

**SEASONAL AND LONG-TERM (1995-2009) CHANGES IN THE
DISTRIBUTION AND ABUNDANCE OF SUBMERGED AQUATIC
VEGETATION AND DREISSENID MUSSELS IN INNER LONG POINT
BAY, LAKE ERIE**

(Thesis Format: Monograph)

by

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ABSTRACT

Invasion by mussels can cause rapid increases in the abundance of submerged aquatic vegetation (SAV) by increasing water clarity and altering nutrient cycling, but rapid expansion of the mussel population is often followed by a decline until a new regional carrying capacity is reached. I sampled Long Point Bay (LPB), Lake Erie, in 2009 to quantify changes in SAV communities and densities of zebra mussels (*Dreissena polymorpha*) since the peak of the latter in the early 1990s, and modeled influences of year, water depth, and substrate type on the probability of SAV detection. I detected a 96% decrease in mussel abundance/m² (\pm SE) between 1992 ($\bar{x} = 457 \pm 86$) and 2009 ($\bar{x} = 19 \pm 2$). The five most abundant SAV species in 1992 had decreased by 2009. Water depth and substrate type influenced probability of detection of SAV species, suggesting that changes in Lake Erie water levels and sediment loading influence SAV communities. Carrying capacity of LPB for waterfowl and other fish and wildlife that use and eat SAV and mussels increased during the mid-1990s, but has since decreased.

Keywords: abundance, distribution, Dreissenid mussels, Lake Erie, Long Point, submerged aquatic vegetation, waterfowl

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List of Abbreviations

ANOVA – Analysis of variance

DER- Daily energy requirement

DUD – Duck use days

IDW – Inverse distance weighted spatial interpolation

LGL – Lower Great Lakes

LPB – Inner Long Point Bay, Lake Erie

MANOVA – Multivariate analysis of variance

SCUBA – Self-contained underwater breathing apparatus

SAV – Submerged aquatic vegetation

TME- True metabolizable energy

1 Introduction

1.1 Coastal Wetlands

Coastal wetlands and associated submerged aquatic vegetation (SAV) include seasonal and relatively permanent coastal-plain freshwater swamps and marshes, coastal beaches, rocky shorelines, estuarine salt marshes, mangrove swamps, seagrass beds, mud flats, oyster reefs, and sand bars (Prince *et al.* 1992, Bildstein *et al.* 1991). Coastal wetlands are among the most productive and ecologically valuable natural habitats, because they are made up of interconnected subsystems whose functions cannot be duplicated elsewhere. Coastal habitats are home to a diversity and abundance of plants and animals and also serve the important role of filtering impurities in the water that flows through them (Beatley *et al.* 2002). The productive plant communities within the coastal wetlands of North America meet the life cycle needs of a diversity of birds as they migrate and exploit available resources (Bildstein *et al.* 1991, Newton 2008).

Because of their productivity and value as transportation arteries, coastal wetlands have been attractive sites for human settlement for centuries (Day *et al.* 1989). Approximately half of the world's wetlands have been drained, filled or degraded in the last century, and less than 3% of the Western Hemisphere land surface consists of coastal wetlands (Bildstein *et al.* 1991). Humans impact coastal wetlands directly through (1) physical alteration, (2) the introduction of toxic materials, (3) enrichment with excessive levels of naturally occurring materials (including nutrients) and heat, and (4) the introduction of exotic species that often replace the diverse native plant communities and form monotypic communities and reduce habitat quality for wildlife (Day *et al.* 1989, Petrie and Knapton 1999, Schummer *et al.* 2012).

1.2 Impact of Exotic Species on Coastal Wetlands

Many of the remaining coastal wetlands have been altered by various stressors, including the introduction of exotic plants and invertebrates (Petrie 1998, Knapton and Petrie 1999, Petrie and Knapton 1999). Invasive species can affect carrying capacity for staging waterfowl and other animals by altering total biomass of submerged aquatic vegetation (SAV) or changing species composition within wetlands (Crowder and Bristow 1988). For instance, the introduction and proliferation of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) (hereafter combined as Dreissenid mussels) has been associated with changes in the abundance, distribution, and community composition of SAV (Blindlow 1992; Knapton and Petrie 1999; Petrie and Knapton 1999). Dreissenid mussels reduce the number of suspended particles in the water column through filtering, and thereby increase water clarity and decrease light attenuation (Knapton and Petrie 1999). Decreased light attenuation enhances benthic photosynthesis and influences the distribution and abundance of SAV (Wetzel 1983). In addition, Dreissenid mussels can alter microbially-mediated nutrient cycling and the nearshore phosphorus cycle (Wilson *et al.* 2006), further decreasing phytoplankton levels. Decreased phytoplankton levels through Dreissenid filtering and the resulting increased water clarity can also increase SAV abundance (Schloesser and Manny 2007).

1.3 Relationships between Dreissenid Mussels and SAV

Following introduction to a suitable, new locale, exotic species often occur in greater abundance than observed in their native range, which often is followed by decline until a new regional carrying capacity is reached (McKillup *et al.* 1988). Dreissenid mussels prefer to anchor to hard substrate, but those types of substrates are not found extensively throughout LPB, so mussels primarily anchor to SAV (Knapton and Petrie 1999). Dreissenid mussel abundance can

influence water clarity and rates of eutrophication because they filter substantial amounts of water (Knapton and Petrie 1999). Because angiosperm SAV species that reproduce via flowering vegetative structures can outcompete algal species in eutrophic systems, changes in abundance of Dreissenid mussels may cause measureable changes in SAV plant community composition (Knapton and Petrie 1999). An angiosperm-dominated SAV community in LPB would provide more nutritious food sources for certain species of waterfowl (Knapton and Petrie 1999) and better spawning habitat for some fish species (Richardson *et al.* 1998).

1.4 Coastal Wetlands of the Lower Great Lakes

Coastal wetlands associated with the lower Great Lakes (LGL) are critically important to a diversity of wetland-dependent organisms. SAV in coastal wetlands of the LGL is food for migrating waterfowl (Knapton and Petrie 1999; Badzinski and Petrie 2006) and provides habitat and nursery areas to fish (Richardson *et al.* 1998). In addition, SAV quantity and species distribution are indicators of local water conditions, affect biogeochemical and sedimentological processes, and protect shorelines from erosion by decreasing nearshore wave action (Moore *et al.* 1996). Despite their importance to fish, wildlife and humans, a substantial number of LGL coastal wetlands have been drained for agriculture and other development (e.g., < 5% of western Lake Erie wetlands remain intact), thereby increasing the importance of remaining coastal wetland habitat for wetland-dependent organisms. Inner Long Point Bay – Lake Erie (LPB) is an important remaining habitat that is in a relatively pristine state. LPB is important because it has a fairly uniform depth of 2 m, which supports an extensive SAV community covering >99% of the bay (Knapton and Petrie 1999).

1.5 Importance of Long Point Bay to Fish and Wildlife

Diving ducks (e.g., *Aythya* spp. and *Bucephala* spp.) feed exclusively in aquatic habitats; thus, the shallow, productive waters of LPB provide foraging habitat necessary to complete migration (Petrie 1998). Expansion of introduced Dreissenid mussels to Lake Erie in the early-1990s led to an initial increase in use of LPB by molluscivorous diving ducks (Petrie and Knapton 1999). Lesser scaup (*Aythya affinis*) and greater scaup (*Aythya marila*), bufflehead (*Bucephala albeola*), and common goldeneye (*Bucephala clangula*) altered traditional migration patterns to take advantage of this novel food source in LPB (Hamilton *et al.* 1994, Petrie 1998, Petrie and Knapton 1999). However, since 2000, diving duck use has declined within LPB, particularly among those species that consume Dreissenid mussels (Badzinski 2007). In addition, the abundance of economically important fish species, such as yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), and smallmouth bass (*Micropterus dolomieu*), has also decreased within LPB since the late 1990s (Ontario Ministry of Natural Resources 2007). Causes of declines in fish populations and diving duck use remain unclear, but it is plausible that a decline in abundance or distribution of Dreissenid mussels may be a direct or indirect contributing factor.

1.6 Seasonal Trends in SAV Biomass

Seasonal changes in SAV biomass may influence availability of food and cover for wetland fish and wildlife. In August, SAV typically reaches maximum aboveground biomass and begins shifting resources to propagules (Rybicki and Landwehr 2007). Specifically, most angiosperm species (e.g., wild celery, *Vallisneria americana* and pondweeds, *Potamogeton* spp.) of SAV typically overwinter as belowground roots, tubers, and seeds (Kufel 2001). In addition to autumn senescence of aboveground SAV biomass, waterfowl and fish can also eat a substantial

portion of available biomass (Marklund *et al.* 2002). In December, aboveground biomass nears zero and belowground biomass occurs as roots, tubers, and dormant seeds (Rybicki and Landwehr 2007). During winter, aboveground biomass in LPB is dominated by muskgrass (*Chara vulgaris*), a charophyte species capable of over-wintering in aboveground form (Kufel 2001). Although potentially important during spring to migrant waterfowl that require adequate food resources to fuel migration to breeding grounds, seasonal reduction of SAV biomass in LPB has not yet been documented.

1.7 Historical Studies and Available Data

Because LPB is an important wetland habitat used by staging waterfowl and other fish and wildlife in the LGL, researchers have quantified the distribution, relative abundance and long-term temporal dynamics of the SAV community; Smith (1979) mapped the distribution of SAV in LPB during the 1960s and 1970s; Knapton and Petrie (1999) and Petrie and Knapton (1999) assessed the distribution and relative abundance of SAV and Dreissenid mussels in the mid-1990s and compared their findings with those of Smith (1979). However, no studies have determined seasonal dynamics of SAV at LPB between autumn and spring. Seasonal abundance is important in determining carrying capacity of LPB for waterfowl, and these data would be beneficial to conservation planners charged with determining habitat suitability and availability through the annual cycle of waterfowl.

1.8 Research Objectives and Predictions

My goal was to examine the relationship between declines in Dreissenid mussel abundance (mussels/m²) and SAV that had appeared to have occurred since the peak mussel population densities in the early 1990s (Petrie and Knapton 1999) to infer potential impacts on fish and wildlife of LPB. My objectives were 1) to examine how SAV distribution and

abundance changed through time (year effect) and was influenced by substrate and water depth. I predicted that changes in the distribution and abundance of SAV would have been consistent with declines in Dreissenid mussel density. I also predicted that my estimates of angiosperm (e.g., wild celery and pondweeds) and charophyte (e.g., muskgrass) SAV collected in 2009 and 2010 in LPB would be greater and lesser, respectively, than the estimates from the 1990s (Petrie and Knapton 1999) 2) to quantify changes in above and belowground SAV biomass between early autumn and late spring to determine the seasonal carrying capacity for waterfowl using LPB. I predicted that SAV aboveground biomass would decrease more between autumn and spring for those species that over-winter as belowground tubers and dormant seeds (wild celery, pondweeds, or *Najas* spp. than for species such as muskgrass and Eurasian milfoil (*Myriophyllum spicatum*), which retain aboveground vegetative structures during winter to a lesser extent; and 3) because seasonal changes in biomass have implications for migrating waterfowl, my last objective was to estimate the energetic carrying capacity within LPB. I predicted that energy available from SAV was great enough to feed the average number of ducks present throughout the autumn and spring migration period at LPB.

2 Methods

2.1 Study Area

My study was conducted at Long Point, Ontario (80° 30' E, 42° 35' N to 80° 03' E, 42° 33' N). Long Point is a sand-spit extending 35 km south-east into Lake Erie, and it has facilitated the formation of the Inner and Outer Long Point Bays and associated freshwater marsh complexes (Petrie 1998). The Inner Bay at Long Point is 78 km² and mean depth (1 to 2 m) varies depending upon annual and periodic changes in regional water budgets (Berst and MaCrimmon 1966). Coverage of the Inner Bay by SAV is > 90% in most locales (Pauls and Knapton 1993, Petrie 1998, Smith 1979). The mean temperature of the Inner Bay (22 °C; Pauls and Knapton 1993, Smith 1979) provides favourable growing conditions for macrophytic SAV, including muskgrass, wild celery, Eurasian milfoil, *Najas* spp., pondweeds, Canada water weed (*Elodea canadensis*), and coontail (*Ceratophyllum demersum*; Petrie 1998). Big Creek is the major tributary of the Inner Bay, and it drains a watershed comprised primarily of agricultural land northwest of Long Point (Berst and MaCrimmon 1966, Leach 1981). Big Creek influences the SAV communities in LPB because it is the primary source of nutrients and sediments in the bay (Leach 1981). LPB substrate is predominantly mud at the mouth of Big Creek, sandy loam over most of the central portion, and sand bordering the eastern and south-eastern portions (Smith 1979).

