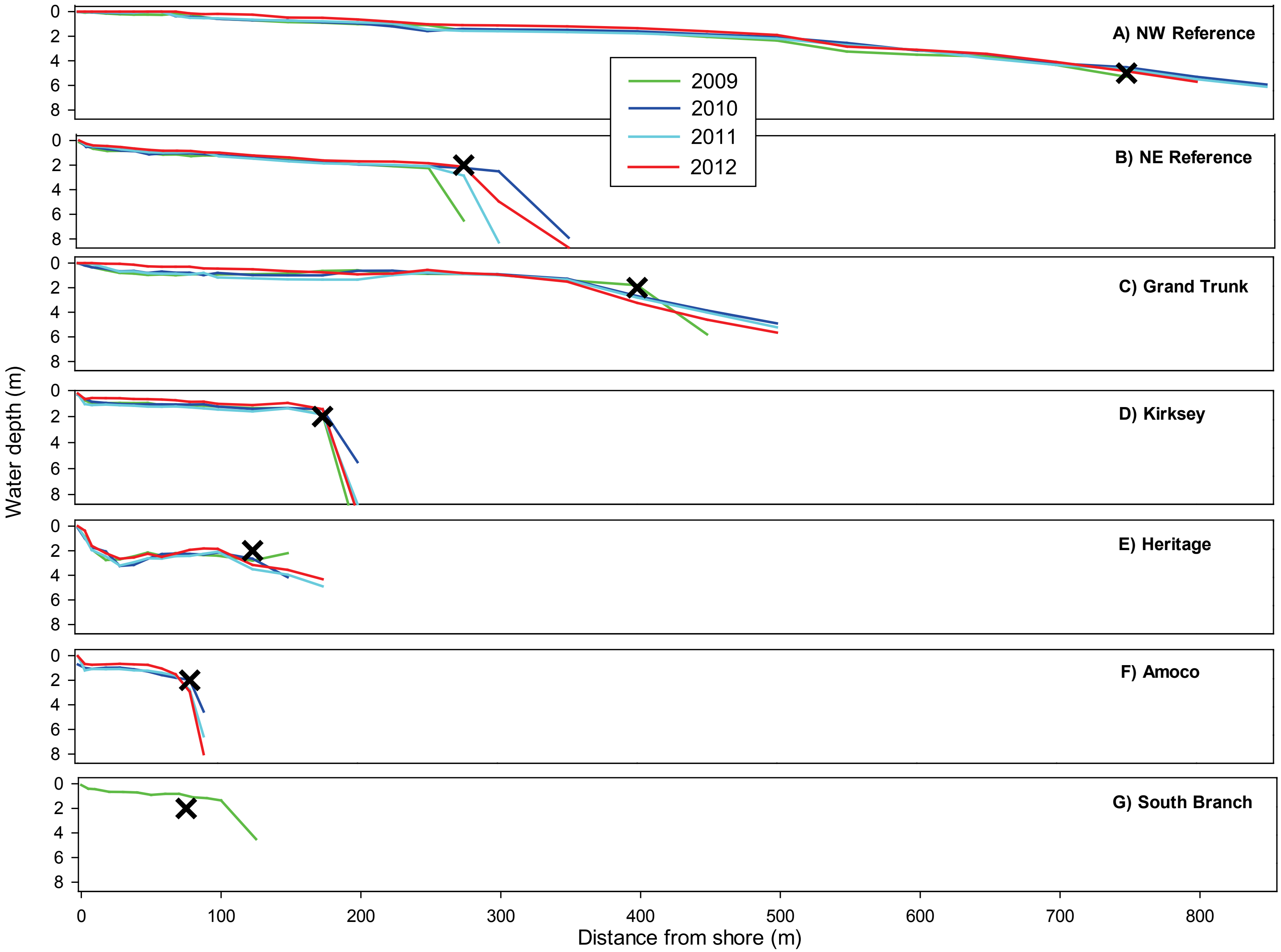

Figure 2. Depth contours at each of the transects sampled from 2009-2012. “X” indicates the approximate farthest extent of macrophyte growth. Sampling at South Branch was discontinued after 2009 due to change in restoration location; Amoco was not sampled in 2009 (see methods).

Macrophyte Cover and Biomass

The most macrophyte cover was observed at the Grand Trunk and Heritage Landing sites, whereas the least macrophyte cover was found at the South Branch (2009) and Amoco (2010, 2011, 2012) sites (Table 4). The only significant change in average cover rank among sampling years was observed at Kirksey, where cover rank was lower in 2011 than in 2010 (p=0.004) and 2012 (p=0.002). Detailed cover data are included in the Appendix.

Macrophyte biomass density and total biomass varied both spatially and temporally during the study period. The greatest values were generally observed at Northwest Reference, Heritage Landing, and Grand Trunk (Figure 3). Biomass density and total biomass were comparatively low at South Branch, Kirksey, and Amoco. At the Northwest Reference site, macrophyte biomass decreased from 2009 to 2011, but increased substantially in 2012 (Figure 3). The temporal trend was opposite at the Northeast Reference site. The Northwest Reference site had more biomass than the Northeast Reference site during all years, except 2011 when biomass was similar between the sites (Figure 3).

Three of the four restoration sites experienced a decrease in macrophyte biomass the first year following restoration (Figure 3). The largest decline was at the Heritage Landing site, but biomass also declined at Kirksey and Grand Trunk in 2011, although it remained similar to or greater than 2009 observations, respectively. In 2012, the second year following restoration, macrophyte biomass increased at all restoration sites to amounts similar to or greater than pre-restoration conditions (Figure 3). Despite the increases observed at Kirksey and Amoco following restoration, macrophyte biomass remained relatively low (Figure 3). Grand mean (i.e., sites pooled) biomass density and total biomass were similar in 2009, 2010, and 2012, and much lower in 2011, though the difference was not statistically significant. Mean (± SE) biomass density ranged from 49 (± 20) g/m^2 in 2011 to 142 (± 57) g/m^2 in 2012; mean (± SE) total biomass ranged from 198 (± 90) kg in 2011 to 493 (± 231) kg in 2012.

Table 4. Mean macrophyte cover rank for transects in Muskegon Lake. Cover ranks: 0-Bare, 1-1–25%, 2-26–50%, 3-51–75%, 4-76–100%. South Branch was sampled only in 2009; Amoco was not sampled 2009.

	Mean Cover Rank			
Site	**2009**	**2010**	**2011**	**2012**
NW Reference	2.67	2.42	2.33	2.93
NE Reference	1.56	2.50	2.47	2.68
South Branch	0.83	--	--	--
Heritage	3.58	3.23	2.77	3.00
Kirksey	1.20	2.82	1.00	2.47
Amoco	--	1.70	0.90	1.64
Grand Trunk	2.77	3.64	3.57	3.27

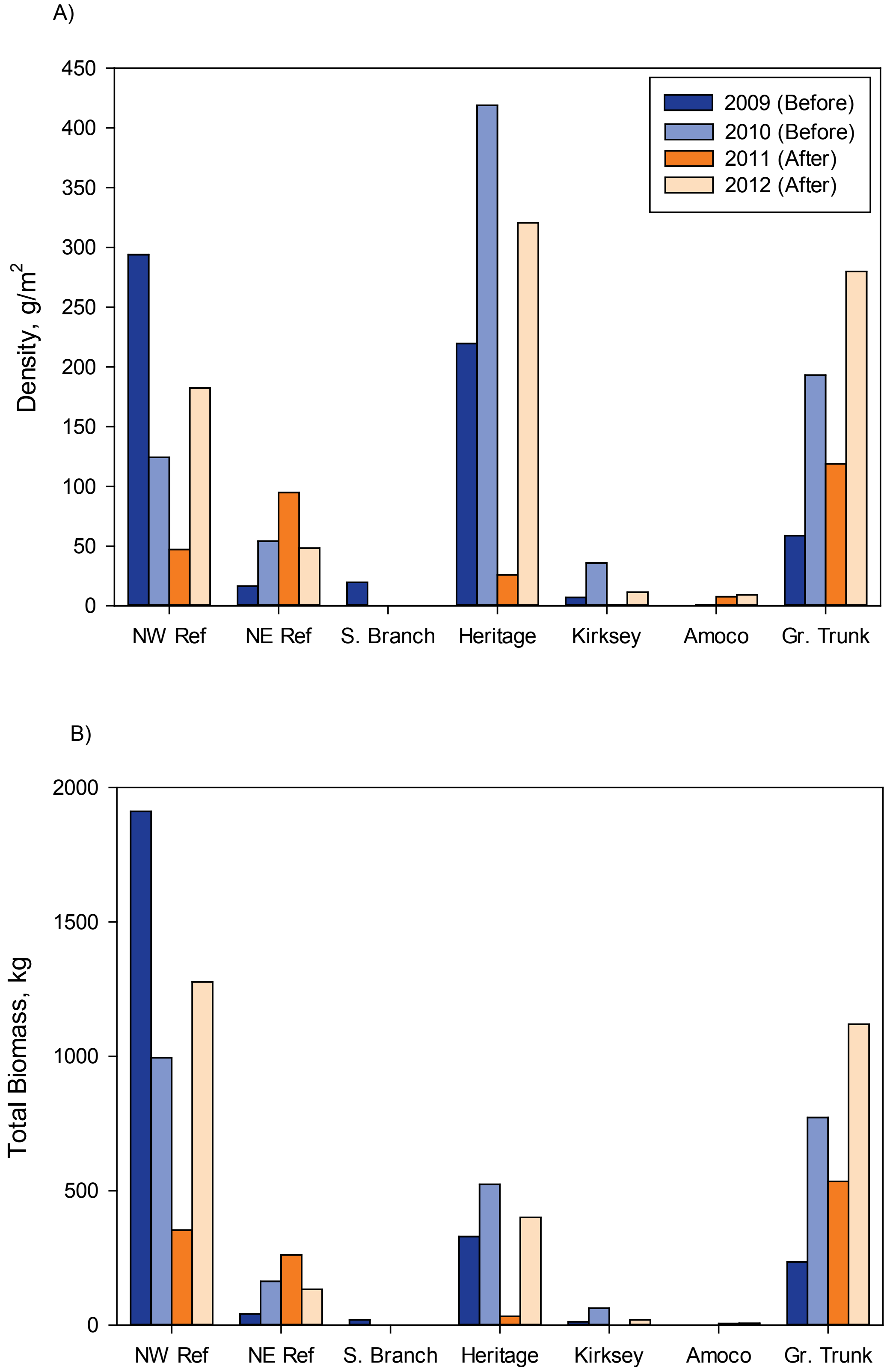

Figure 3. Macrophyte biomass density (g/m^2) (A) and total biomass (kg) (B) at each survey site before (2009 and 2012) and after (2011 and 2012) restoration.

