2011

Aquatic Plants in Lake Simcoe: Distribution, Environmental Controls and Utility as Ecological Indicators

Technical Progress Series in Lake Monitoring: Report No. 1

Lake Simcoe
Region
Conservation
Authority

Results of this research are also published:

Ginn, B.K. 2011. Distribution and limnological drivers of submerged aquatic plant communities in Lake Simcoe (Ontario, Canada): Utility of macrophytes as bioindicators of lake trophic status. Journal of Great Lakes Research 37: 83-89.

Lake Simcoe Region Conservation Authority. 2011. Aquatic plants in Lake Simcoe. LSRCA Newsletters in Lake Science No. 1.

This research was funded by Environment Canada's Lake Simcoe Clean-up Fund, Lake Simcoe Conservation Foundation, and the Lake Simcoe Region Conservation Authority with its municipal partners.

SUMMARY

Species composition, distribution, and biomass of submerged aquatic plants (or macrophytes) were studied in Lake Simcoe (Ontario, Canada) as was the use of aquatic plants as indicators of lake trophic status. While previous studies in this lake targeted eutrophic Cook's Bay, this study covered the entire lake area, identified other areas of high plant biomass, and recorded 16 macrophyte species; the community was dominated by *Ceratophyllum demersum* (39% of the total biomass), the invasive species *Myriophyllum spicatum* (27%), *Elodea canadensis* (11%) and *Chara* spp. (10%). Canonical correspondence analysis (CCA) identified four significant limnological variables related to plant biomass: (a) depth, likely a proxy for light levels; (b) substrate type, related to nutrient availability, stability, and wave exposure; (c) phosphorus loading from the closest tributary; and (d) subwatershed area. Since initial (1971) macrophyte surveys on Lake Simcoe, the community has been dramatically altered by expansion of an invasive species (i.e. *M. spicatum*) resulting in declines of native shallow-water species (particularly *Chara* spp.). The arrival of invasive zebra mussels (*Dreissenia polymorpha*) ~1995 and reductions in phosphorus loading have increased water clarity, extending the maximum depth of plant colonization (6.0 m in 1984 to 10.5 m in 2008), and almost tripled macrophyte biomass (1.2 kg · m^{-2} in 1984 to 3.1 kg · m^{-2} in 2008). Increased plant biomass, and a loss of species diversity, due to the spread of *M. spicatum* are interpreted by macrophyte indices as a decrease in lake ecological status, which likely explains why these indices did not follow recorded trends in reduced phosphorus loading.

RECOMMENDATIONS:

In order to monitor for changes in species distribution, maximum depth of colonization, and further develop the use of macrophytes as environmental indicators, it is recommended that limited surveys in target locations be carried out twice during the ice-free season in late spring (e.g. June) and autumn (e.g. late September) to capture both seasonal changes in species composition and plant biomass. A full survey of Lake Simcoe on the scale of this project should be carried out every five years to monitor for critical ecological changes in the aquatic plant community and future invasions by exotic plant species.

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INTRODUCTION

Lake Simcoe (44^{o}25'N, 79^{o}24'W) is a large (surface area 722 km^2; maximum depth 42 m; mean depth 15 m) currently mesotrophic (total phosphorus (TP) ~14 µg L^{-1}) lake in southern Ontario which has undergone environmental changes consistent with increased phosphorus (P) inputs due to human activites and has experienced a subsequent loss of coldwater fish habitat (Evans et al. 1996). While many studies have focused on the pelagic zone of this lake (e.g. Evans et al. 1996; Winter et al. 2007, 2011), the nearshore zone (0-20 m depth, covering 67% of the lake area) has been relatively ignored. Yet, it is the nearshore zone that exhibits the most visible effects of both aquatic and terrestrial environmental changes: zebra mussel (*Dreissenia polymorpha*) colonization; increased nutrient flow due to altered terrestrial surface run-off, removal of natural vegetative cover, and changes in land use; habitat loss resulting from shoreline hardening; dense patches of aquatic plants; loss of species diversity; and higher nutrient concentrations.