2.2 Study Design and Sample Collection

I used a grid generated with geographic information system (GIS) software to uniformly distribute 321 sampling stations throughout LPB (Figure 1). I used GPS coordinates to navigate to sampling stations in the field. I collected SAV and Dreissenid mussels at the 321 stations from 5-29 August 2009 and 28 April – 25 May 2010 to estimate SAV and Dreissenid mussel

availability to ducks foraging during autumn and spring. SAV and Dreissenid mussel were sampled at 100 stations selected using random stratification from 30 November – 7 December 2009. I collected SAV and Dreissenid mussels during these periods to enable comparisons of seasonal biomass of food available to migrating ducks at LPB. A handheld GPS unit was used to navigate to sampling stations throughout LPB. At each sampling station, I recorded water depth and water clarity using a Secchi disc marked at 5 cm intervals. Using a digital thermometer (± 0.1 °C; Fisher Scientific 0666426), I also recorded water temperature at each sampling station. I used a Self-Contained Underwater Breathing Apparatus (SCUBA) when diving to the substrate where I collected SAV, Dreissenid mussel, and benthic substrate samples. I estimated SAV percentage cover using a modified Braun-Blanquet scale of abundance and ascended to the surface to record values. To create continuous values for multivariate analysis I modified the Braun-Blanquet scale using categories 1-4 instead of 0-5. Using scissors I clipped all aboveground SAV in a 0.5m x 0.5m quadrat at substrate level and placed the clippings in a modified mesh bag to capture and strain samples. Tuber and substrate samples were collected using three horizontal scoops of substrate with a perforated metal can (sample volume = 0.03 m^3) to emulate maximum foraging depth for diving ducks (Badzinski 2003). Dreissenid mussels were removed from SAV samples on the deck of the boat, where I bottled and labelled each of the mussel samples separately. Finally, I differentiated between above and belowground SAV samples, and froze samples until further processing.

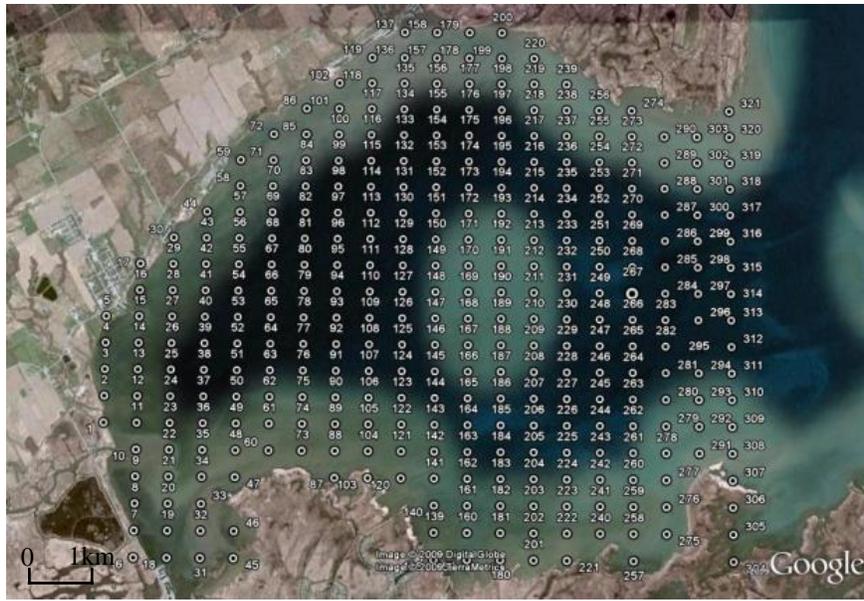


Figure 1. Locations for sampling Dreissenid mussels, SAV distribution and abundance, water depth, and substrate type within Long Point Bay, Lake Erie.

2.3 Laboratory Procedures

All species-specific aboveground vegetation samples were blotted dry using paper towel. I weighed each sample using a digital balance (± 0.001 g; A&D Company Ltd. FX3000i) and recorded values as wet mass. Belowground plant parts (i.e., roots, turions/tubers, and rhizomes) were separated from benthic substrate using a fine mesh sieve (2 mm \times 2 mm; Fisher Scientific U.S. standard brass). Substrate type was classified into one of three groups (mud, sandy loam, or sand) using the modified Wentworth scale (Wentworth 1922). Three substrate classifications were selected based on previously reported substrate types within LPB (Smith 1979). Dry mass of sub-samples was obtained to allow for estimation of dry mass for aboveground samples (by species). I selected sub-samples from aboveground samples for each species and oven-dried them separately at 80 °C to constant mass (± 0.001 g). I ensured that sub-samples represented the range of wet masses observed in samples of each species. Thereafter, I used linear regression to estimate dry mass using wet mass measurements (Table 1.). The only species I detected in

belowground sampling was wild celery tubers and occurrence was negligible, accounting for 0.05% and 0.58% in autumn and spring respectively, of the total SAV biomass and were included with the aboveground parts of wild celery in my analysis. The numbers of all dreissenid mussels were counted at each sample site.

Table 1. Linear regressions for conversion of wet weights to dry weights for species of SAV sampled at Long Point Bay, Lake Erie, autumn 2009 and spring 2010.

| Species | n | Intercept | β | R^2 |
|---------------------------------|----------|------------------|---------------------------|-------------------------|
| <i>Chara vulgaris</i> | 23 | 2.5306 | 0.2544 | 0.99 |
| <i>Myriophyllum spicatum</i> | 32 | 0.2487 | 0.1524 | 0.98 |
| <i>Najas</i> spp. | | | | |
| <i>Najas flexilis</i> | 29 | 0.6847 | 0.1218 | 0.99 |
| <i>Najas guadalupensis</i> | 14 | 0.1009 | 0.1557 | 0.98 |
| <i>Potamogeton richardsonii</i> | 19 | 0.0341 | 0.1309 | 0.95 |
| <i>Potamogeton pusillus</i> | 25 | 0.6916 | 0.1141 | 0.99 |
| <i>Vallisneria americana</i> | 26 | 0.3649 | 0.1003 | 0.97 |

2.4 Data Mapping and Analysis

2.4.1 SAV Distribution and Abundance

Abundance and distribution data from previous studies (1976, 1991, and 1992) were obtained from Bird Studies Canada archives. In 1976, only cover data (using the Braun-Blanquet scale) for each plant species were available. In 1991 and 1992, cover data for each plant species were available, as well as water depth, Secchi depth, and Dreissenid mussel abundance. I used inverse distance-weighted (IDW) spatial interpolation (Spatial Analyst tool, ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) to estimate species-specific distributions and changes in SAV and Dreissenid mussel distribution in LPB (Watson and Philip 1985, Neckles et al. 2012). I mapped the abundances of Dreissenid mussels and the six most abundant SAV species for 1976, 1991, 1992, and 2009 to provide a graphical representation of community changes in LPB. The modified Braun-Blanquet scale described above (to ensure data were ordinal) was used to map SAV. Using abundance of Dreissenid mussels (mussels/m²) I was able to develop maps and show changes in relative abundance among sampling periods. To test for temporal variation in mussel abundance, I used repeated measures analysis of variance (ANOVA). Spatial interpolation provides a visual representation of SAV coverage in LPB, but does not provide statistical comparisons of abundance among years. Therefore, multivariate analysis of variance (MANOVA) was used to test for changes in plant community (e.g., SAV) among years using SAV relative abundance data. I included muskgrass, wild celery, Eurasian milfoil, *Najas* spp., slender pondweed (*Potamogeton pusillus*) and Richardson's pondweed (*Potamogeton richardsonii*) cover (modified Braun-Blanquet) as response variables and year as a repeated measure to account for sampling the same points through time. I included latitude and longitude as covariates to control for spatial autocorrelation and substrate as a covariate to control for potential changes to growing conditions. I inspected

studentized residual plots from all models for normal distribution. I log-transformed SAV data to normalize the residual distribution (Littell et al. 2007). I selected a 0.10 (α) level of significance *a priori* because it is appropriate for observational data (Tacha et al. 1982). I used Wilks' lambda and F-tests (type III sum of squares) to evaluate statistical significance of year effects within multivariate (MANOVA) and univariate analyses, respectively.

Backwards elimination logistical regression was used to determine factors influencing likelihood of detecting a species at a sampling station for the 6 most common species of SAV. I included Dreissenid mussel abundance, substrate type, year, water depth, depth \times depth, and substrate \times year as fixed effects and latitude and longitude as covariates to correct for spatial autocorrelation. I included substrate \times year to detect if changes in the likelihood of detecting SAV changed through time within substrate types and within years among substrate types. Secchi disk reading was not included, because it was strongly correlated with water depth ($p < 0.01$; $r=0.90$), but subject to greater error than water depth because of daily differences in turbidity. I compared means of reduced models using post-hoc Tukey's adjustment.

2.4.2 Energetic Carrying Capacity

Biomass of SAV, species-specific nutritional quality of plants, and information on energy requirements of ducks were used to determine how many waterfowl the SAV in LPB could feed during autumn, winter, and spring (i.e., SAV energetic carrying capacity). I compared the energy available from SAV (kcal/m^2) and requirements of migrating waterfowl using LPB to determine energy surplus or deficit and how many ducks SAV could feed during winter if LPB remained ice-free (i.e., consistent with climate change scenarios – see further discussion below). I determined available energy by calculating g/m^2 (dry mass) for each plant species within LPB. A true metabolizable energy (TME) value was assigned to each plant species from published

literature (Table 2). TME values represent energy available to waterfowl corrected for endogenous (non-food) excretory energy and are appropriate for modeling of carrying capacity (Sibbald 1976). Using inputs of dry biomass, TME and area in LPB, I calculated available energy in LPB based on autumn 2009 and spring 2010 sampling.

I used data from standardized, aerial waterfowl surveys that were conducted approximately once every two weeks, autumn and spring 1990-2006 (Long Point Waterfowl, unpublished data) to estimate waterfowl usage of LPB. Duck Use Days (DUD) were determined for each species by adding abundances on days of counts to estimates of abundance between surveys. Duck abundances between surveys were estimated by averaging abundances from two consecutive surveys and multiplying by the number of non-survey days between aerial surveys (Korschgen *et al.* 1985). I calculated the energy needs of each waterfowl species that commonly eats SAV using species-specific daily energy requirements (DER; Table 3). DER incorporates the energetic costs of feeding and non-feeding behaviours and excludes the demands related to reproduction, molt, and migration in waterfowl (Baldassarre and Bolen 2006). Because SAV is a portion of total diet in waterfowl, I adjusted species-specific DER using data on waterfowl diets (Petrie 1998), and the equation (see also Table 3):

$$\text{Adjusted DER} = \text{DER} \times \% \text{ stems/leaves in diet}$$

To calculate energy needs of waterfowl derived from SAV in each season and year at LPB, I multiplied adjusted DER by total seasonal DUDs for each species for autumn and spring and summed energy requirements across species within seasons and years.

I considered autumn migration to be 15 September – 15 December (100 days) and spring migration to be 1 March – 14 May (75 days). Autumn and spring migrations are separated by a 75 day wintering period when LPB is typically ice covered (Long Point Waterfowl, unpublished

data; Bellrose 1980, Assel 2003). However, climate change scenarios and recent trends suggest an increasing number of ice-free days at LPB (Assel 2003). To determine the energetic capacity of SAV in LPB to feed waterfowl into winter, I calculated surplus energy by subtracting spring energy needs of waterfowl using LPB 1990 - 2006 from estimates of energy available during spring 2010. By subtracting the energy requirement in spring from energy available I determined the surplus (or deficit) of energy estimated to be available for overwintering waterfowl. I divided surplus energy by DER from stems and leaves (163.5 kcal/day; average of grazing and diving ducks adjusted for stems/leaves only; Table 3) to determine available DUDs for each wintering period between 1990-2006.

Table 2. True metabolizable energy (TME) values (kcal/g) used to calculate energetic carrying capacity for food items in Long Point Bay, Lake Erie during summer/fall 2009.

| Food Item | TME (kcal/g) | Source |
|-------------------------------|-------------------------|---------------------|
| <i>Ceratophyllum demersum</i> | 0.49 | Brasher et al. 2007 |
| <i>Chara vulgaris</i> | 0.57 | Boyd 1968 |
| <i>Myriophyllum spicatum</i> | 0.55 | Boyd 1968 |
| <i>Najas</i> spp. | 0.82 | Brasher et al. 2007 |
| <i>Potamogeton</i> spp. | 0.82 | Brasher et al. 2007 |
| <i>Vallisneria americana</i> | | |
| aboveground | 0.78 | Donnermeyer 1982 |
| belowground | 0.88 | Donnermeyer 1982 |

Table 3. Daily energetic requirements (DER) of species and guilds (bold) and the percentage of diet consisting of stems/leaves of waterfowl species using SAV habitat within Long Point Bay, Lake Erie (LPB). DER (guild) represents the mean of all species.

| Species | DER (kcal/day) | % of diet consisting of stems/leaves |
|--|---------------------------|---|
| Grazers | 268* | |
| American wigeon (<i>Anas americana</i>) | 255* | 90.5 [†] |
| Gadwall (<i>Anas strepera</i>) | 280* | 96.7 [†] |
| Divers | 274* | |
| Bufflehead (<i>Bucephala albeola</i>) | 213** | 29.3 [†] |
| Canvasback (<i>Aythya valisineria</i>) | 347* | 88 [†] |
| Common goldeneye (<i>Bucephala clangula</i>) | 249*** | 51.7 [†] |
| Redhead (<i>Aythya americana</i>) | 311* | 72.8 [†] |
| Ring-necked duck (<i>Aythya collaris</i>) | 234* | 24.7 ^{††} |
| Scaup (<i>Aythya affinis</i> and <i>Aythya marila</i>) | 280* | 9.3 [†] |

* Straub 2008

**McKinney and McWilliams 2012

*** DER migration = 3xBMR and DER wintering = 3xBMR (King 1974)

[†] Petrie 1998

^{††} Mendall 1958

3 Results

3.1 Long-term Changes

3.1.1 Overall Changes

I detected an influence of sampling year on abundance of Dreissenid mussels in LPB ($F_{2,960}=25.7$, $P<0.001$) (Figure 2). Post-hoc comparisons indicated a 2110% increase in Dreissenid mussel abundance between 1991 (mean number per site: 20.6) and 1992 (mean number per site: 456.8), and a 96% decrease between 1992 and 2009 (mean number per site: 18.9) ($P < 0.001$), with no difference between 1991 and 2009 ($P = 0.999$). There was also an overall influence of sampling year on the percent cover of the six most abundant SAV species in LPB between 1976 and 2009 (MANOVA: Wilks' $\lambda = 0.90$, $F_{3,316} = 11.8$, $P < 0.001$) (Figures 3-9).