Community Composition

At all sites except Kirksey and Amoco, emergent and shallow-water vegetation, such as cattail (*Typha* spp.), common reed (*Phragmites australis*), willow (*Salix* sp.), sedges (*Schoenoplectus* spp.), and bladderwort (*Utricularia* spp.) dominated the nearshore portion of the transect (Tables 5-8). The transect at the Northwest Reference site had a particularly long portion (70-90 m) characterized by this type of vegetation. Several sites had a stretch of bare sediment with or without macroalgae (*Chara* sp. or filamentous) before transitioning to submerged aquatic vegetation, such as coontail (*Ceratophyllum demersum*), water celery (*Vallisneria americana*), pondweed (*Potamogeton* spp.), and Eurasian watermilfoil (*Myriophyllum spicatum*), at approximately 1 m depth (Tables 5-8).

Table 5. Dominant taxa based on relative abundance along each of the macrophyte transects in 2009. Loc. = distance from shore in meters.

Loc.	NW Reference	NE Reference	South Branch	Heritage	Kirksey	Grand Trunk
0	• *Typha angustifolia* • *Phragmites australis* • *Schoenoplectus pungens* • *Utricularia vulgaris*	• *Salix* sp. • *Scirpus americanus*	• *Salix* sp.	• *Salix* sp. • *Vallisneria americana* • *Ceratophyllum demersum* • *Elodea canadensis*	• *Vallisneria americana* • *Potamogeton pectinatus* • *Potamogeton perfoliatus* • Filamentous green algae	• *Typha angustifolia* • *Lythrum salicaria* • *Nasturtium microphyllum*
5			BARE			
10		BARE				• *Utricularia vulgaris* • *Ceratophyllum demersum* • *Myriophyllum spicatum*
20						
30				• *Ceratophyllum demersum*		• *Ceratophyllum demersum*
40		• *Chara* sp. • Filamentous green algae				
50						
60						• *Ceratophyllum demersum* • *Myriophyllum spicatum* • *Nymphaea odorata* • *Potamogeton pusillus* • *Potamogeton crispus* • *Potamogeton perfoliatus* • *Elodea canadensis* • *Vallisneria americana*
70						
80			• *Elodea canadensis* • *Vallisneria americana*			
90		• *Chara* sp. • *Najas flexilis* • *Vallisneria americana*				
100	BARE					
125						
150					BARE	
175					• *Ceratophyllum demersum*	
200						
225						
250						• *Vallisneria americana*
275	• *Vallisneria americana* • Filamentous green algae • *Ceratophyllum demersum*					
300						
350						
400						
450						
500						
550						
600						
650						

Table 6. Dominant taxa based on relative abundance along each of the macrophyte transects in 2010. Loc. = distance from shore in meters.

Loc.	NW Reference	NE Reference	Amoco	Heritage	Kirksey	Grand Trunk
0	• *Typha angustifolia* • *Phragmites australis* • *Schoenoplectus pungens*	• *Typha angustifolia* • *Salix sp.*	• Filamentous green algae	• *Salix exigua* • *Schoenoplectus tabernaemontani*	• *Vallisneria americana* • *Potamogeton pectinatus* • *Potamogeton perfoliatus* • *Potomogeton pusillus* • Filamentous green algae	• *Typha x glauca* • *Lythrum salicaria* • *Nasturtium microphyllum* • *Sparganium eurycarpum*
5		• *Najas flexilis* • Filamentous green algae		• *Nymphaea odorata*		
10				• *Ceratophyllum demersum* • *Elodea canadensis*		• *Ceratophyllum demersum* • *Myriophyllum spicatum* • *Nymphaea odorata*
20		• *Chara* sp.	• *Vallisneria americana* • Filamentous green algae			
30				BARE		
40				• *Ceratophyllum demersum* • *Elodea canadensis*		
50						
60						
70						
80	BARE					
90						
100						
125		• *Myriophyllum spicatum* • *Heteranthera dubia* • *Vallisneria americana*			BARE	
150					• *Vallisneria americana*	
175					BARE	
200						
225						• *Vallisneria americana*
250	• *Vallisneria americana* • *Ceratophyllum demersum* • *Myriophyllum spicatum* • *Najas flexilis*					
275						
300						
350						
400						
450						BARE
500						
550						
600						
650						
700						
750						
800						

Table 7. Dominant taxa based on relative abundance along each of the macrophyte transects in 2011. Loc. = distance from shore in meters.

Loc.	NW Reference	NE Reference	Amoco	Heritage	Kirksey	Grand Trunk
0	• *Typha angustifolia* • *Phragmites australis* • *Schoenoplectus pungens* • *Utricularia intermedia*	• Filamentous green algae • *Najas flexilis* • *Vallisneria americana* • *Chara* sp.	BARE	• *Salix exigua* • *Impatiens capensis*	• Filamentous green algae	• *Typha angustifolia* • *Lythrum salicaria*
5				• *Nymphaea odorata* • *Ceratophyllum demersum* • *Vallisneria americana*	BARE	
10						
20					• *Vallisneria americana*	• *Ceratophyllum demersum* • *Myriophyllum spicatum* • *Nymphaea odorata* • *Elodea canadensis*
30					BARE	
40					• *Vallisneria americana* • *Potamogeton pectinatus* • *Potamogeton perfoliatus*	
50			• *Vallisneria americana* • *Potamogeton perfoliatus* • *Potamogeton pectinatus*			
60				• *Elodea canadensis* • *Ceratophyllum demersum* • *Vallisneria americana*		
70						
80	• *Najas flexilis* • *Chara* sp. • Filamentous green algae					
90						
100						
125				• *Ceratophyllum demersum*	BARE	
150					• *Vallisneria americana* • *Potamogeton perfoliatus*	
175						
200		• *Myriophyllum spicatum* • *Ceratophyllum demersum* • *Vallisneria americana* • *Najas flexilis* • *Potamogeton pusillus*				
225	• *Vallisneria americana* • *Ceratophyllum demersum* • *Myriophyllum spicatum* • *Najas flexilis* • *Potamogeton pusillus* • *Potamogeton perfoliatus*					• *Vallisneria americana* • *Ceratophyllum demersum* • *Potamogeton perfoliatus*
250						
275						
300						
350						
400						
450						
500						
550						
600						
650						
700						
750						

Table 8. Dominant taxa based on relative abundance along each of the macrophyte transects in 2012. Loc. = distance from shore in meters.

Loc.	NW Reference	NE Reference	Amoco	Heritage	Kirksey	Grand Trunk
0	• *Typha angustifolia* • *Phragmites australis* • *Schoenoplectus pungens*	• *Typha* x *glauca* • *Schoenoplectus pungens* • *Salix exigua*	• Filamentous green algae • *Vallisneria americana* • *Potamogeton pectinatus* • *Potamogeton perfoliatus*	• *Salix exigua* • *Impatiens capensis*	• Filamentous green algae • *Vallisneria americana*	• *Typha angustifolia* • *Typha* x *glauca* • *Lythrum salicaria* • *Impatiens capensis*
5		• Filamentous green algae • *Vallisneria americana* • *Chara* sp.		• Filamentous green algae	• *Vallisneria americana* • *Potamogeton perfoliatus* • *Potamogeton perfoliatus*	
10				• *Ceratophyllum demersum* • *Elodea nutallii*		
20						• *Ceratophyllum demersum* • *Nymphaea odorata* • *Elodea nuttallii* • *Myriophyllum spicatum*
30						
40						
50						
60						
70						
80						
90	• *Najas flexilis* • *Chara* sp. • Filamentous green algae • *Potamogeton pectinatus*	• *Myriophyllum spicatum* • *Vallisneria americana* • *Najas flexilis* • *Heteranthera dubia*				
100						
125				• *Ceratophyllum demersum*	BARE	
150					• *Potamogeton pectinatus*	
175					• *Vallisneria americana*	
200						
225	• *Vallisneria americana* • *Myriophyllum spicatum* • *Najas flexilis* • *Potamogeton perfoliatus* • Filamentous green algae					
250						
275		• *Ceratophyllum demersum*				• *Ceratophyllum demersum* • *Elodea nuttallii* • *Myriophyllum spicatum* • *Vallisneria americana* • *Najas guadalupensis* • *Potamogeton pusillus*
300						
350						
400						
450						
500						
550	• *Ceratophyllym demersum* • *Najas flexilis*					
600						
650						
700						

In terms of weighted mean relative abundance, water celery (*Vallisneria americana*) was the dominant submergent macrophyte at 5 of the 7 locations (Tables 9-12). At Heritage Landing and Grand Trunk, coontail (*Ceratophyllum demersum*) had the greatest weighted mean relative abundance (Tables 9-12). The extensive length of wet meadow area at the Northwest Reference site accounts for the relatively high proportion of narrow-leaf cattail (*Typha angustifolia*) and common reed (*Phragmites australis*) at that site (Tables 9-12).

Average Coefficient of Conservatism (C) values were fairly similar among sites, ranging from 3.2 at Northeast Reference in 2009 to 4.4 at Northwest Reference in 2010 and Kirksey in 2012 (Tables 9-12). Average C-values were also similar among sampling years, but Heritage Landing, Kirksey, and Grand Trunk did have slightly lower values in 2011 than the previous sampling years (Tables 9-12, Figure 4).

In 2009, one species (*Ranunculus flabellaris*) was identified at both Northwest Reference and Kirksey that has a C-value of 10 (Table 9), meaning that it requires high quality conditions for growth. In 2010, 5 species with a C-value of 10 were found: *Cladium mariscoides, Hydrocotyle umbellata, Ranunculus flabellaris, Utricularia intermedia,* and *Utricularia minor.* All of these species were found at the Northwest Reference site, except for *Ranunculus flabellaris*, which was found at Grand Trunk (Table 10). Three species with a C-value of 10 were found in 2011, all at the Northwest Reference site: *Cladium mariscoides, Hydrocotyle umbellata,* and *Utricularia intermedia* (Table 11). In 2012, only two species with C-values of 10, *Cladium mariscoides* and *Hydrocotyle umbellata,* were found at the Northwest Reference site (Table 12); the shallow-water habitat where *Utricularia intermedia* is usually found was dry in 2012 due to low water levels. Where species with a C-value of 10 were found, they comprised 3% or less of the macrophyte community, in terms of weighted mean relative abundance (Tables 9-12).

Non-native species were assigned a C-value of 0 (Bourdaghs et al. 2006) and included purple loosestrife (*Lythrum salicaria*), Eurasian watermilfoil (*Myriophyllum spicatum*), water cress (*Nasturtium microphyllum*), common reed (*Phragmites australis*), curly-leaf pondweed (*Potamogeton crispus*), narrow-leaf cattail (*Typha angustifolia*), and hybrid cattail (*Typha* x *glauca*) (Tables 9-12). *Myriophyllum spicatum* was the only non-native species that was found at all sites; most other non-natives were found only at one or both of the reference sites and/or Grand Trunk (Tables 9-12). Curly-leaf pondweed (*Potamogeton crispus*) was also found at Kirksey and Amoco in 2011 and at Heritage in 2012 (Tables 11 and 12). In 2012, *Phragmites australis* was found at Heritage (Table 12). With the exception of *Typha angustifolia* and *Phragmites australis* at the Northwest Reference site, all non-native species comprised less than 10% of the macrophyte community, in terms of weighted mean relative abundance (Tables 9-12).

In contrast to average C-values, taxa richness varied greatly among the sites (Tables 9-12, Figure 4). Taxa richness ranged from 4 at Amoco in 2011 to 55 at Northwest Reference in 2012 (Tables 11-12, Figure 4). Most of the variability in richness among sites was due to differences in emergent taxa; submergent taxa richness was fairly consistent among sites (Tables 9-12, Figure 4). Taxa richness was less variable among sampling years; however, richness was lower at Heritage Landing, Amoco, and Grand Trunk in 2011 than in previous sampling years and increased again in 2012 (Tables 9-12, Figure 4).

Table 9. Coefficient of Conservatism (C) and weighted mean relative abundance (%) for taxa found along each macrophyte transect in 2009. E = emergent, S = submergent, F = floating. – indicates that no C-value was available for that taxon.

Species	**Type**	**C**	**NW Ref**	**NE Ref**	**S. Branch**	**Heritage**	**Kirksey**	**Grand Trunk**
Carex hystericinia	E	2	1					
Ceratophyllum demersum	S	1	13	4		63	3	23
Chara sp.	S	—		18		<1		
Cicuta bulbifera	E	5	<1					
Elodea canadensis	S	1	<1	<1	10	23	<1	6
Filamentous green algae	—	—	7	11	3		18	<1
Heteranthera dubia	S	6	<1	2	10	1		1
Impatiens capensis	E	2	<1					
Juncus articulatus	E	3	<1					
Juncus canadensis	E	6	<1					
Juncus sp.	E	—	<1					
Lemna minor	F	5	<1					<1
Lemna trisulca	F	6						<1
Lythrum salicaria	E	0	<1	1				4
Myriophyllum spicatum	S	0	2	2	<1	5	1	10
Najas flexilis	S	5	6	23		<1		
Najas guadalupensis	S	7						1
Nasturtium microphyllum	E	0						2
Nymphaea odorata	F	6	<1			1		10
Peltandra virginica	E	6						<1
Phragmites australis	E	0	10					
Potamogeton crispus	S	0						3
Potamogeton illinoensis	S	5					4	
Potamogeton nodosus	S	6						<1
Potamogeton pectinatus	S	3	<1	<1		<1	19	3
Potamogeton perfoliatus	S	6		<1		<1	16	5
Potamogeton pusillus	S	4	3	1		<1	1	4
Potamogeton zosteriformis	S	5				1	<1	<1
Ranunculus flabellaris	S	10	<1				<1	
Sagittaria sp.	E	—						<1
Sagittaria latifolia	E	1	<1					
Salix sp.	E	—			8			<1
Salix exigua	E	1		4		2		
Schoenoplectus acutus	E	5	4					
Schoenoplectus pungens	E	5	6	8				
Schoenoplectus tabernaemontani	E	4	<1			1		
Spirodela polyrhiza	F	6						<1
Typha angustifolia	E	0	27	1				8
Utricularia vulgaris	S	6	8					5
Vallisneria americana	S	7	12	24	70	3	39	14
Mean C			3.6	3.0	3.5	3.8	4.2	3.9
Submergent Richness			10	10	4	11	10	13
Total Richness			25	14	5	14	10	24

Table 10. Coefficient of Conservatism (C) and weighted mean relative abundance (%) for taxa found along each macrophyte transect in 2010. See Table 7 for table explanation.

Species	**Type**	**C**	**NW Ref**	**NE Ref**	**Amoco**	**Heritage**	**Kirksey**	**Grand Trunk**
Carex comosa	E	5	<1					
Ceratophyllum demersum	S	1	2	8	<1	38		33
Chara sp.	S	–	2	23				
Cicuta bulbifera	E	5	<1					<1
Cladium mariscoides	E	10	<1					
Cuscuta gronovii	E	3	<1					
Elodea canadensis	S	1	<1			31		3
Elodea nuttallii	S	5	<1	6	<1			2
Eupatorium perfoliatum	E	4	<1					
Filamentous green algae	–	–	3	3	31		8	5
Galium tinctorium	E	5	<1					
Heteranthera dubia	S	6	1	10		6		2
Hydrocotyle umbellata	E	10	<1					
Impatiens capensis	E	2	<1			<1		<1
Juncus articulatus	E	3	<1					
Juncus canadensis	E	6	2					
Juncus debilis	E	–						<1
Lemna minor	F	5	<1					<1
Lemna trisulca	F	6	<1					<1
Lythrum salicaria	E	0	<1	1				2
Myriophyllum spicatum	S	0	7	9	2	9	1	10
Najas flexilis	S	5	7	6	<1	<1	1	
Najas guadalupensis	S	7						2
Nasturtium microphyllum	E	0	<1					2
Nymphaea odorata	F	6				7		9
Phragmites australis	E	0	10					
Polyganum punctatum var. *confertiflorum*	E	5						<1
Potamogeton crispus	S	0		<1				<1
Potamogeton pectinatus	S	3	<1		4		8	2
Potamogeton perfoliatus	S	6	2	<1	4	<1	8	2
Potamogeton pusillus	S	4	2	<1	2	<1	11	1
Potamogeton zosteriformis	S	5					<1	<1
Ranunculus flabellaris	S	10						<1
Salix sp.	E	–						<1
Salix exigua	E	1		2		1		
Salix petiolaris	E	1	<1					
Schoenoplectus pungens	E	5	6	1				
Schoenoplectus tabernaemontani	E	4	<1			1		<1
Sparganium eurycarpum	E	5						1
Typha angustifolia	E	0	19	2				
Tyhpa x *glauca*	E	0						3
Utricularia sp.	S	–						
Utricularia geminiscarpa	S	8	2					
Utricularia intermedia	S	10	2					
Utricularia minor	S	10	2					
Utricularia vulgaris	S	6						2
Unknown sedge	E	–				<1		
Vallisneria americana	S	7	28	30	56	7	64	16
Various grasses	E	–	2					
Mean C			4.5	3.1	4.4	3.6	4.3	4.0
Submergent Richness			14	10	8	8	7	13
Total Richness			34	14	8	13	7	27

Table 11. Coefficient of Conservatism (C) and weighted mean relative abundance (%) for taxa found along each macrophyte transect in 2011. See Table 7 for table explanation.

Species	**Type**	**C**	**NW Ref**	**NE Ref**	**Amoco**	**Heritage**	**Kirksey**	**Grand Trunk**
Carex comosa	E	5	<1					
Carex hystericinia	E	2	<1					
Ceratophyllum demersum	S	1	3	7		57	2	47
Chara sp.	S	–	2	15				
Cicuta bulbifera	E	5	<1					
Cirsium muticum	E	6	<1					
Cladium mariscoides	E	10	<1					
Cuscuta gronovii	E	3	<1					
Eleocharis sp.	E	–	<1					
Elodea canadensis	S	1	<1	<1		11		4
Elodea nuttallii	S	5	<1					1
Filamentous green algae	–	–	6	11	2	<1	7	3
Galium tinctorium	E	5	<1					
Heteranthera dubia	S	6	2	2		<1		2
Hydrocotyle umbellata	E	10	<1					
Impatiens capensis	E	2	<1			1		<1
Juncus sp. 1	E	–	<1					
Juncus sp. 2	E	–	<1					
Juncus sp. 3	E	–	<1					
Juncus sp. 4	E	–	<1					
Juncus articulatus	E	3	1					
Juncus effusus	E	3	<1					
Lemna minor	F	5	1					1
Lemna trisulca	F	6						<1
Lythrum salicaria	E	0	1					3
Myriophyllum spicatum	S	0	6	6		2	1	2
Myosotis laxa	E	6	<1					
Najas flexilis	S	5	8	14		2	1	
Najas guadalupensis	S	7						1
Nasturtium microphyllum	E	0	<1					<1
Nymphaea odorata	F	6	<1			6		4
Peltandra virginica	E	6	<1					<1
Phragmites australis	E	0	14					
Pilea pumila	E	5	<1					
Polyganum virginianum	E	4	<1					
Potamogeton crispus	S	0			4		2	2
Potamogeton illinoensis	S	5		<1				
Potamogeton pectinatus	S	3	1	1	17		8	1
Potamogeton perfoliatus	S	6	2	1	33	<1	13	2
Potamogeton pusillus	S	4	3	4		5	2	2
Rumex sp.	E	–	<1					
Salix exigua	E	1				1		
Salix petiolaris	E	1	<1					
Sagittaria latifolia	E	1	<1					
Schoenoplectus acutus	E	5	2			<1		
Schoenoplectus pungens	E	5	7					
Schoenoplectus tabernaemontani	E	4	<1					
Scutellaria galericulata	E	5	<1					
Spirodela polyrhiza	F	6						<1
Typha angustifolia	E	0	18					9
Tyhpa x *glauca*	E	0	1					<1
Tyhpha latifolia	E	1	<1					
Utricularia sp.	S	–						1
Utricularia intermedia	S	10	3					
Vallisneria americana	S	7	16	38	44	13	66	13
Various grasses	E	–	<1					
Mean C			3.9	3.8	4.0	3.7	3.3	3.4
Submergent Richness			12	11	4	8	8	12
Total Richness			48	11	4	12	8	22

Table 12. Coefficient of Conservatism (C) and weighted mean relative abundance (%) for taxa found along each macrophyte transect in 2012. See Table 7 for table explanation