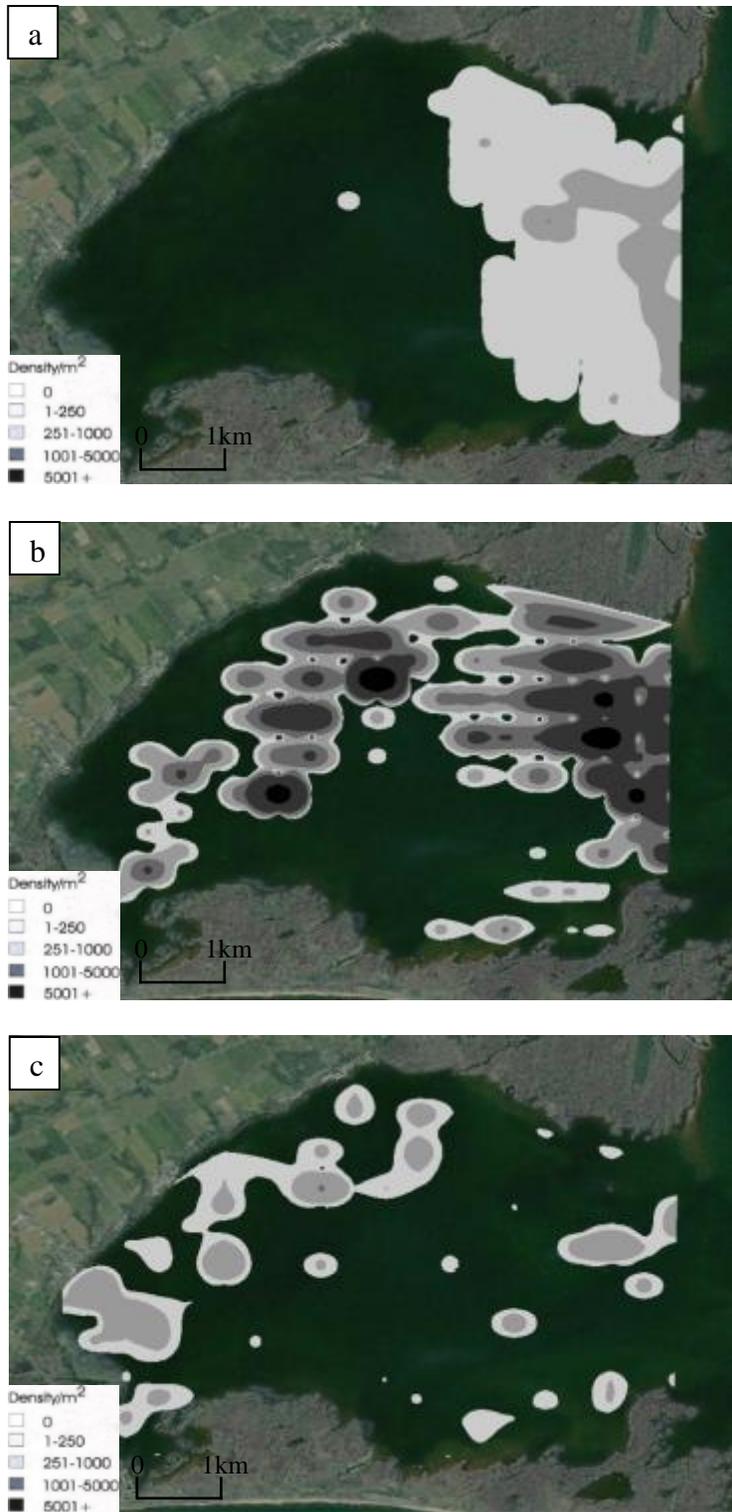


Figure 2. Distribution and abundance (mussels/m²) of Dreissenid mussels in Long Point Bay – Lake Erie a) 1991 b) 1992 and c) 2009.

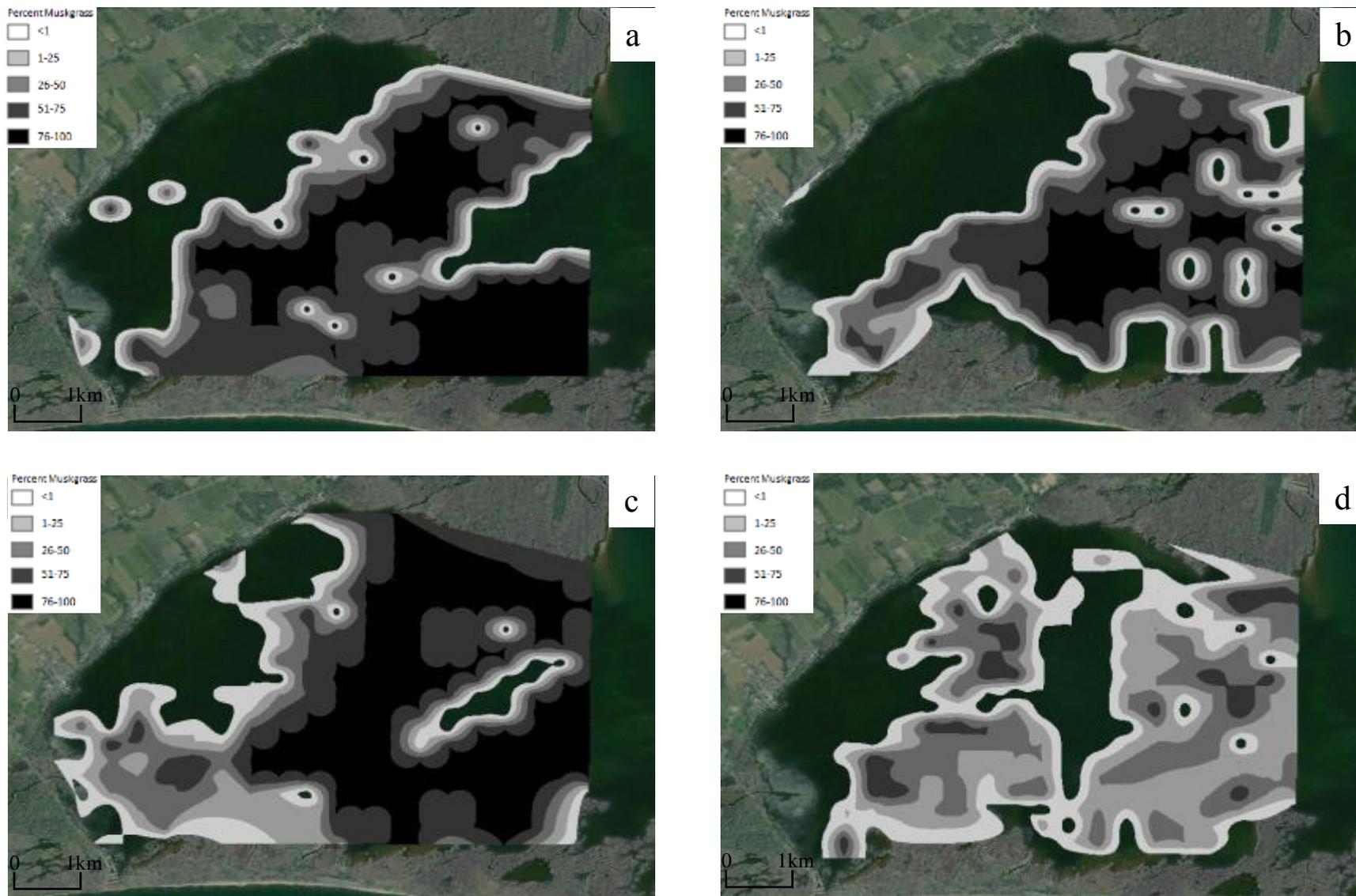


Figure 3. Distribution and abundance (percent cover) of muskgrass (*Chara vulgaris*) in Long Point Bay – Lake Erie a) 1976 b) 1991 c) 1992 and d) 2009.

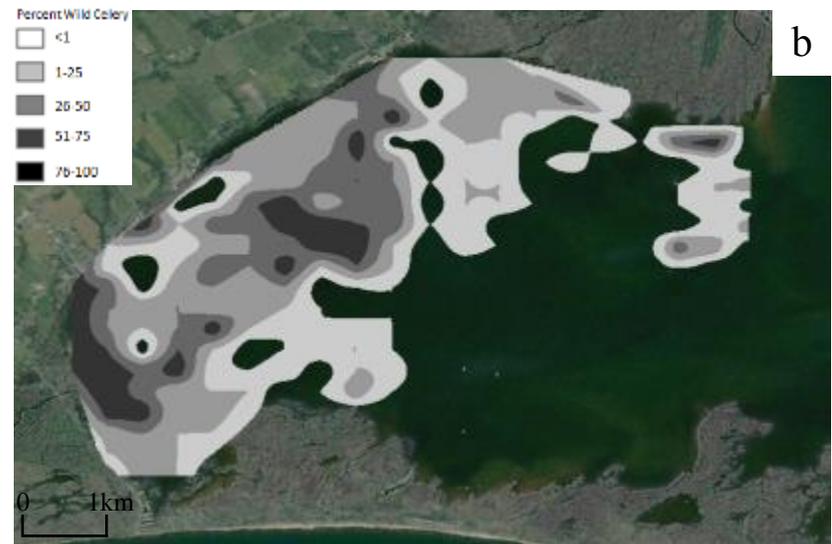


Figure 4. Distribution and abundance (percent cover) of wild celery (*Vallisneria americana*) in Long Point Bay – Lake Erie a) 1976 b) 1991 c) 1992 and d) 2009.

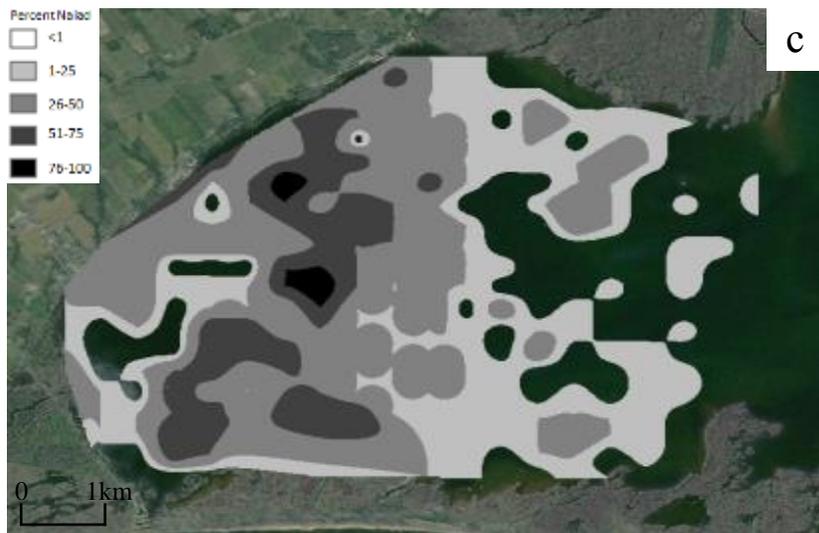
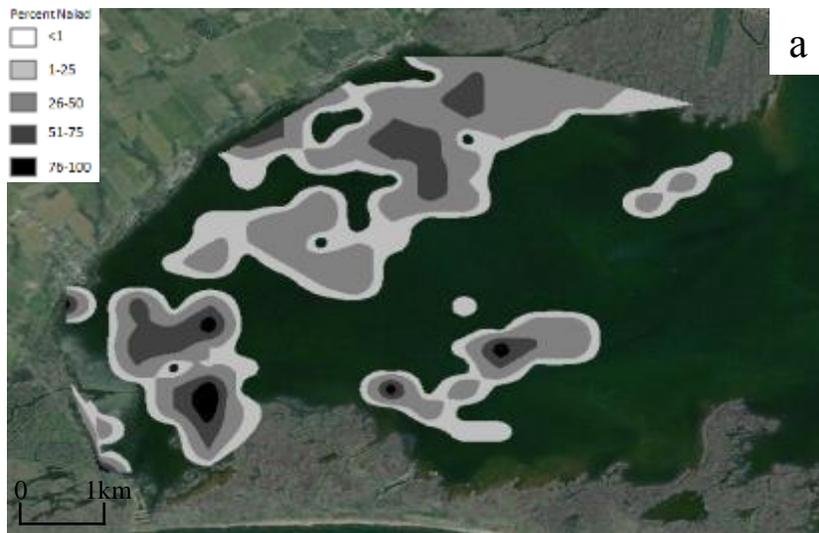


Figure 5. Distribution and abundance (percent cover) of *Najas* spp. in Long Point Bay – Lake Erie a) 1976 b) 1991 c) 1992 and d)

2009

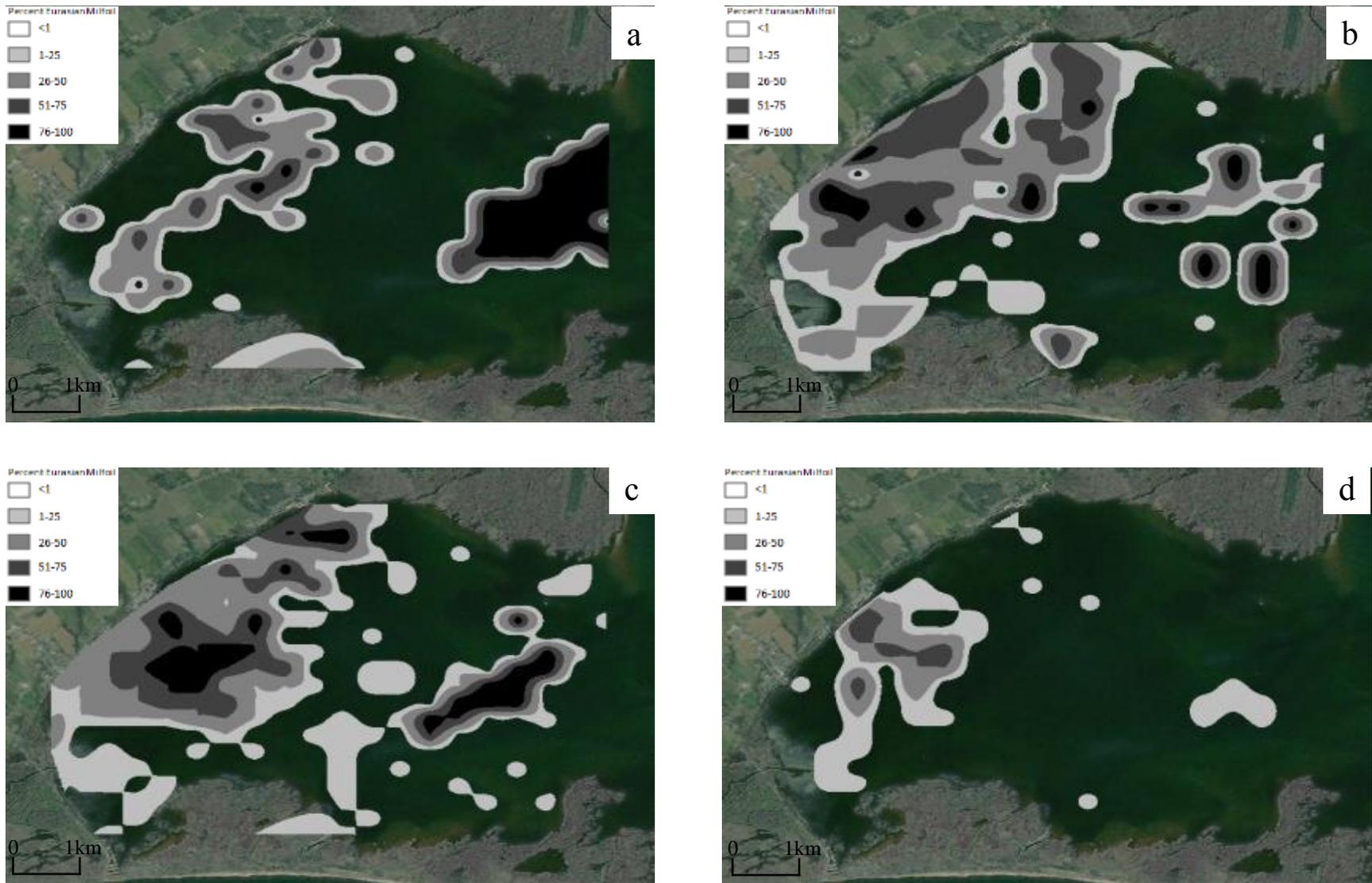


Figure 6. Distribution and abundance (percent cover) of Eurasian milfoil (*Myriophyllum spicatum*) in Long Point Bay – Lake Erie a) 1976 b) 1991 c) 1992 and d) 2009.

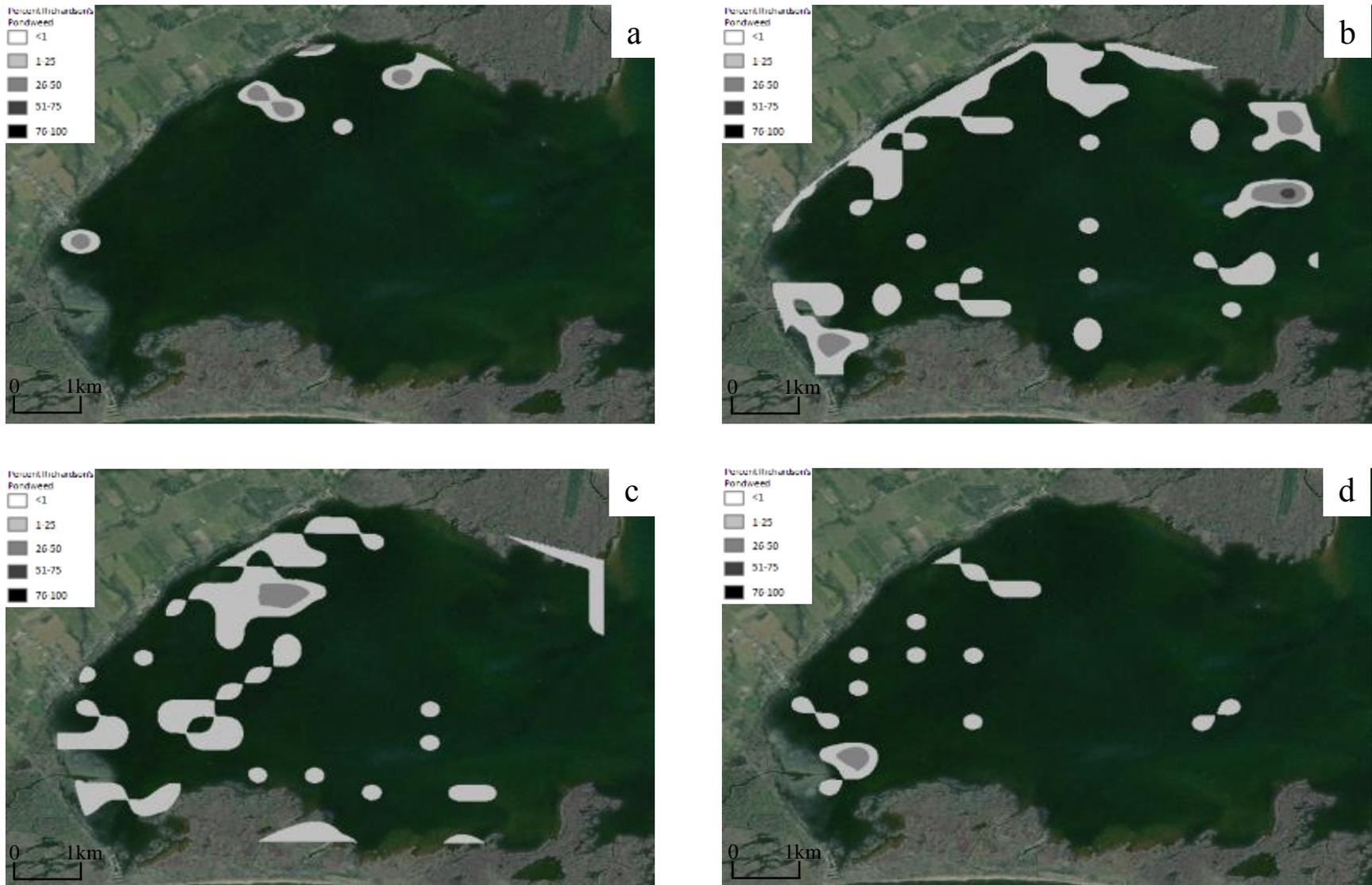


Figure 7. Distribution and abundance (percent cover) of Richardson's pondweed (*Potamogeton richardsonii*) in Long Point Bay – Lake Erie a) 1976 b) 1991 c) 1992 and d) 2009.

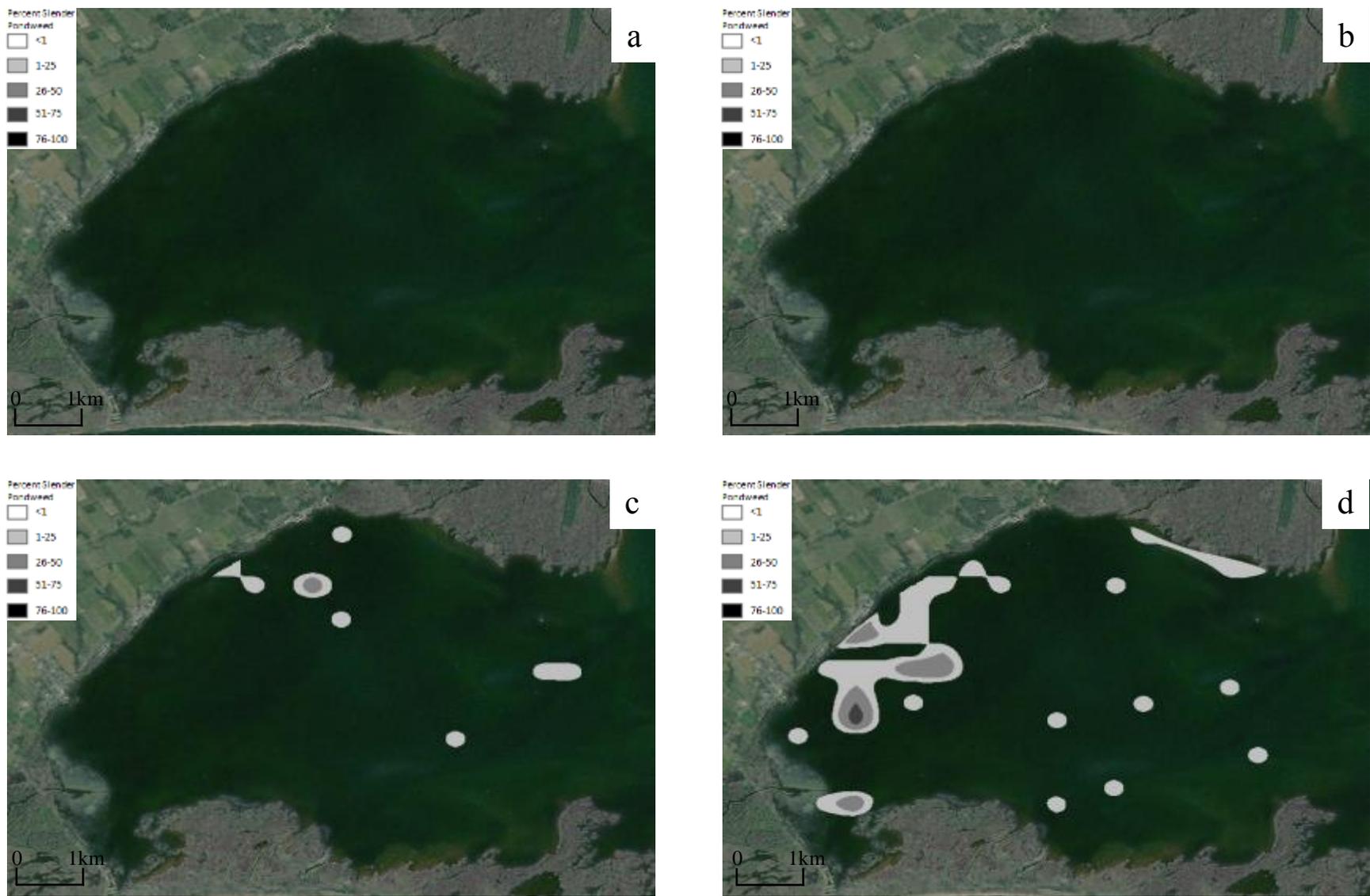


Figure 8. Distribution and abundance (percent cover) of slender pondweed (*Potamogeton pusilus*) in Long Point Bay – Lake Erie a)