Species	Type	C	NW Ref	NE Ref	Amoco	Heritage	Kirksey	Grand Trunk
Carex comosa	E	5	<1					
Ceratophyllum demersum	S	1	10	10		63		36
Chara sp.	S	–	3	12				
Cirsium muticum	E	6	<1					
Cladium mariscoides	E	10	<1					
Cuscuta gronovii	E	3	<1					
Eleocharis sp.	E	–	<1					
Elodea canadensis	S	1	<1			<1		1
Elodea nuttallii	S	5	<1	1		22		9
Epilobium coloratum	E	3						<1
Eupatorium perfoliatum	E	4	<1					
Eutrochium maculatum	E	4	<1					
Filamentous green algae	–	–	4	14	16	3	3	3
Galium tinctorium	E	5	<1					
Heteranthera dubia	S	6	1	10		1	<1	2
Hydrocotyle umbellata	E	10	<1					
Impatiens capensis	E	2	<1			1		4
Juncus sp. 1	E	–	<1					
Juncus sp. 2	E	–	<1					
Juncus sp. 3	E	–	<1					
Juncus sp. 4	E	–	<1					
Juncus sp. 5	E	–	<1					
Juncus acuminatus	E	8	<1					
Juncus articulatus	E	3	<1					
Juncus brachycephalus	E	7	<1					
Juncus effusus	E	3	<1					
Leersia oryzoides	E	3	<1					
Lemna minor	F	5	<1					<1
Lemna trisulca	F	6						<1
Lycopus sp.	E	–	<1					
Lythrum salicaria	E	0	<1					4
Moss	E	–	<1					
Myriophyllum spicatum	S	0	6	9	2	4	<1	8
Myosotis laxa	E	6	<1					
Najas flexilis	S	5		12			2	
Najas guadalupensis	S	7	13					2
Nasturtium microphyllum	E	0	<1					<1
Nuphar variegata	F	7						<1
Nymphaea odorata	F	6				1		11
Peltandra virginica	E	6	<1					<1
Phragmites australis	E	0	14	<1		<1		
Pilea pumila	E	5	<1					
Polyganum punctatum	E	5	<1					<1
Pontederia cordata	E	8	<1					<1
Potamogeton crispus	S	0				<1		<1
Potamogeton illinoensis	S	5	<1					
Potamogeton pectinatus	S	3	1	1	20	<1	34	2
Potamogeton perfoliatus	S	6	2	1	7	1	20	<1
Potamogeton pusillus	S	4	<1	1	2	<1	<1	1
Potamogeton zosteriformis	S	5				<1		1
Rumex sp.	E	–	<1					
Salix exigua	E	1		1		1		
Sagittaria latifolia	E	1	<1					
Schoenoplectus acutus	E	5	<1					
Schoenoplectus pungens	E	5	3	1				
Schoenoplectus tabernaemontani	E	4	<1					
Scutellaria lateriflora	E	5	<1					
Sparganium eurycarpium	E	5						<1
Spirodela polyrhiza	F	6						<1
Typha angustifolia	E	0	25					4
Tyhpa x glauca	E	0	<1	1				3
Unknown emergent 1	E	–	<1					
Unknown emergent 2	E	–	<1					
Utricularia vulgaris	S	6						1
Vallisneria americana	S	7	13	30	53	2	40	4
Various grasses	E	–	<1					
Verbena hastata	E	4	<1					
Mean C			4.2	3.3	4.0	3.1	4.4	3.9
Submergent Richness			12	10	5	11	7	13
Total Richness			55	14	5	15	7	28

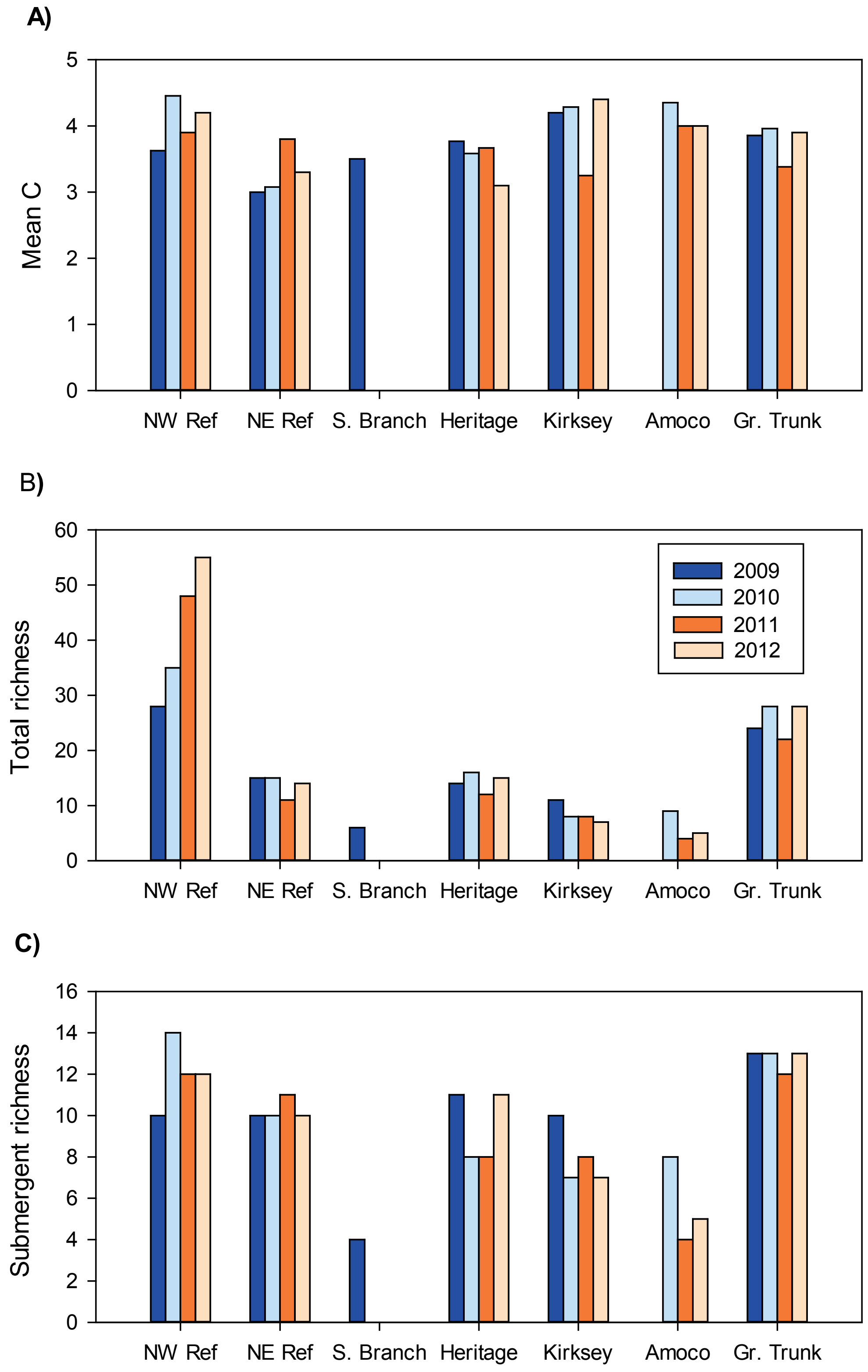

Figure 4. Mean coefficient of conservatism [C] values (A), total richness (B), and submergent richness (C) at each of the transects before (2009-2010) and after (2011-2012) restoration.

Substrate Characterization

Sediment organic matter was much greater at Grand Trunk than at the other sites, averaging 16% to 25% (Figure 5). All other sites had mean sediment organic matter values between 0.3% and 2%, except for Heritage Landing, which had 5% to 8% sediment organic matter (Figure 5). No temporal trends were evident in the data.

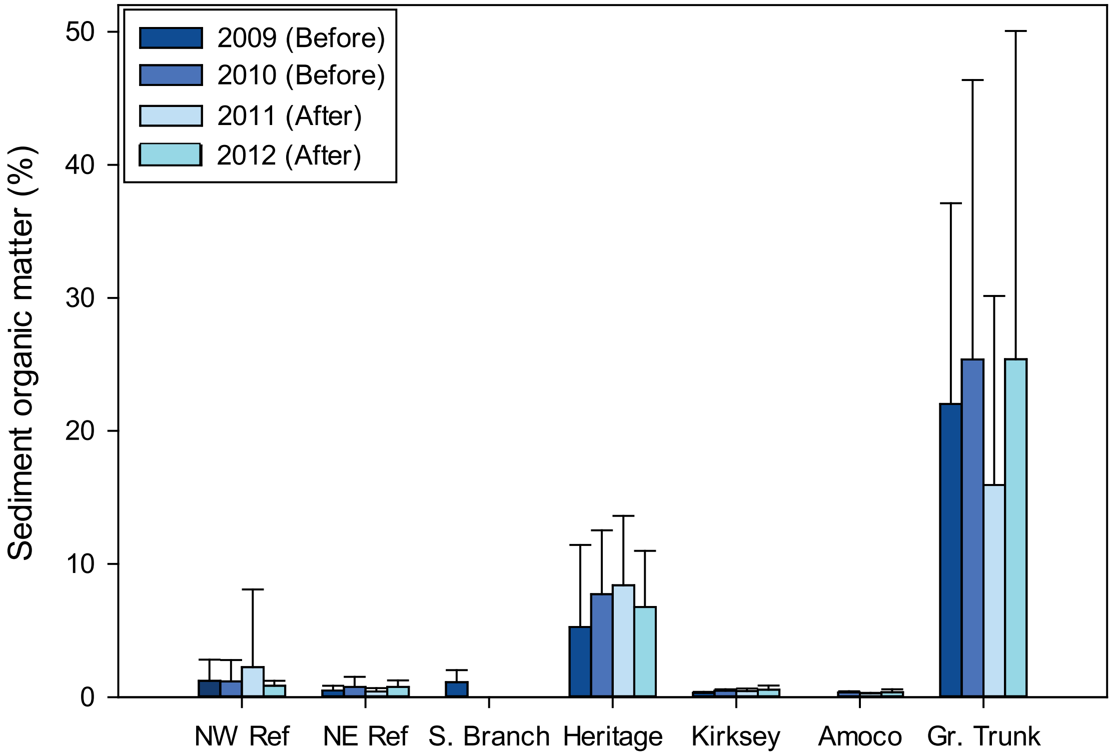

Figure 5. Average (± SD) sediment organic matter (%) at each macrophyte transect before (2009 and 2010) and after (2011 and 2012) restoration.