1976 b) 1991 c) 1992 and d) 2009

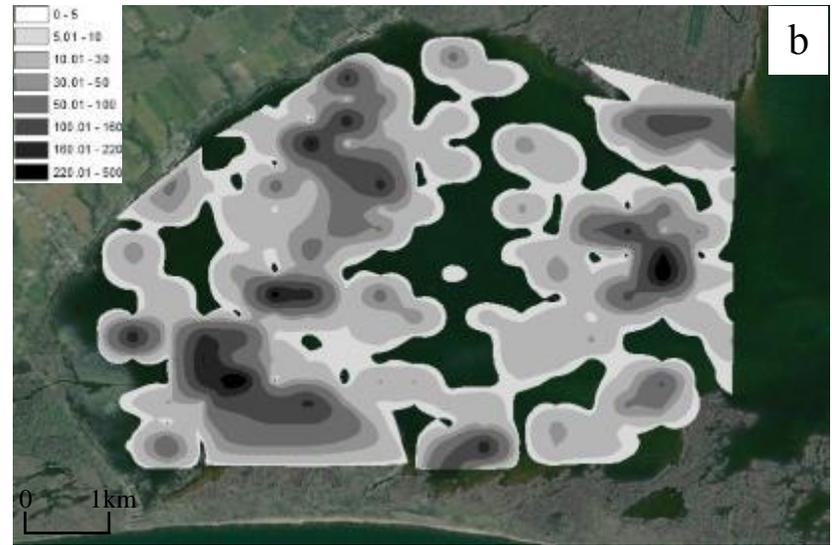
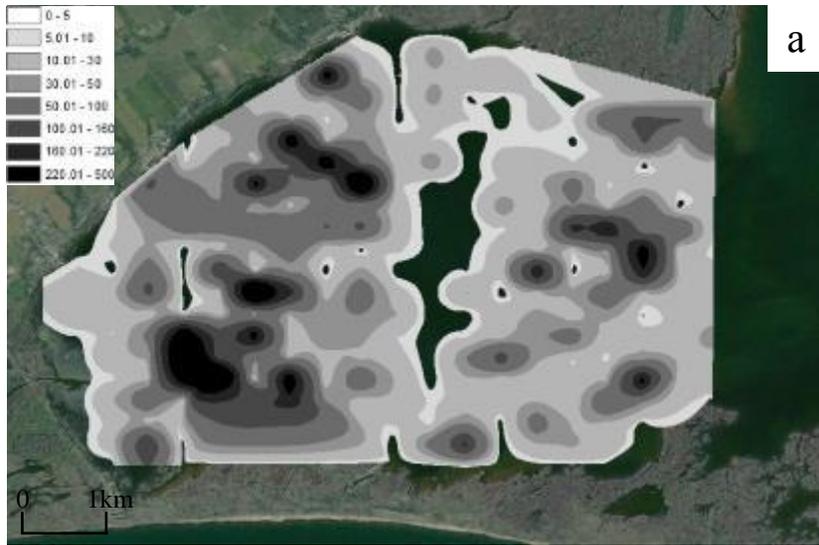


Figure 9. Total energy available (kcal/m^2) from submerged aquatic vegetation in autumn 2009 (a and c) and spring 2010 (b and d)

both with (a and b) and without (c and d) muskgrass (*Chara vulgaris*) in Long Point Bay – Lake Erie

3.1.2 Species-specific Changes

Sampling year had an influence on the likelihood of detection for each of the six most abundant SAV species' (Table 4). Wild celery ($P < 0.001$; Figure 10), Richardson's pondweed ($P < 0.001$; Figure 10) and Eurasian milfoil ($P < 0.001$; Figure 10) had the highest detection probability in sampling years 1991 and 1992. *Najas* spp. ($P < 0.001$; Figure 10) and muskgrass ($P < 0.001$; Figure 10) were more likely to be detected in 1992, while slender pondweed ($P < 0.001$; Figure 10) was the only species with a higher detection probability in 2009.

Species responses to substrate type were varied; detection probability of muskgrass ($P \leq 0.006$; Figure 11) was greater on sand and sandy loam substrate, whereas slender pondweed ($P = 0.018$; Figure 11) and Eurasian milfoil ($P < 0.001$; Figure 11) were more likely to be detected on mud substrate. The effects of substrate and sampling year had an interactive influence on the detection probability of wild celery, *Najas* spp., and Richardson's pondweed. Both wild celery ($P = 0.070$; Figure 13) and Richardson's pondweed ($P = 0.019$; Figure 13) had a higher detection probability across all sampling years in mud substrate. *Najas* spp. ($P < 0.001$; Figure 13) was more likely to be detected sandy loam during 1992, though this changed to mud in 1992 and 2009.

The likelihood of detecting Eurasian pondweed ($P < 0.001$; Figure 12), Richardson's pondweed ($P = 0.002$; Figure 12), and slender pondweed ($P = 0.054$; Figure 12) increased with water depth. The detection probability of muskgrass decreased with increasing water depth among all substrate types and sampling years (depth \times depth) (Table 4, Figure 12). *Najas* spp. occurrence was similar among water depths ($P = 0.641$; Table 4, Figure 12).

Table 4. Results of the multiple logistic regression of the SAV distribution data (n=321).

Specific SAV species' presence or absence was the response variable and the 11 site characteristics were the explanatory variables.

| Species | Effect | Estimate | Error | Degrees of freedom | P | X ² |
|-------------------|------------------|----------|--------|--------------------|--------|----------------|
| Wild Celery | Intercept | -1243.2 | 213.6 | 1 | <0.001 | 33.8 |
| | Substrate | | | 2 | 0.034 | 6.8 |
| | Mud | -0.319 | 0.251 | 1 | | |
| | Sandy Loam | -0.142 | 0.153 | 1 | | |
| | Depth | -0.018 | 0.007 | 1 | 0.011 | 6.5 |
| | Year | | | 2 | 0.067 | 5.5 |
| | 1991 | 0.179 | 0.157 | 1 | | |
| | 1992 | 0.162 | 0.162 | 1 | | |
| | Depth × Depth | <0.001 | <0.001 | 1 | 0.027 | 4.9 |
| | Substrate × Year | | | 4 | 0.035 | 10.4 |
| Muskgrass | Intercept | 1567.5 | 237.3 | 1 | <0.001 | 43.6 |
| | Substrate | | | 2 | <0.001 | 22.1 |
| | Mud | -0.56 | 0.208 | 1 | 0.007 | 7.2 |
| | Sandy Loam | 0.671 | 0.144 | 1 | <0.001 | 21.7 |
| | Depth | 0.013 | 0.007 | 1 | 0.047 | 3.9 |
| | Year | | | 2 | <0.001 | 36.3 |
| | 1991 | -0.6 | 0.134 | 1 | <0.001 | 19.9 |
| | 1992 | 0.828 | 0.141 | 1 | <0.001 | 34.6 |
| | Depth × Depth | <0.001 | <0.001 | 1 | <0.001 | 11.6 |
| Eurasian Milfoil | Intercept | -927.3 | 299.2 | 1 | <0.001 | 16.4 |
| | Substrate | | | 2 | 0.001 | 17.7 |
| | Mud | 0.419 | 0.213 | 1 | 0.049 | 3.9 |
| | Sandy Loam | -0.649 | 0.152 | 1 | <0.001 | 17.7 |
| | Year | | | 2 | <0.001 | 90.5 |
| | 1991 | 0.874 | 0.141 | 1 | <0.001 | 38.6 |
| | 1992 | 0.625 | 0.139 | 1 | <0.001 | 20.3 |
| | Depth × Depth | <0.001 | <0.001 | 1 | <0.001 | 11.6 |
| | Depth × Year | | | 2 | <0.001 | 90.5 |
| <i>Najas</i> spp. | Intercept | -220.3 | 196.6 | 1 | 0.262 | 1.3 |
| | Substrate | | | 2 | <0.001 | 44.1 |
| | Sandy Loam | 0.603 | 0.135 | 1 | <0.001 | 20.1 |
| | Year | | | 2 | <0.001 | 104.4 |
| | 1991 | 0.357 | 0.117 | 1 | 0.002 | 9.3 |

Table 4. Cont

| Species | Effect | Estimate | Error | DF | P | X² |
|-----------------------|------------------|-----------------|--------------|-----------|----------|----------------------|
| <i>Najas</i> spp. | Substrate × Year | | | 4 | <0.001 | 33.3 |
| Richardson's pondweed | Intercept | -618.4 | 240.1 | 1 | 0.01 | 6.6 |
| | Substrate | | | | | |
| | Mud | 0.9420 | 0.734 | 1 | | |
| | Sandy Loam | 0.1756 | 0.798 | 1 | | |
| | Depth | -0.020 | 0.007 | 1 | 0.002 | 9.3 |
| | Year | | | 2 | <0.001 | 23.7 |
| | 1991 | 2.787 | 0.635 | 1 | | |
| | 1992 | 2.115 | 0.647 | 1 | | |
| | Depth × Depth | <0.001 | <0.001 | 1 | 0.002 | 9.9 |
| | Substrate × Year | | | 4 | 0.047 | 9.7 |
| Slender pondweed | Intercept | -1243.2 | 213.6 | 1 | <0.001 | 33.9 |
| | Substrate | | | 2 | 0.024 | 7.5 |
| | Mud | 1.245 | 0.755 | 1 | | |
| | Sandy Loam | -0.512 | 0.572 | 1 | | |
| | Depth | -0.018 | 0.007 | 1 | 0.054 | 3.7 |
| | Year | | | 2 | <0.001 | 5.9 |
| | 1991 | -13.720 | 153.7 | 1 | | |
| 1992 | -2.056 | 0.483 | 1 | | | |

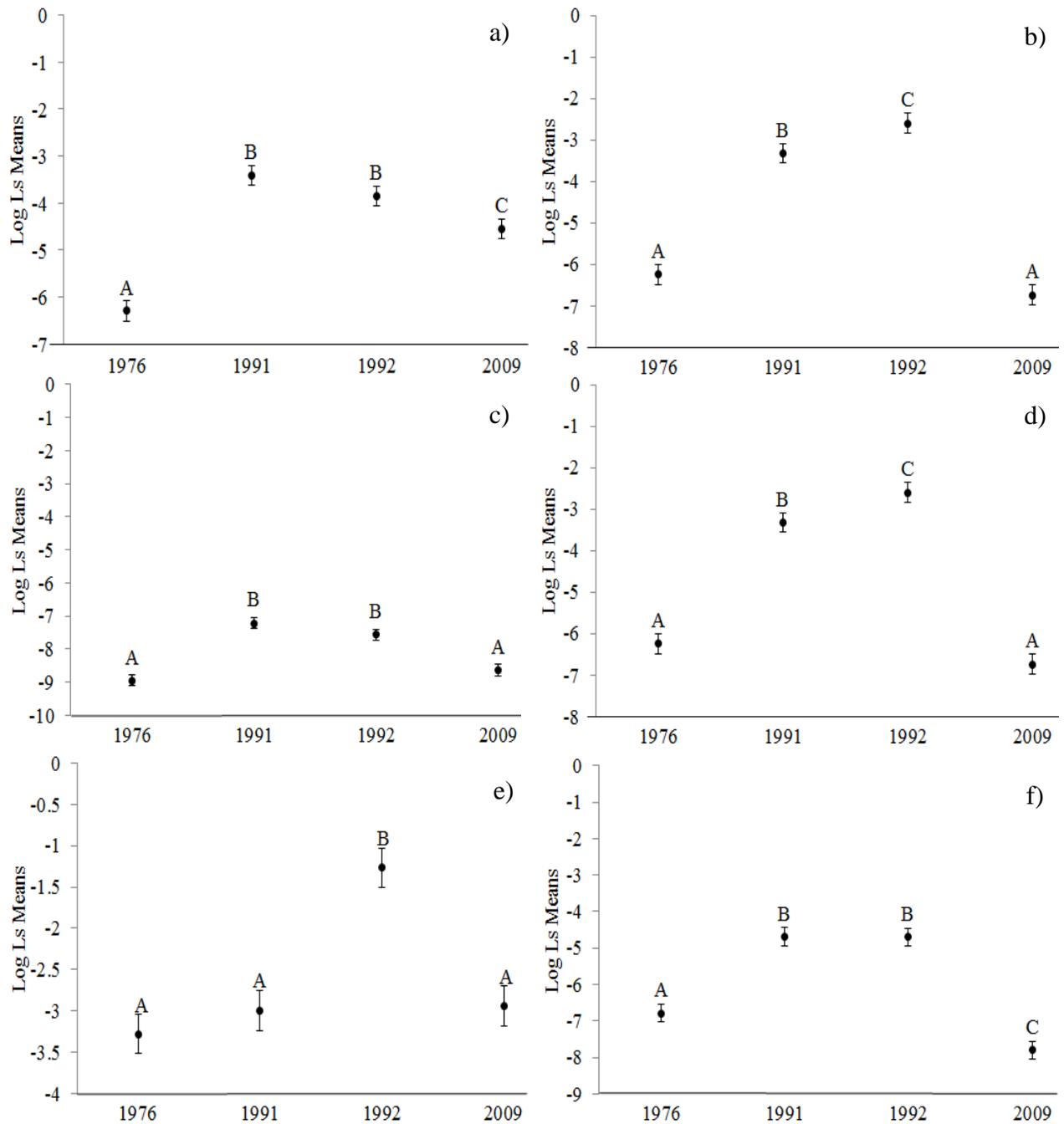


Figure 10. Least-squared means (log transformed) of percent abundance (\pm SE) for the most abundant species of SAV in LPB: a) Wild celery b) *Najas* spp. c) Slender pondweed d) Richardson's pondweed e) Muskgrass and f) Eurasian milfoil. Years with the same letter are not significantly different ($P > 0.10$).

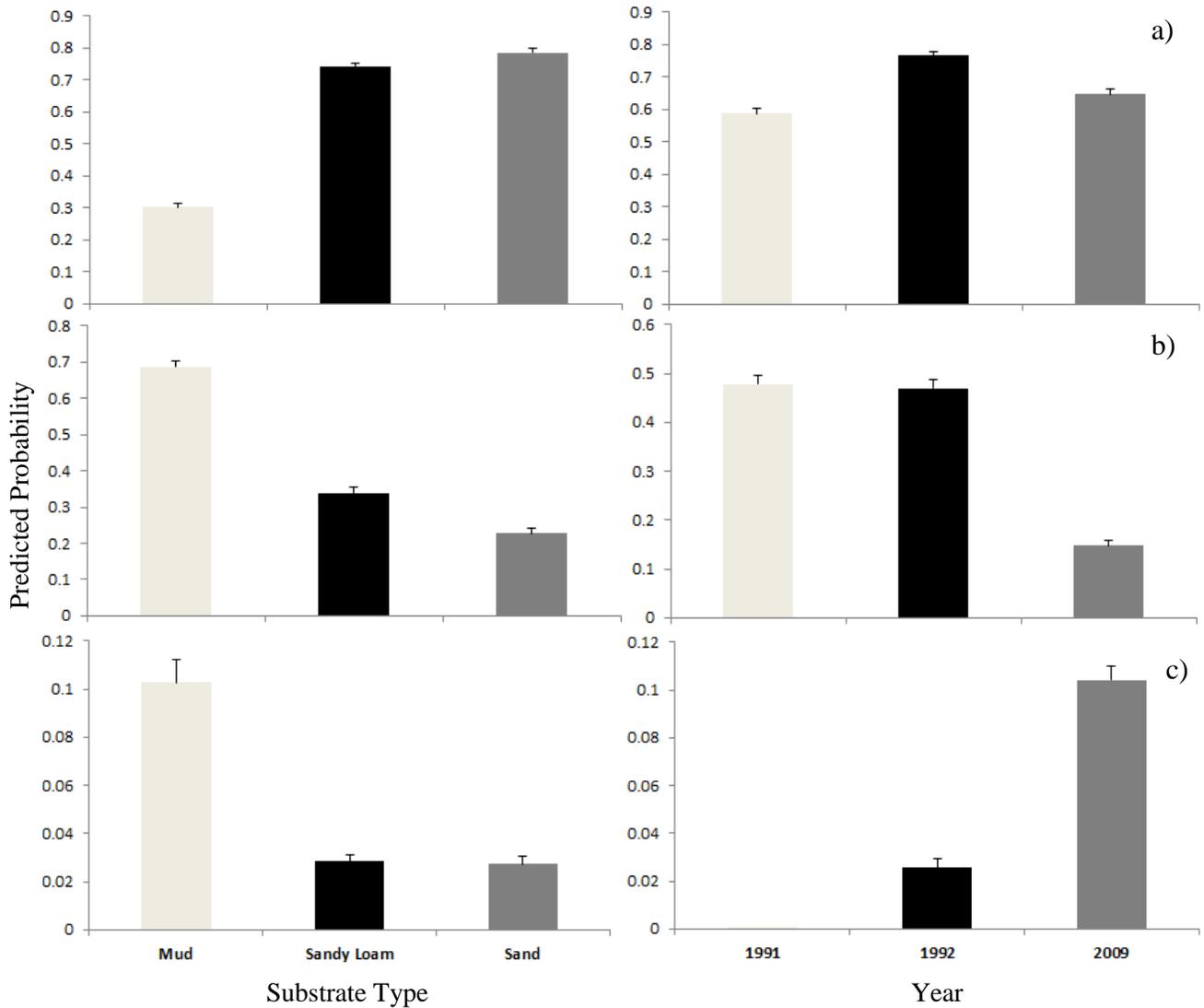


Figure 11. Relationship between the predicted probability (\pm SE) of SAV presence (a) muskgrass b) Eurasian milfoil c) slender pondweed) and the effects of substrate and year in Long Point Bay – Lake Erie in 1991, 1992, and 2009.

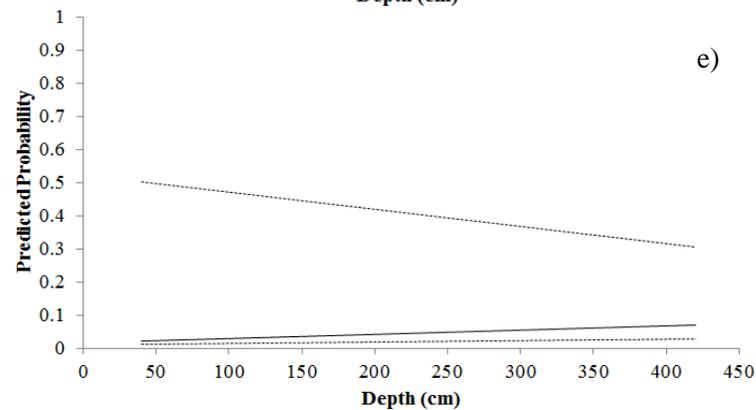
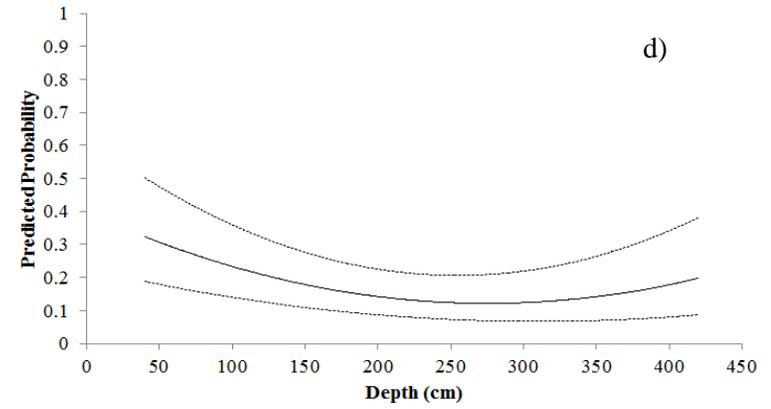
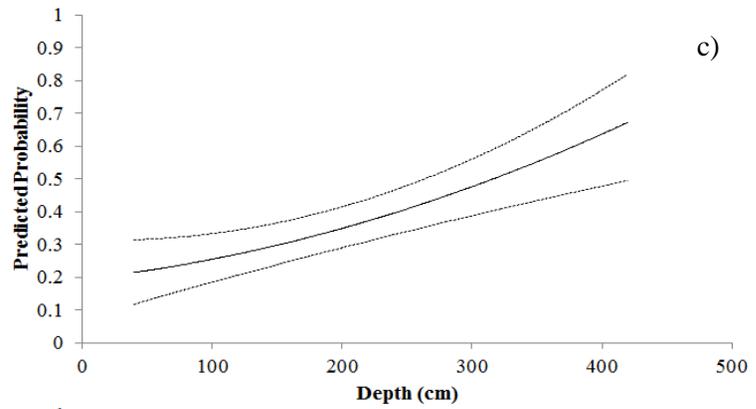
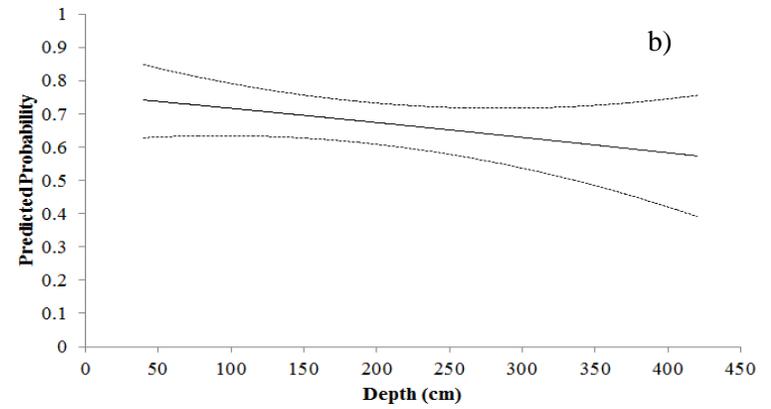
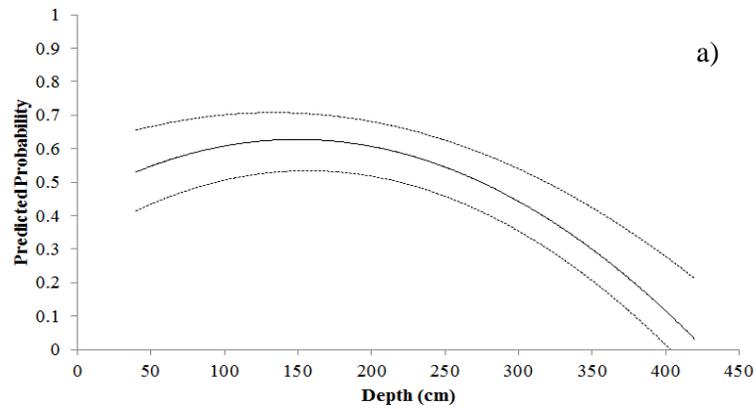


Figure 12. Relationship between the predicted probability of SAV presence (a) wild celery b) muskgrass c) Eurasian milfoil d) Richardson's pondweed e) slender pondweed) and water depth (\pm 90% confidence intervals) in Long Point Bay – Lake Erie in 1991, 1992, and 2009.

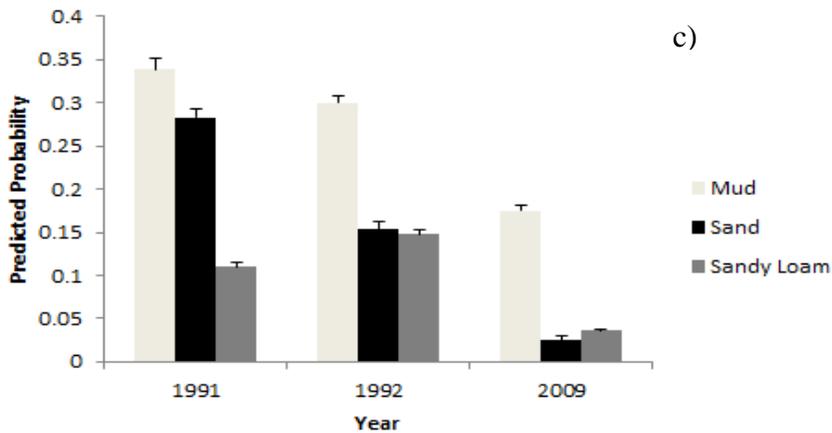
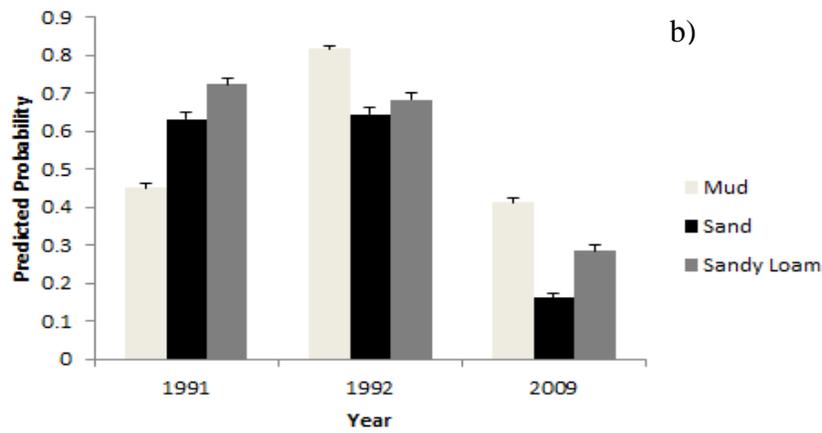
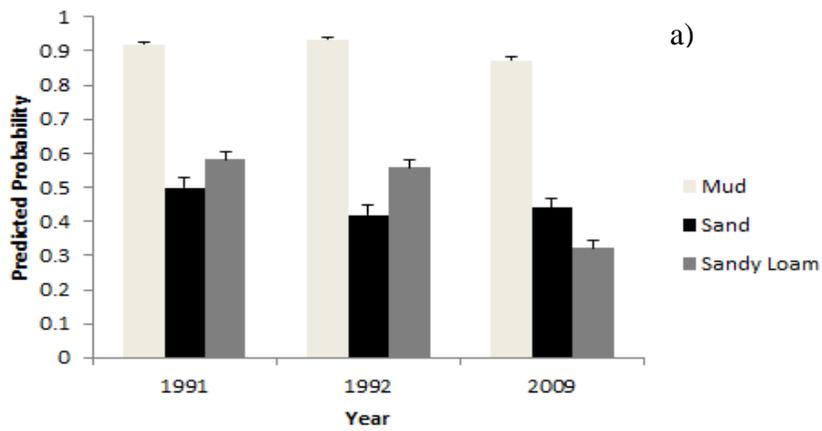


Figure 13. Relationship between the predicted probability (\pm SE) of SAV presence (a) wild celery b) *Najas* spp. c) Richardson's pondweed) and the interactive effects of substrate and year in Long Point Bay – Lake Erie in 1991, 1992, and 2009.