Discussion

The ecological significance of aquatic macrophytes is considerable. The structural complexity of macrophytes provides essential habitat for invertebrates, fish, and breeding marsh birds (Jude and Pappas 1992, Thomaz et al. 2008, Cvetkovic et al. 2010, Grabas et al. 2012, Jurca et al. 2012), in addition to the other ecosystem services, such as sediment stabilization and nutrient cycling (Barko et al. 1991, Madsen et al. 2001). Although fish distribution in Great Lakes coastal wetlands is significantly affected by both macrophytes and water quality, macrophytes have been shown to be the better predictor of fish community (Cvetkovic et al. 2010). Fish depend on macrophytes for refugia from predators, protection from wind and wave disturbances, shelter from sunlight, and cooler water temperatures (Jude and Pappas 1992, Lougheed et al. 2001, Cvetkovic et al. 2010). The high primary productivity of macrophyte beds also supports a rich zooplankton and invertebrate food source (Jude and Pappas 1992). The macrophyte communities of Great Lakes coastal wetlands, such as those found in Muskegon Lake, are particularly attractive to fishes due to their connection with both a major river and a Great Lake (Jude and Pappas 1992, Larson et al. submitted).

In terms of biomass, the macrophyte community of Muskegon Lake is within the mean range of 55-170 g/m^2 reported for temperate lakes (Squires and Lesack 2003), but biomass was quite variable throughout the lake. Differences in littoral zone morphology (i.e., slope; Duarte and Kalff 1986, Barko et al. 1991, Partanen et al. 2002) and exposure (i.e., protection from waves and wind; Keddy 1983, Cvetkovic at al. 2010, Cooper et al. In Press) among the sites likely played a role in the spatial variability observed in biomass. The very shallow depth and gradual gradient in the first 70-90 m of the Northwest Reference site supported a productive wet meadow, where the majority of the biomass was located. In contrast, the majority of biomass at Grand Trunk and Heritage Landing was in the form of submergent and floating macrophytes. These sites are located in protected embayments that are subjected to very little physical disturbance compared to the other sites. Kirksey and Amoco are both located off of points and subjected to wind and wave action, which likely contributes to the low biomass at those sites.

In addition to littoral zone morphology and exposure, macrophyte biomass also appears to be linked to sediment organic matter in Muskegon Lake. Several studies have documented a positive relationship between sediment organic matter and macrophyte biomass (Sand-Jensen and Søndergaard 1979, Duarte and Kalff 1986, Squires and Lesack 2003). With the exception of Northwest Reference, the sites with the greatest biomass also had the greatest sediment organic matter. The large amount of submergent vegetation at Grand Trunk and Heritage Landing contributes directly to the greater organic matter content of the sediments. Upon seasonal senescence, submergent vegetation decomposes rapidly and enriches the sediments with organic matter and nutrients (Barko et al. 1991). This enrichment, in turn, fuels greater macrophyte biomass during the next growing season (Barko et al. 1991, Squires and Lesack 2003), creating a positive feedback loop. Sediment organic matter at Grand Trunk was similar to the average organic matter content (24%) reported by Barko and Smart (1986) for lakes with a broad range a sediment types and geographic range. Squires and Lesack (2003) encountered many sediments with organic matter content less than 10% and attributed lower organic matter to higher rates of inorganic sedimentation from riverine inputs. The less protected sites in Muskegon Lake may be more influenced by inorganic sediment inputs from Muskegon River, as they all had ≤ 1%

organic matter. Alternatively, less protected sites could experience greater flushing of organic sediments, which may be more flocculent and susceptible to removal.

The maximum taxon richness observed (Northwest Reference: 25; 34, 48, and 55 during 2009, 2010, 2011, and 2012, respectively) was similar to what has been reported for other area lakes (Pigeon Lake [28]: Jude et al. 1981, Little Black Lake [29]: Steinman et al. 2011) that have abundant and diverse macrophyte growth. Similar to biomass, the high taxon richness at Northwest Reference was most likely due to the extensive wet meadow area at the beginning of that transect, where macrophyte diversity was high. Wet meadows are known to be the most species-rich habitat type in Great Lakes coastal wetlands (Keddy and Reznicek 1986, Wilcox et al. 2005). Interestingly, Grand Trunk, which is considered a highly disturbed site, had the second highest taxon richness. A 10-m section of wet meadow at Grand Trunk supported substantial macrophyte diversity. However, the wet meadow area does not entirely explain the high diversity at that site; Grand Trunk had the highest submergent taxa richness among sites in 2009, 2011, and 2012, and the second highest in 2010. Lougheed et al. (2001) reported a range of 0-15 submergent plant taxa in 62 Great Lakes coastal wetlands. Nearly all of the sites in Muskegon Lake exceeded the average of 6 submergent taxa that Lougheed et al. (2001) reported, and both Northwest Reference and Grand Trunk approached the upper end of the range of 15. Although taxa richness was high at Grand Trunk, it had one of the lowest average C-values, which suggests a community more tolerant of degraded conditions.

Average Coefficient of Conservatism values have been shown to be effective indicators of condition in Great Lakes coastal wetlands (Bourdaghs et al. 2006). In a survey of 55 Great Lakes coastal wetlands, Bourdaghs et al. (2006) reported an average C-value of 5.42 based on the State of Michigan’s values. The highest C-value that we observed in Muskegon Lake was 4.4, and several sites had values below 4, suggesting that the species present in Muskegon Lake are more tolerant of degradation than the average condition in Great Lakes coastal wetlands. However, the presence of species with C-values of 8 and above at the Northwest Reference site is encouraging in that it indicates Muskegon Lake has the ability to support species of high quality; if the appropriate environmental conditions are provided in the restored areas, there is a readily available species pool present to colonize these regions. All of the high C-value species were in the wet meadow area, further highlighting the importance of restoring these areas along the south shoreline.

Given the heavy recreational use and shoreline development of Muskegon Lake, the presence of non-native and tolerant species is not surprising. Most Great Lakes coastal wetlands contain 2-7 exotic species in wet meadow zones and up to 3 non-native submergents (Albert and Minc 2004). Muskegon Lake fell well within this range, with 5 non-natives associated with wet meadow areas and 2 non-native submergent species. The distribution of the hybrid cattail (*Typhya* x *glauca*) and common reed (*Phragmites australis*) should be closely monitored, as both species are known to expand into structurally uniform and monotypic stands to the detriment of wet meadow habitat (Frieswyk and Zedler 2007, Tulbure et al. 2007).

Filamentous green algae were relatively abundant at all sites throughout the study. A consortium of different taxa was found entangled among the vascular macrophytes. The genus *Cladophora* has experienced a resurgence in coastal Great Lakes habitats (Auer et al. 2010) and is of ecological and environmental concern because of its association with beach fouling, avian botulism, and human pathogens (Higgins et al. 2008). Muskegon Lake also harbors *Enteromorpha flexuosa*, a filamentous green alga of marine origin, which can reach bloom conditions (Lougheed and Stevenson 2004). We did not identify the filamentous green algae by species, although the growth dynamics of these autotrophs clearly bear watching.

Our macrophyte assessment data serve both as an indication of short-term restoration effects on the macrophyte community and as a valuable baseline for future investigations of restoration success. Two years of pre-restoration baseline data (2009 and 2010) give an indication of the natural year-to-year variability in the macrophyte community of Muskegon Lake. Biomass, taxa richness, and mean C-values tended to be greater in 2010 than in 2009, thus providing a range of baseline conditions rather than a single baseline value. Sediment organic matter, on the other hand, was very similar between the two years.

In 2011, changes were observed in the macrophyte communities that suggest possible short-term impacts from restoration work. At Heritage Landing and Amoco, restoration activities in early 2011 included underwater fill removal within the immediate location of our transects. The decrease in macrophyte biomass and species richness at Heritage Landing is likely a result of mechanical disturbance caused by fill removal. Amoco did not appear to be affected as significantly, most likely due to the very low biomass and cover at that site prior to restoration. Although declines in macrophyte community metrics were observed also at Kirksey and Grand Trunk, it is more difficult to relate them directly to restoration activities. At Kirksey, no underwater restoration occurred and at Grand Trunk, underwater fill removal was adjacent to, but not directly within, our transect. Therefore, direct negative impacts from disturbance would not be expected at these sites.

Our results suggest that the macrophyte community had recovered to at least pre-restoration biomass levels and species richness in 2012. Heritage Landing had the most dramatic increase (12 ×) in macrophyte biomass between 2011 and 2012, suggesting that the potential negative impacts of underwater fill removal observed in 2011 were short-lived. The Amoco site had greater biomass in 2012 than in any other year sampled, also pointing to a restoration benefit. However, C-values at Heritage were the lowest of any year sampled in 2012 due to the presence of two non-native species not previously found at that site (*Phragmites australis* and *Potamogeon crispus*). Although these species accounted for less than 1% of the macrophyte community, their abundances should be monitored in the future.

The increases in macrophyte metrics observed at nearly all sites in 2012, regardless of whether underwater restoration occurred, could mean that 2012 was simply a "good year" for macrophytes in Muskegon Lake. Water levels in Lake Michigan were 60 cm below the long-term average in August 2012 (USACE 2012) and water depths at our sampling locations were 20-50 cm lower in 2012 than in any other sampling year. The greater light availability afforded by lower water levels is favorable for macrophyte growth, and the newly exposed sediment allows the germination of new taxa. Indeed, Bucak et al. (2012) found that a 30 cm decline in water level resulted in greater macrophyte density in a mesocosm experiment. A long-term study of shallow, eutrophic lakes in Sweden concluded that water level was among the most important factors causing fluctuations in coverage of submersed macrophytes (Blindow 1992).

The differences observed between the two reference sites reflect the different morphometric conditions at these sites, and demonstrate the degree of spatial variability exhibited by macrophyte growth in Muskegon Lake, even along the more natural north shore. Compared to Northwest Reference, the Northeast Reference site had a steeper gradient and a shorter littoral zone. Biomass, taxa richness, and mean C-values were substantially lower at Northeast Reference than at Northwest Reference in 2009, 2010, and 2012. In 2011, macrophyte community metrics were more similar between the reference sites than in previous years. Species composition was also very different between the two reference sites. Northwest Reference had an extensive stand of *Typha* and *Phragmites* before transitioning to submerged vegetation, dominated by *Vallisneria americana* and *Ceratophyllum demersum*. In contrast, Northeast Reference had only a narrow band of *Schoenoplectus pungens*, *Salix*, and *Typha* before transitioning to a submerged community dominated by the macroalga *Chara* and *Vallisneria americana*. Future macrophyte assessments that aim to evaluate restoration effects should use the reference sites as a "barometer" for change in the lake, rather than as explicit targets for success. In other words, if changes occur at the restoration sites, but not at the reference sites, they can be attributed to restoration efforts rather than environmental changes.

As most climate change models predict an increase in extreme events and conditions (Changnon 2007), it is likely that we will see continued fluctuations in Muskegon Lake water levels, and therefore our restoration efforts should take into account both adaptation and resilience (cf. Folke et al. 2010). Minimizing hardened features along shorelines, thereby allowing coastal wetland vegetation to migrate both landward and lakeward, depending on lake levels, will maximize structural and functional diversity in these systems. In addition, changing water levels may have significant implications for sediment nutrient release, also influencing system responses (cf. Steinman et al. 2012). Future monitoring of the macrophyte community in Muskegon Lake will be instrumental in teasing out environmental effects and changes resulting from restoration.

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APPENDIX

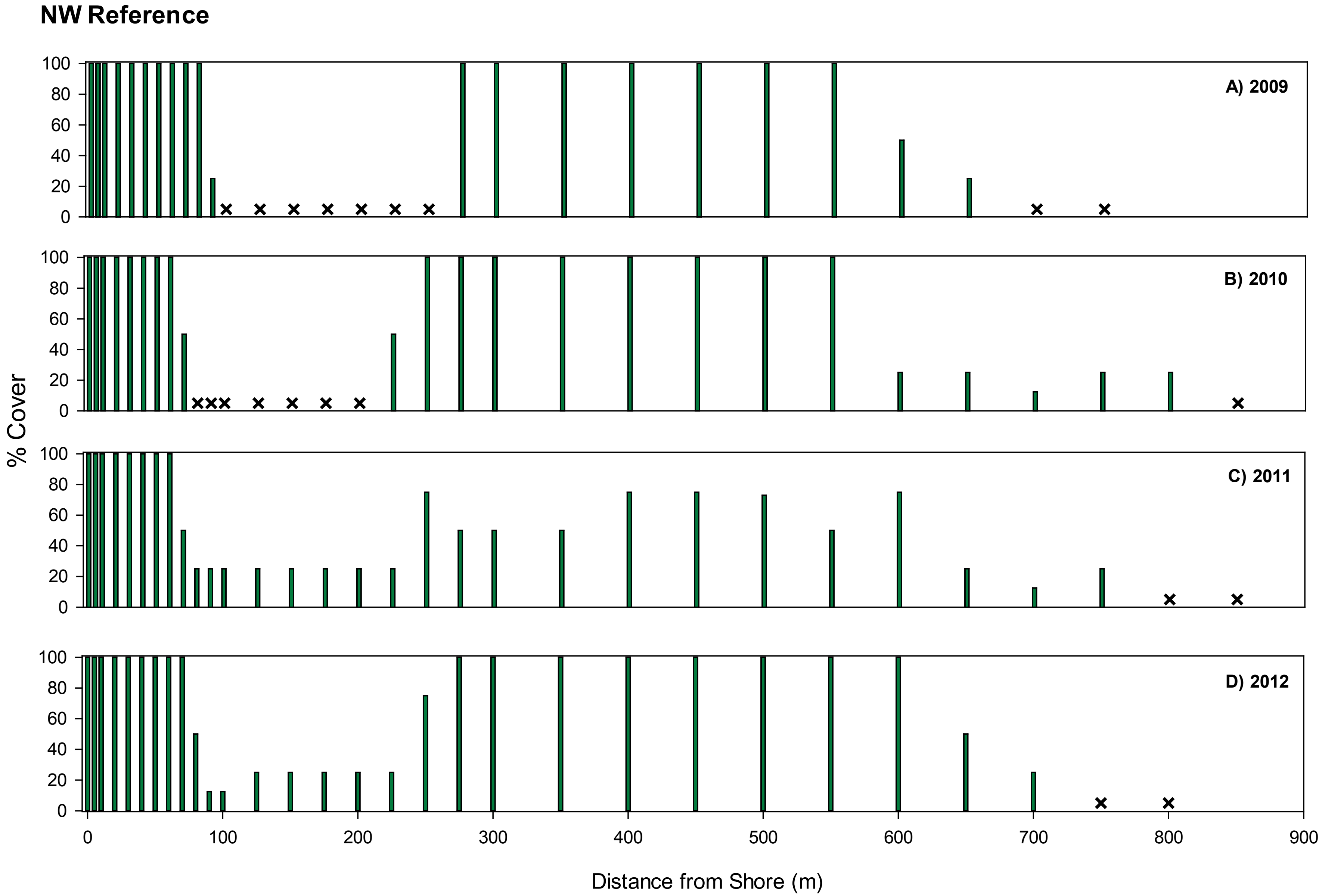

Figure A1. Macrophyte % cover (based on cover ranks) at the Northwest Reference site from 2009-2012. X indicates 0% cover for a given point along the transect.

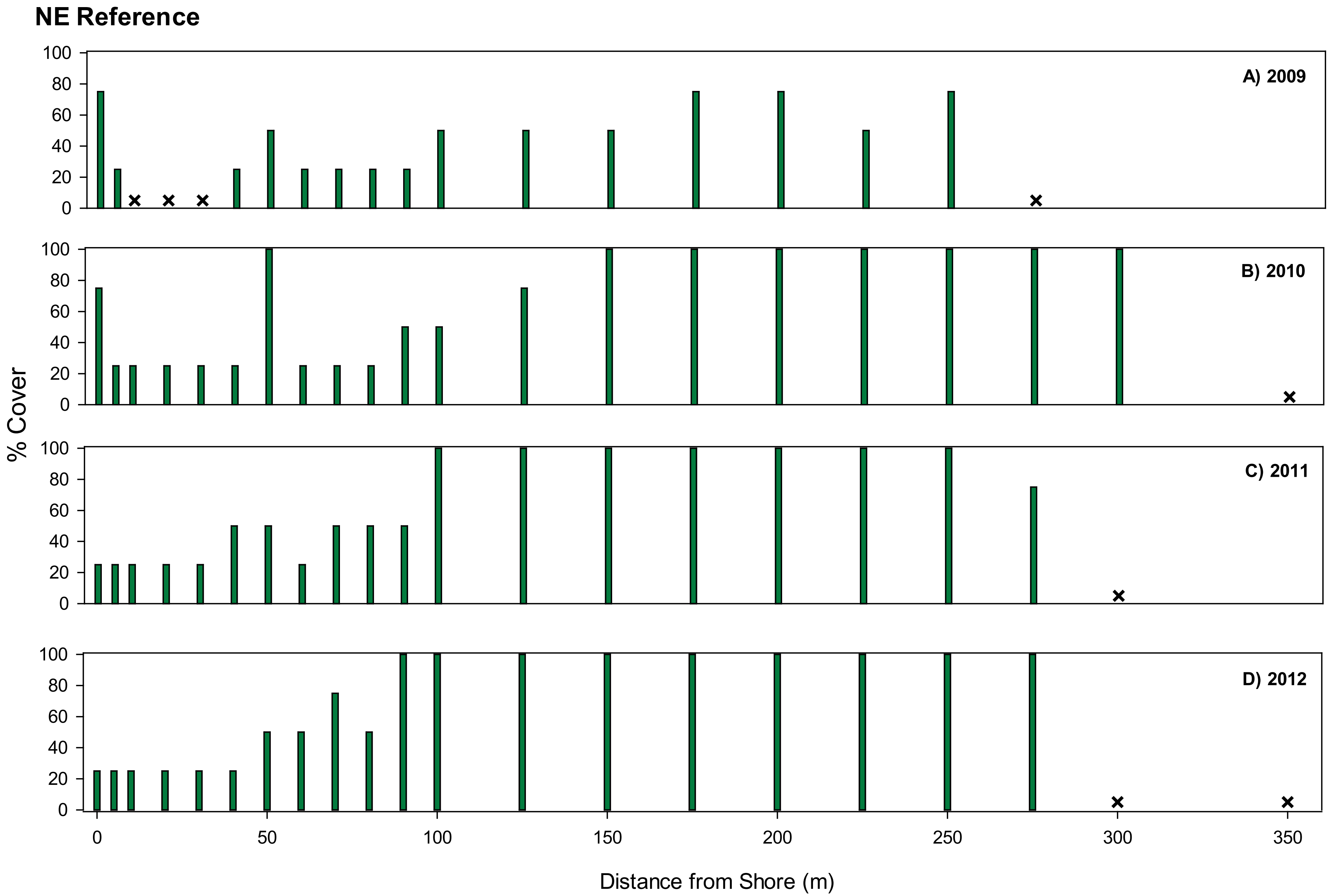

Figure A2. Macrophyte % cover (based on cover ranks) at the Northeast Reference site from 2009-2012. X indicates 0% cover for a given point along the transect.

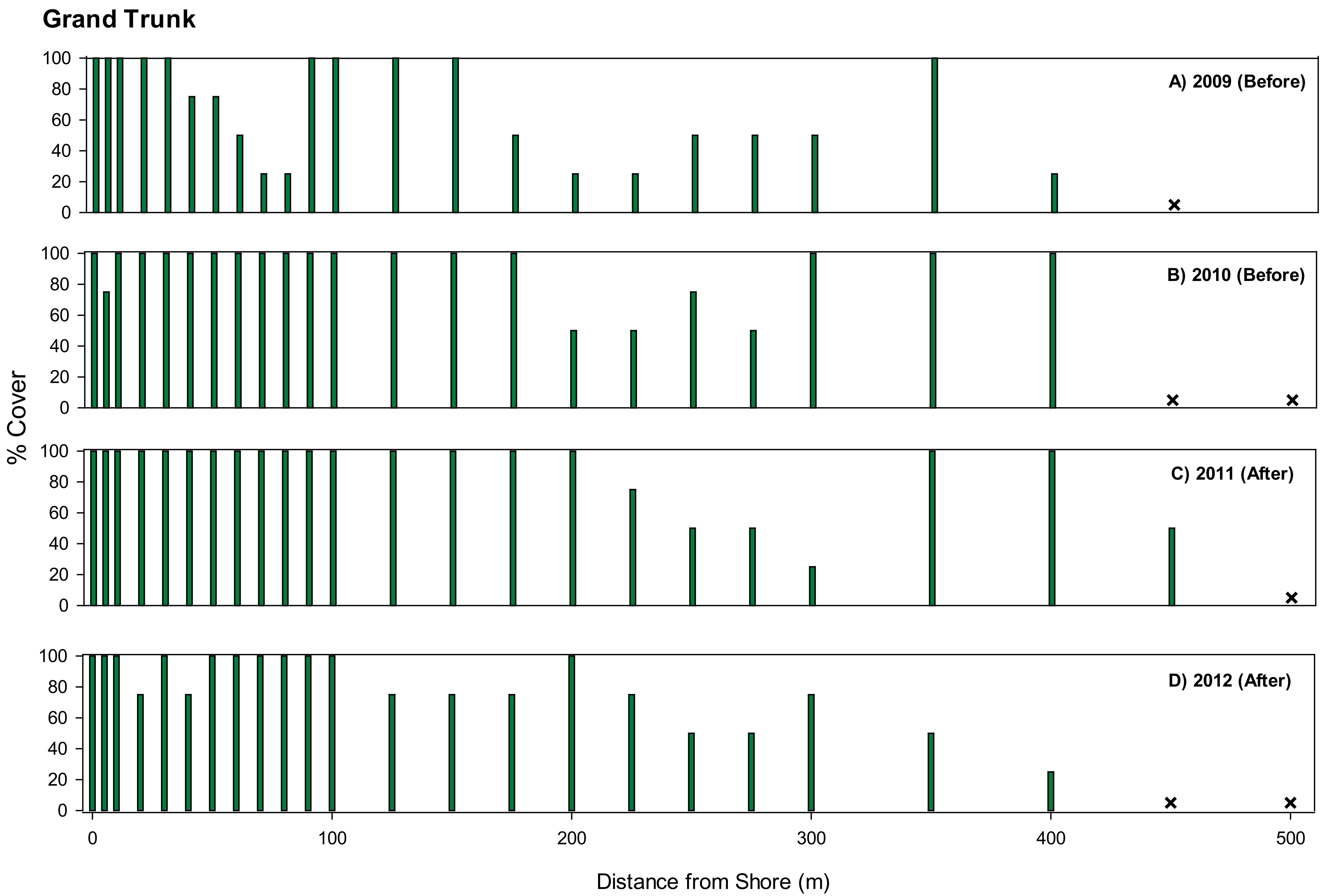

Figure A3. Macrophyte % cover (based on cover ranks) at the Grand Trunk site from 2009-2012. X indicates 0% cover for a given point along the transect.