3.2 Seasonal Changes in Energetic Carrying Capacity

Muskgrass and wild celery provided the majority of SAV biomass within LPB during both autumn and spring (Table 5). Mean biomass ($\text{g/m}^2 \pm \text{SE}$) of muskgrass during autumn was 60.6 ± 11.6 , and spring mean biomass was 41.2 ± 3.4 . Wild celery had a mean biomass of 3.2 ± 0.5 and 0.6 ± 0.5 , during autumn and spring, respectively.

Based on the annual energy necessary to feed migrating diving and grazing ducks using LPB, a surplus of available energy from SAV existed during autumn and spring when using SAV data from 2009-2010 (Table 6 and Figures 15-18). I estimated that the mean adjusted energy need of diving and grazing ducks migrating through LPB in autumn was 3.48×10^8 kcals, 1990 - 2005. I calculated that there were 3.46×10^9 kcals available in LPB in autumn 2009, leaving a surplus of 3.11×10^9 kcals available in LPB. However, because muskgrass is not consumed in abundance by waterfowl in LPB (Petrie 1998), I removed it from the analysis to better estimate available energy from SAV. My adjusted available energy estimate (muskgrass excluded) in autumn was 7.63×10^8 kcals, which represented a surplus of 4.16×10^8 kcals. In spring, required energy, adjusted for stems/leaves only, was 1.62×10^8 kcals. The available energy (muskgrass excluded) was 3.46×10^8 kcals, with a surplus of 1.84×10^8 kcals.

I also estimated required and available DUDs if LPB remained ice-free throughout winter, exposing SAV to an additional 75 days of foraging. Using the surplus energy estimate from spring 2010, between 1990-2006 (excluding 1998, in which I estimated a substantial deficit of energy of -6×10^7 kcals) the estimated ducks that LPB could feed each day for a 75 day wintering period ranged from 3,466 (2.6×10^5 DUDs) in 2000 to 24,000 (1.8×10^6 DUDs) in 1994, with an average of 16,000 (1.2×10^6 DUDs).

Table 5. Seasonal biomass (g/m^2 ; mean \pm SE), given by species of SAV in Long Point Bay, Lake Erie, Ontario autumn 2009 and spring 2010.

| Species | Spring Mean Biomass ($\text{g/m}^2 \pm \text{SE}$) | Autumn Mean Biomass ($\text{g/m}^2 \pm \text{SE}$) |
|---------------------------------|--|--|
| <i>Ceratophyllum demersum</i> | 0.48 \pm 0.26 | 0.82 \pm 0.21 |
| <i>Chara vulgaris</i> | 41.18 \pm 8.35 | 60.55 \pm 11.61 |
| <i>Myriophyllum spicatum</i> | 1.59 \pm 0.76 | 3.20 \pm 1.25 |
| <i>Najas spp.</i> | 1.17 \pm 0.5 | 3.60 \pm 1.05 |
| <i>Potamogeton richardsonii</i> | 0.07 \pm 0.08 | 0.53 \pm 0.24 |
| <i>Potamogeton pusillus</i> | 1.36 \pm 1.43 | 1.54 \pm 0.67 |
| <i>Vallisneria americana</i> | | |
| aboveground | 0.61 \pm 0.49 | 3.20 \pm 0.49 |
| belowground | 0.27 \pm 0.07 | 0.04 \pm 0.01 |

Table 6. Seasonal estimates of average required (1990-2006) and available energy (kcal; energetic carrying capacity) in LPB, Lake Erie 2009.

| Season | Avg. Required[†] | Avg. Required^{††} | Total Carrying Capacity | Carrying Capacity* |
|---------------|----------------------------------|-----------------------------------|--------------------------------|---------------------------|
| Autumn | 937,739,965 | 347,873,962 | 3,455,303,332 | 763,413,993 |
| Spring | 410,099,844 | 162,824,152 | 2,177,911,921 | 346,950,470 |

[†] Total energy required

^{† †} Total energy required after stems/leaves adjustment

* Muskgrass removed from available energy

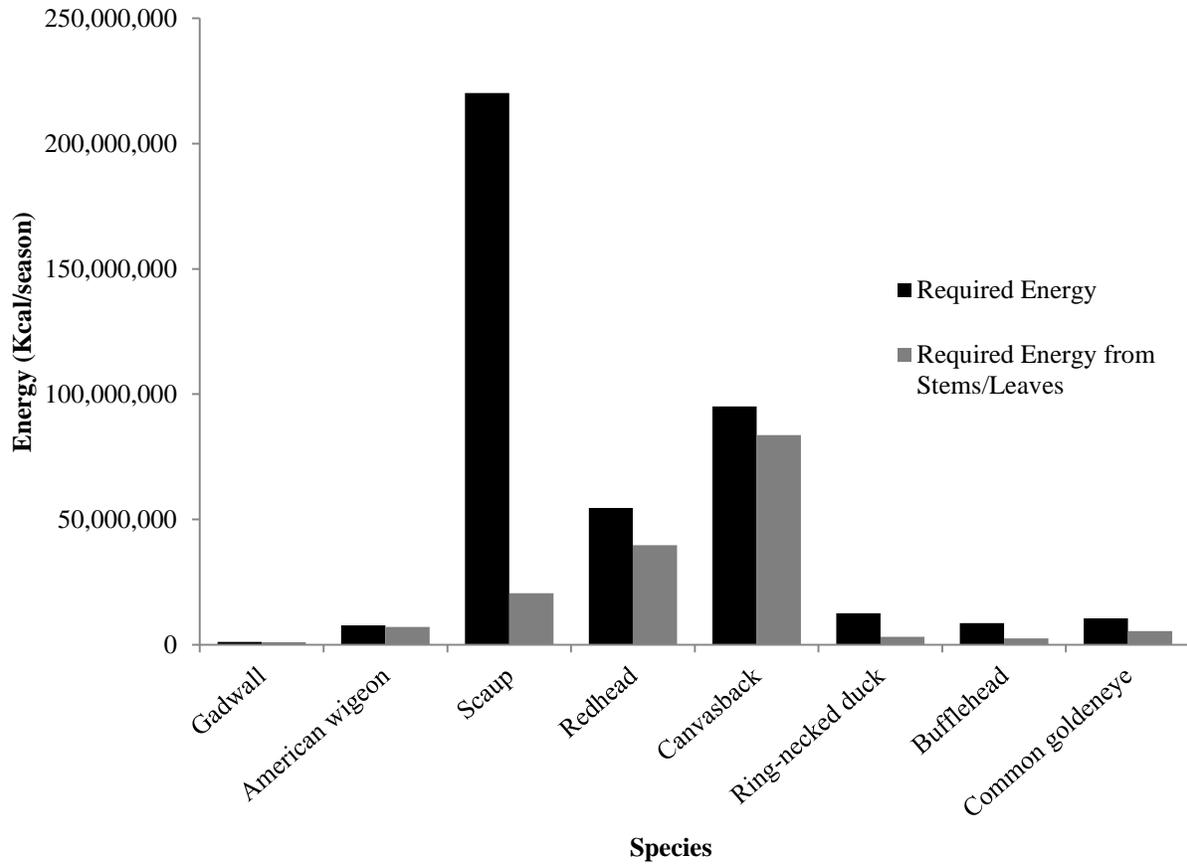


Figure 14. Total required energy and the total required energy from stems/leaves for SAV consuming waterfowl species within LPB (Petrie 1998)

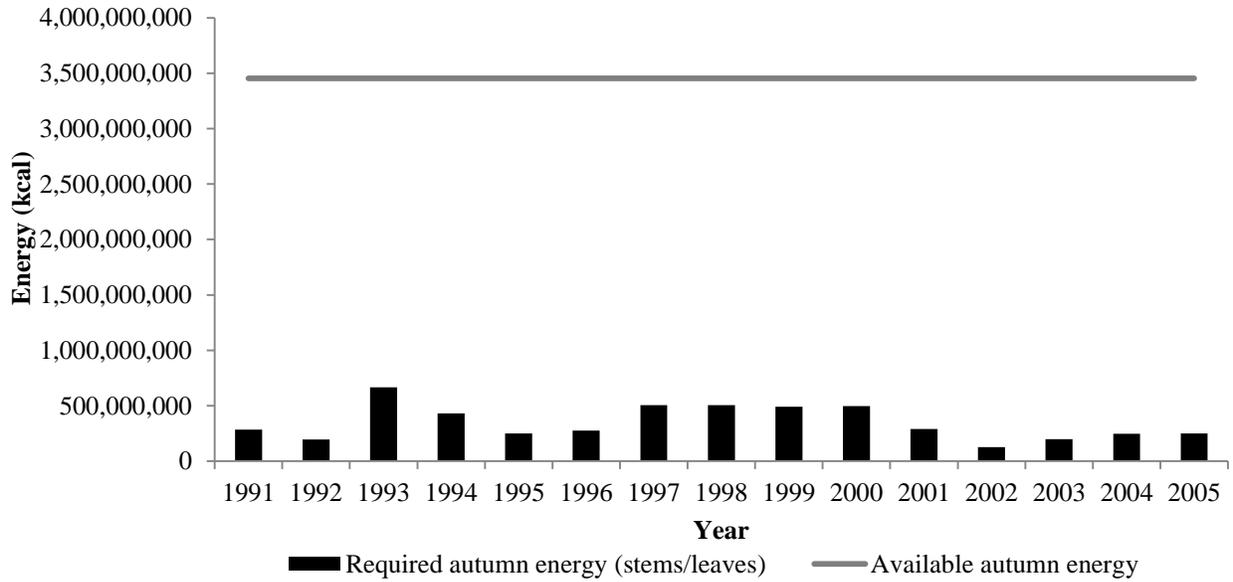


Figure 15. Available autumn energy and the required energy from the stems/leaves of SAV within LPB (with Muskgrass).

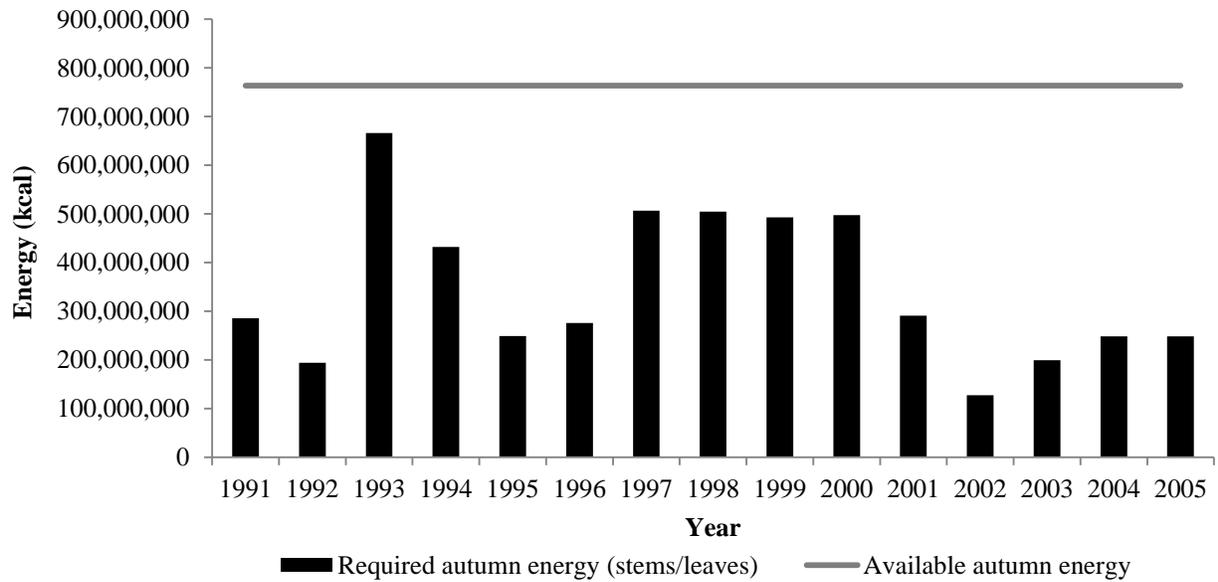


Figure 16. Available autumn energy and the required energy from the stems/leaves of SAV within LPB (without Muskgrass).