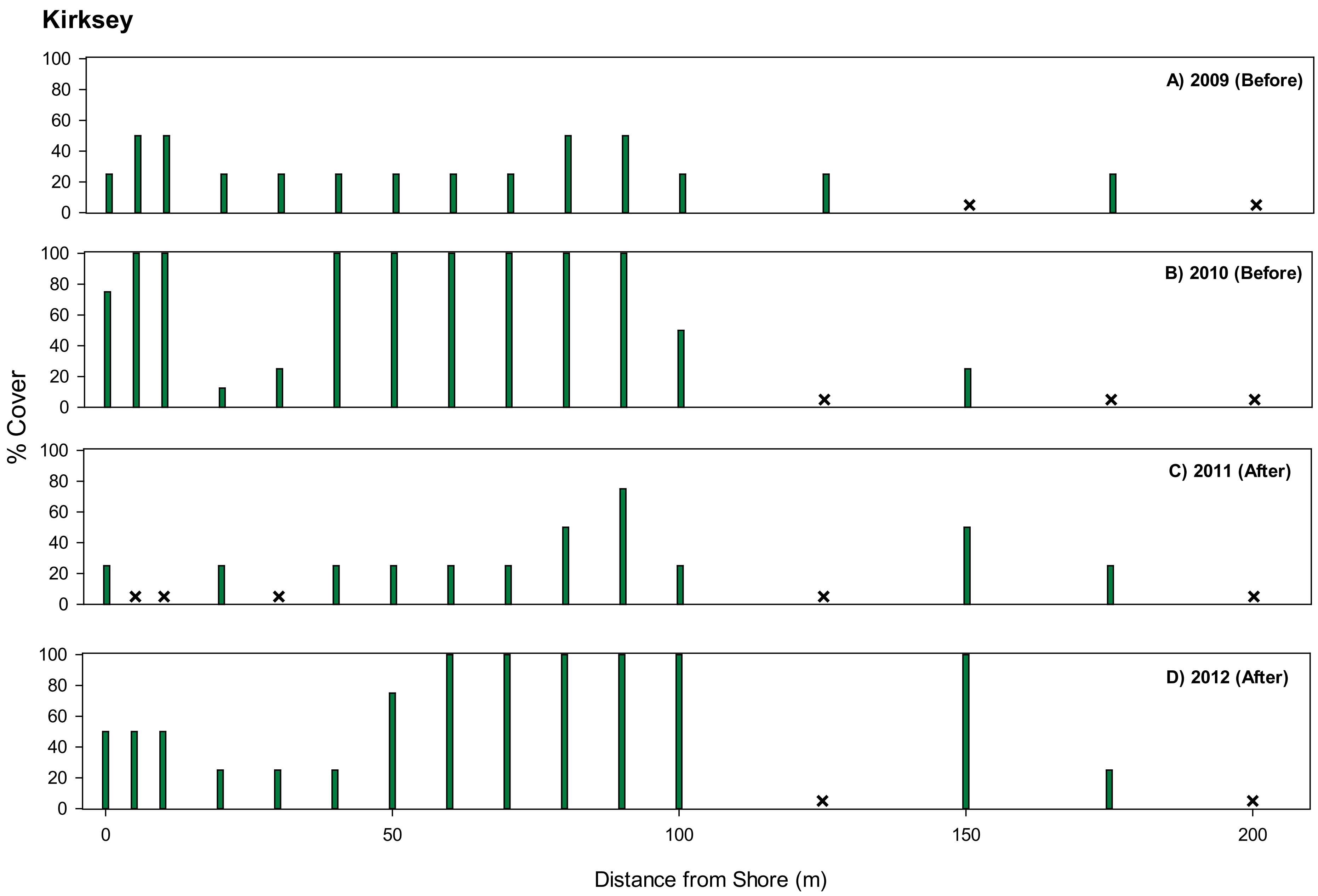

Figure A4. Macrophyte % cover (based on cover ranks) at the Kirksey site from 2009-2012. X indicates 0% cover for a given point along the transect.

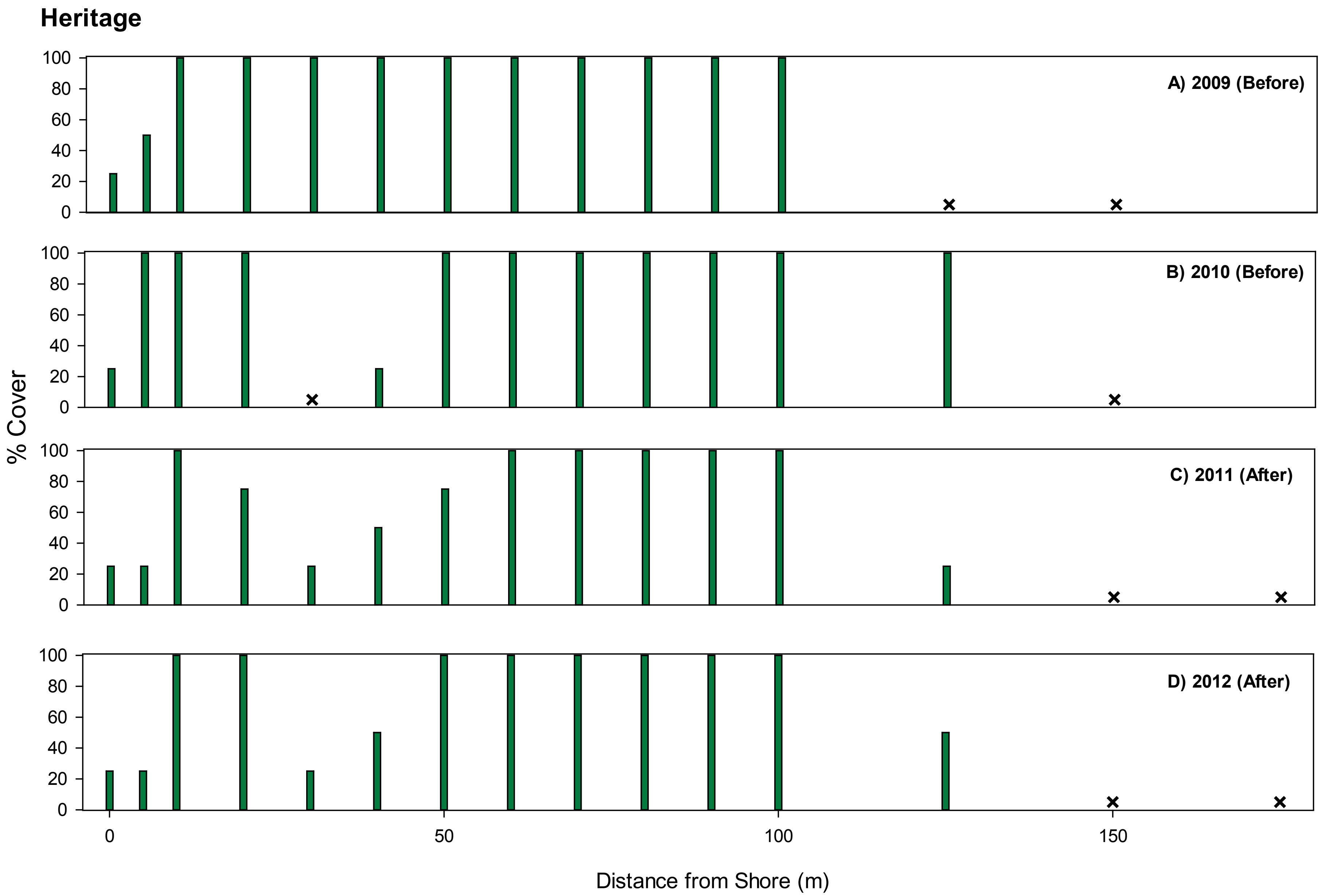

Figure A5. Macrophyte % cover (based on cover ranks) at the Heritage site from 2009-2012. X indicates 0% cover for a given point along the transect.

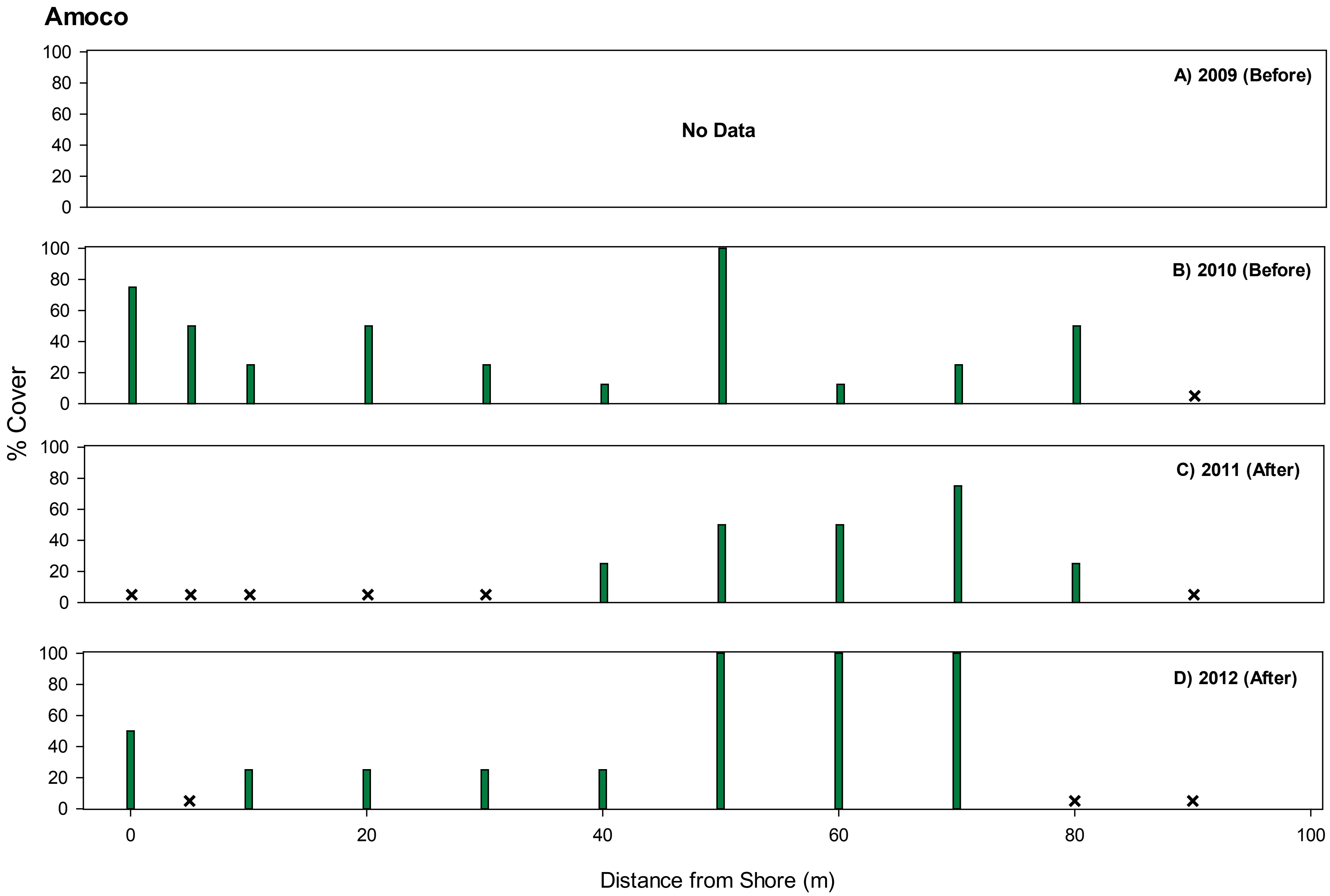

Figure A6. Macrophyte % cover (based on cover ranks) at the Heritage site from 2009-2012. X indicates 0% cover for a given point along the transect.

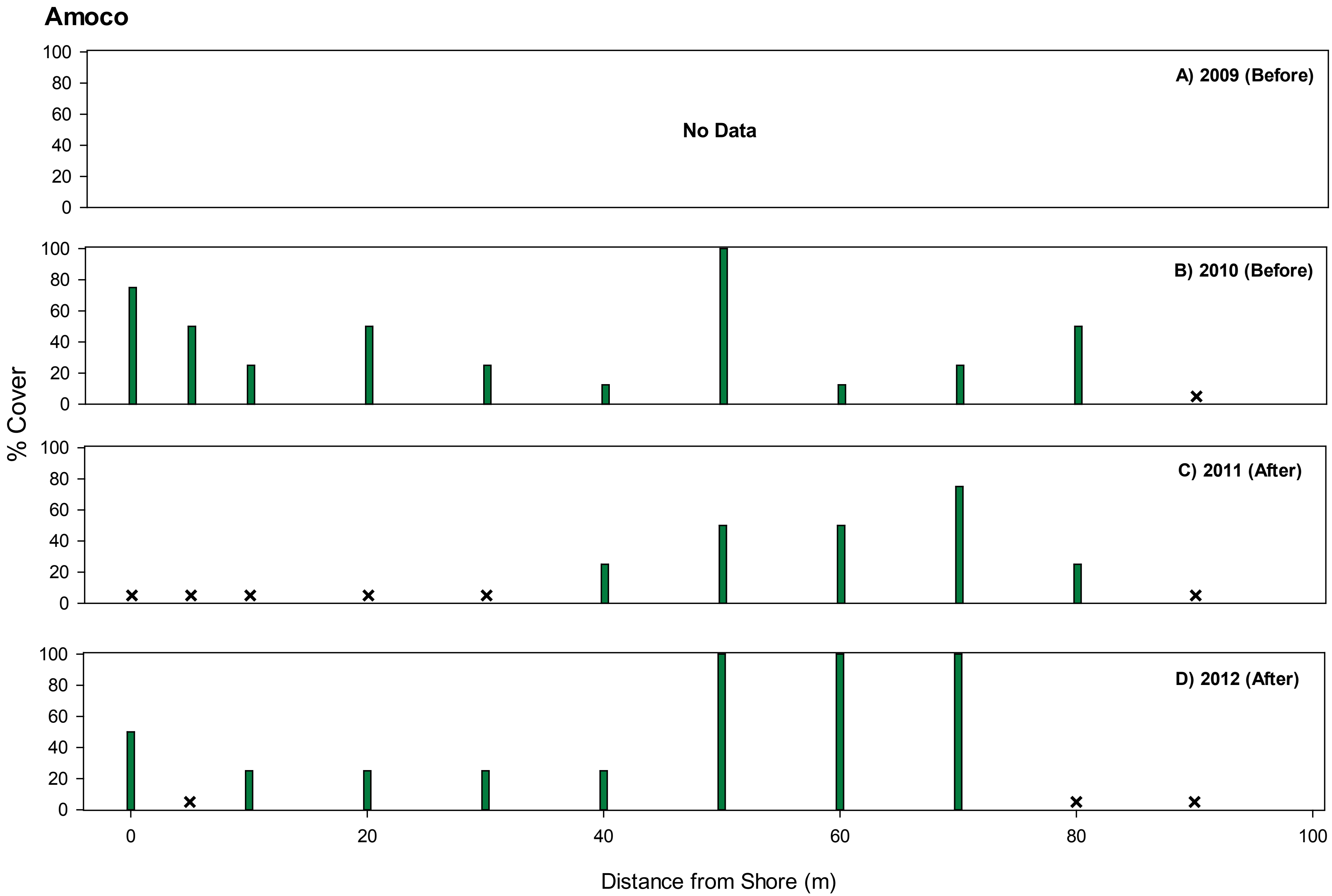

Figure A7. Macrophyte % cover (based on cover ranks) at the Amoco site from 2009-2012. X indicates 0% cover for a given point along the transect.

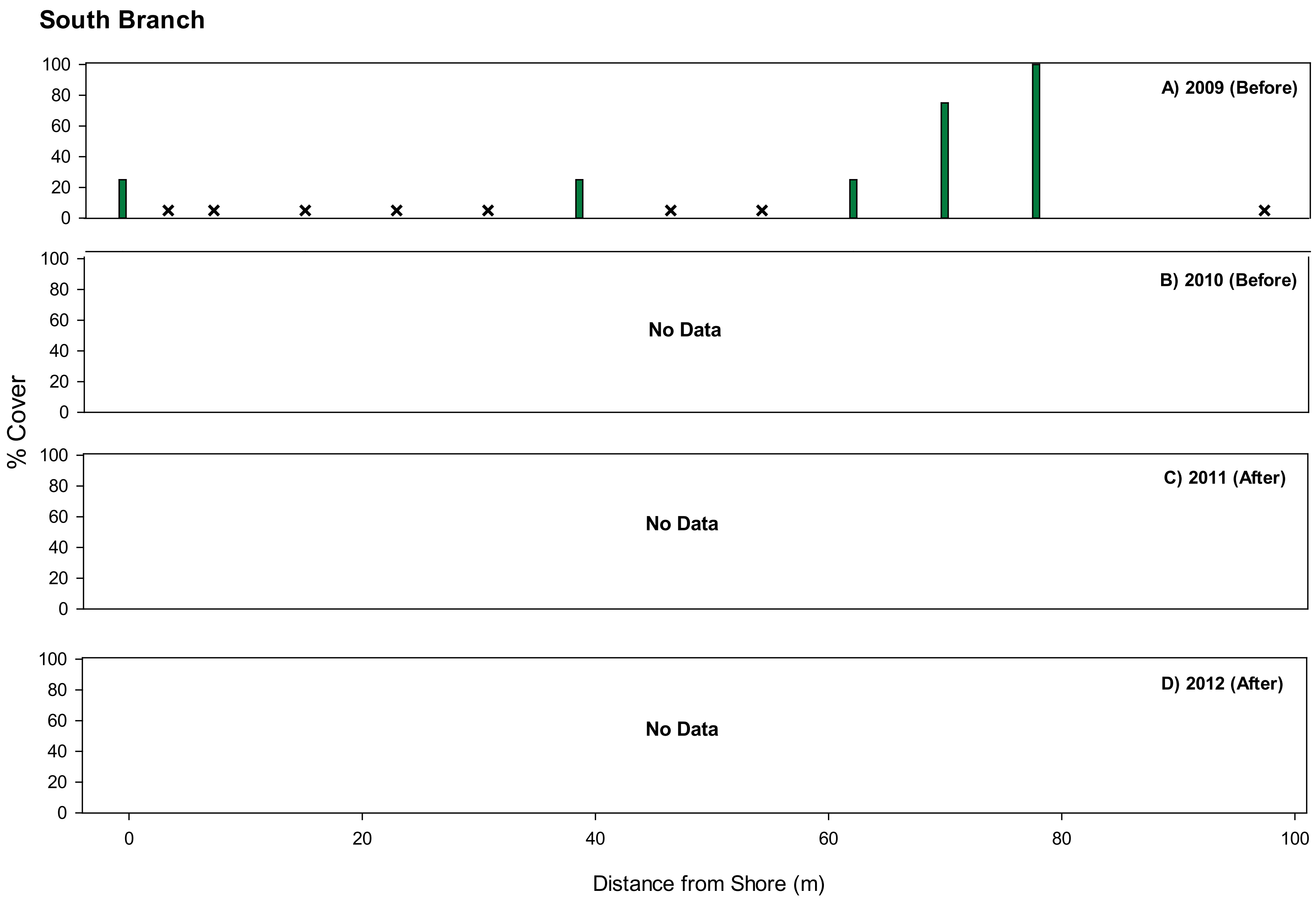

Figure A8. Macrophyte % cover (based on cover ranks) at the Amoco site from 2009-2012. X indicates 0% cover for a given point along the transect.