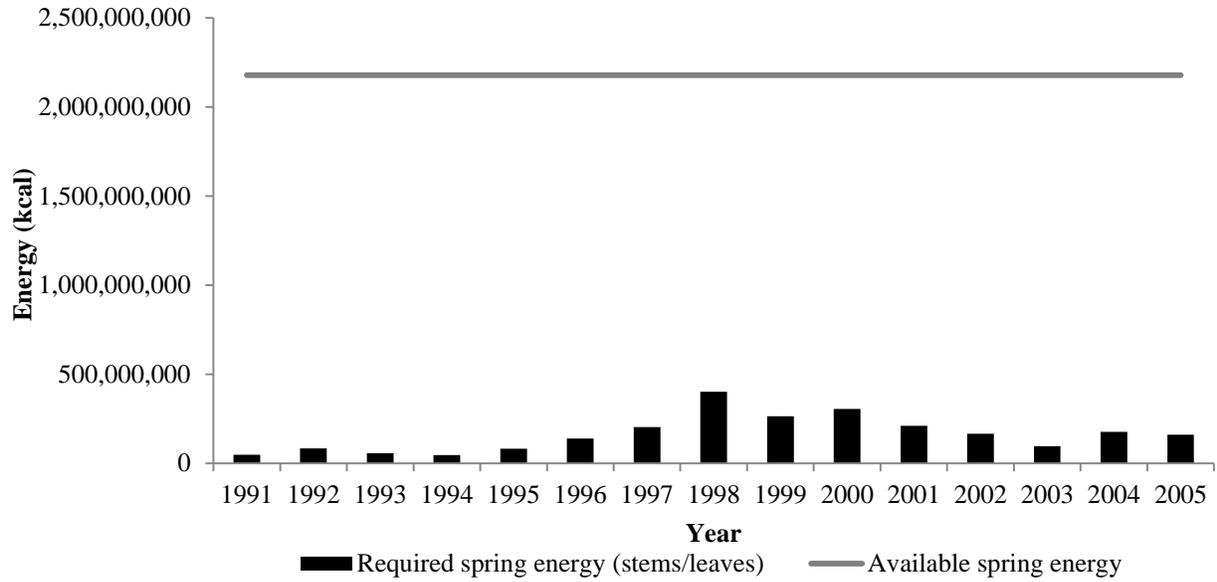


Figure 17. Available spring energy and the required energy from the stems/leaves of SAV within LPB (with Muskgrass).

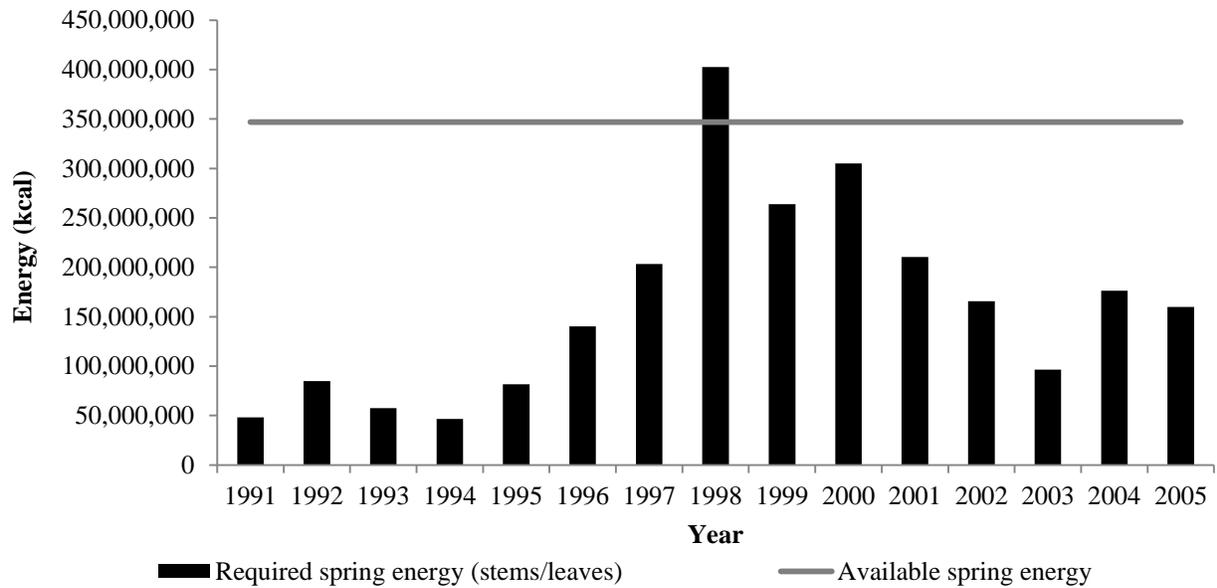


Figure 18. Available spring energy and the required energy from the stems/leaves of SAV within LPB (without Muskgrass).

4 Discussion

4.1 Long-term Changes

A diversity of fish and wildlife rely on SAV for food and cover in the Great Lakes region. The distribution and abundance of SAV, and consequently its availability to fish and wildlife, is a function of several environmental factors including light quantity, interspecific competition, nutrient availability, herbivory, ice and storm damage, fluctuating water levels, temperature and pH (Knapton and Petrie 1999, Petrie and Knapton 1999). However, Knapton and Petrie (1999) determined that the introduction of Dreissenid mussels to the Inner Bay in the early 1990s had the most pronounced recent influence on SAV. I initiated this study, in part, to assess the abundance and distribution of Dreissenid mussels and SAV in LPB to make comparisons to prior studies. Although the distribution of Dreissenid mussels in LPB has not changed since 1992, total abundance has decreased substantially. The increase in Dreissenid mussel abundance in the early-1990s resulted in increased water transparency and declines in all phytoplankton taxa and chlorophyll concentrations in Lake Erie (Holland 1993). The decline in particulate matter within the water column has likely contributed to the overall decline in Dreissenid mussels since 1992, because they feed on phytoplankton. Furthermore, predation by both fish and waterfowl also likely contributed to the decline in abundance of Dreissenid mussels (Mitchell 1995, Petrie and Knapton 1999). As predicted, I detected changes in the SAV community that are consistent with decreases in water clarity based on declining Dreissenid mussel abundance.

With the exception of slender pondweed, the 5 most abundant SAV species in LPB have experienced declines in abundance since 1992. Although this response was predicted for charophyte species in LPB (muskgrass), it contradicted the predicted increase in angiosperm species abundance expected with more eutrophic conditions. Carter and Rybicki (1986) determined that the resurgence of SAV within the tidal Potomac River could not be conclusively

attributed to either nutrient loading or water clarity. Because nutrient enrichment and light availability are interrelated, it is possible that a synergistic effect could better explain SAV growth within LPB. Although angiosperm SAV species are known to proliferate in eutrophic water (Smith 1979), it is possible that there is a point at which there is not enough light available to stimulate growth, regardless of nutrient availability. Inputs of nitrogen and phosphorus from fertilizer applications can result in declines of SAV and enhancement of phytoplankton growth (Twilley *et al.* 1985). Increased abundance of suspended particles in the water column decrease light availability for SAV and reductions in growth are often observed. As such, the decline in filter-feeding Dreissenid mussels in LPB and an associated increase in phytoplankton growth may have reduced light availability for SAV below a threshold that retards growth of these plants. My results suggest that SAV abundance is related to Dreissenid mussel densities within LPB, with increased SAV and mussels in the 1990s. Further, SAV abundance decreased along with a 96% decrease in mussel density between the mid-1990s and 2009.

Water depth and substrate type greatly influenced probability of detection for most species of SAV I observed in LPB. My models could be used to predict future changes in SAV communities in LPB, with decreasing water depth resulting from changes in climate and changes in sediment loading from Big Creek. Winter precipitation and run-off are predicted to decrease in the Great Lakes region, which would reduce spring run-off into LPB from Big Creek and water coming from other areas of the Great Lakes watershed (Steen *et al.*, 2006; Notaro *et al.*, 2014). Soil conservation practices aimed at reducing siltation in the Big Creek watershed coupled with decreased flood intensity and duration from spring snow melt may reduce development of mud substrate in LPB (Petrie 1998). My models predict that decreasing water levels would favor wild celery and possibly muskgrass, whereas Eurasian milfoil would decrease

in LPB. Shifts in substrate type are difficult to predict, but my models suggest that decreases in mud substrate would favor muskgrass relative to other SAV in LPB. Combined, decreased water levels and mud substrate would favor muskgrass over other SAV in LPB. Muskgrass, while eaten by waterfowl, is less preferred relative to pondweeds and wild celery (Bellrose 1980; Petrie 1998). Considering that 83% of the SAV community was musk grass in 2009, a scenario of increasing musk grass would decrease plant diversity and quality of foods available to waterfowl in LPB.

Further monitoring of SAV and Dreissenid mussels within LPB is necessary given the importance of SAV to migrating waterfowl, especially diving ducks and dabbling ducks that require an abundance of these plants to fuel migration (Petrie 1998, Baldassarree and Bolen 2006). Additionally, it would be beneficial for future studies to assess nutrient inputs and levels in LPB, because they influence SAV growth and were not analyzed as part of this study. Nutrient inputs also are important when considering substrate types in LPB. Big Creek flows into northwest LPB, an area that is covered with dense, diverse stands of SAV. The Big Creek delta is the only section of LPB that has a mud substrate, and this study shows the importance of this substrate type to a variety of plants. Sediment from Big Creek watershed is deposited in LPB as mud substrate and likely contributes substantially to turbidity, light attenuation, and nutrient loading in LPB. Further research on landscape change and these inputs into LPB is necessary to increase our ability to predict future changes to SAV in LPB. This study establishes a new baseline for SAV and Dreissenid mussel distribution and abundance which can be used to detect the ecological impacts of future invasive species introductions.

4.2 Energetic Carrying Capacity

Availability of food from SAV for waterfowl using LPB, particularly diving ducks, is at a maximum in the end of summer prior to autumn migration. In August, SAV typically reaches

maximum aboveground biomass and begins shifting resources to propagules by late-September (Rybicki and Landwehr 2007). Aboveground biomass senesces throughout the autumn, and is further depleted through foraging by waterfowl and other wildlife. Remaining biomass is available to spring migrating waterfowl after ice break-up, and was predicted to be potentially limiting to foraging carrying capacity for waterfowl during the spring migration period.

Consistent with my prediction, data suggest that food availability and thus energetic carrying capacity in LPB currently meets and exceeds the requirements of migrating waterfowl in both the autumn and spring seasons (Figures 15-18). Considering all species of SAV, there is a 10-fold surplus of energy in LPB. However, previous studies suggest that some species of SAV are avoided relative to their abundance. Specifically, in a study of waterfowl collected at LPB, it was found that only Redhead and American wigeon consume muskgrass consistently (Petrie 1998), whereas it only occurred in trace amounts in other species. I determined that muskgrass was > 80% of the plant community (dry weight) in autumn and spring, providing the majority of potential available energy. When I excluded muskgrass from my analysis, energy available and surplus were greatly reduced. Habitat managers should assess the utility of muskgrass for the species of fish and wildlife that use LPB and, if justified, consider methods to reduce its abundance while concurrently increasing availability of other SAV species to increase food availability for waterfowl.

Over the past 30-years, percentage of ice cover has decreased and length of open water periods has increased at the Great Lakes during winter (Assel 2003). Further, it is predicted that a greater frequency of no-ice conditions will continue to increase with increased warming during winter (Lofgren et al. 2002). I estimated potential increased foraging pressure if LPB was ice-free throughout winter using a 75-day winter period that traditionally excluded all waterfowl

from LPB. Decreased winter ice cover and associated increases in waterfowl foraging pressure has the potential to decrease availability of SAV during spring migration.

My estimates suggested a wide range of available winter DUDs using energy needs of waterfowl from 1990-2006 waterfowl surveys. In some years I detected an energy deficit in LPB, but the 16-year mean suggests that LPB could support slightly over 16,000 ducks each day for the 75 day wintering period without influencing availability of these plant foods for spring migrating waterfowl. In winter 2011-2012, an estimated 30,000 redheads and canvasback spent 60 days at and around LPB in open water areas (M. Schummer, personal observation), suggesting that recent trends in decreased ice cover during winter may currently have energetic implications for spring migrating waterfowl in the Great Lakes basin. Specifically, this would suggest that substantially less SAV biomass may be available to spring migrating waterfowl requiring fuel to reach their breeding grounds. I was only able to compare the requirements for wintering waterfowl with one year of availability data because my seasonal estimates are the only ones on record. Thus, I suggest caution when interpreting estimates, because greater energy needs of ducks (i.e., deficit years, Figure 18 – 1998) relative to availability suggest greater availability of SAV or other foods eaten by waterfowl. Indeed, variation in abundance and distribution of SAV is only quantified during 4 autumn periods (1976 – 2009) and I suggest that variation among years and understanding mechanisms for these changes would greatly improve our understanding of energetic carrying capacity of SAV in LPB. Further, the implication of a greater number of ice-free days and associated foraging pressure could also be assessed. I also suggest that waterfowl may shift to forage on muskgrass in years of greater foraging pressure or decreased availability of preferred SAV. If waterfowl shift to forage on muskgrass when other selected SAV plants decrease in abundance, there is substantially more food available in LPB

than was required by waterfowl that used LPB 1990–2006. Concurrently studying SAV and Dreissenid mussel availability with waterfowl diets would help refine my energetic carrying capacity estimates and our understanding of the potential influence of climate change on SAV and waterfowl in LPB. In addition to understanding annual SAV and foraging dynamics, using models that predict waterfowl migration based on weather severity to estimate how decreased ice coverage and increasing temperatures may increase use of LPB by waterfowl during winter (Schummer et al. 2010).

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