Development within the Lake Simcoe watershed was primarily agricultural until 1960-70's when urbanization rapidly increased. Currently, agricultural use dominates the watershed (47% of catchment area), urban areas and roadways occupy ~12%, and the remainder is highly fragmented natural cover (forests, wetlands, grasslands) (LSRCA 2008). Phosphorus (P) loading to Lake Simcoe increased from a model-estimated, pre-settlement (pre-1800), 32 t · y^{-1} (Nicholls 1997) to a peak 100 t · y^{-1} (Winter et al. 2011) ~1990 resulting in ecological changes consistent with cultural eutrophication (algal blooms, dense macrophyte biomass, hypoxic – anoxic bottom waters, etc.) and the concurrent recruitment failures for many coldwater fish species (lake trout, *Salvelinus namaycush*; lake whitefish, *Coregonus clupeaformis*; and lake herring, *Coregonus artedii*). Since 1990, mitigation efforts have reduced P-loading to ~72 t · y^{-1} (Winter et al. 2011), although this varies with annual precipitation. The Lake Simcoe Protection Plan (2009) has set a P-loading target of 44 t · y^{-1} for recovery to an ecologically sustainable state. One of the most significant environmental changes in Lake Simcoe was the ~1995 establishment of invasive zebra mussels (*D. polymorpha*) which, as in other locations and combined with P-reductions, have resulted in increased water clarity (Secchi depth: 1.0 – 4.5 m, 1972-1985; 2.5 – 8.0 m, 2000-2008) (Eimers et al. 2005, Winter et al. 2011) from removal of algae and suspended particles. Currently, Lake Simcoe is meso-eutrophic with offshore areas having a mean (2008) total phosphorus (TP) concentration of ~14 µg · L^{-1} (Winter et al. 2011), whereas nearshore areas have a higher mean TP ~ 21.9 µg · L^{-1} (range: 12.0 - 48.0 µg · L^{-1}).

While macrophytes are found in almost all lakes, and create an important habitat for fish and invertebrates (predominantly as feeding and nursery areas), they can rapidly increase in density and biomass under increased nutrient inputs (especially P); interfering with nutrient and biogeochemical cycling, water and sediment chemistry, dissolved oxygen concentrations, lake productivity, alter biological communities (e.g. fish, invertebrates, plankton, waterfowl), and recreational activities (Barko et al. 1986, Carpenter and Lodge 1986, Alexander et al. 2008), quickly reaching what lake users consider "nuisance levels" (see Chambers et al. 1999). As macrophyte biomass and species composition show quantifiable changes in response to lake trophic status, plants can dominate many lake habitats, and they can be surveyed at a relatively low cost, macrophytes can serve as an important indicator of environmental status; although this practice is more widely used in Europe than in North America (Palmer et al. 1992, Melzer 1999, Nichols et al. 2000). As bioindicators, macrophytes emphasize ecological conditions of the nearshore zone, which drives lake productivity, is heavily impacted by ecological degradation, and receives the most interaction / attention from lake users (Vadeboncoeur et al. 2002, Clayton and Edwards 2006). Macrophyte indices of ecological status often incorporate aspects such as trends in native and invasive plant species, trends in lake trophic status, nutrient levels, and water clarity (Thiebault et al. 2002, Schneider 2007). Given the importance of macrophytes to the entire lake ecosystem, management is an important issue and plants are often the most common environmental complaint received from lake users (Chambers et al. 1999).

In Lake Simcoe, previous studies on macrophytes (Millard and Veal 1971; Neil et al. 1985, 1991; Stantec 2007) have targeted Cook's Bay, and area with a high P loading (from agricultural and urban run-off), high macrophyte biomass, and large diurnal changes in hypolimnetic dissolved oxygen (1.3 mg · L^{-1} just before sunrise to 15.7 mg · L^{-1} in late afternoon)

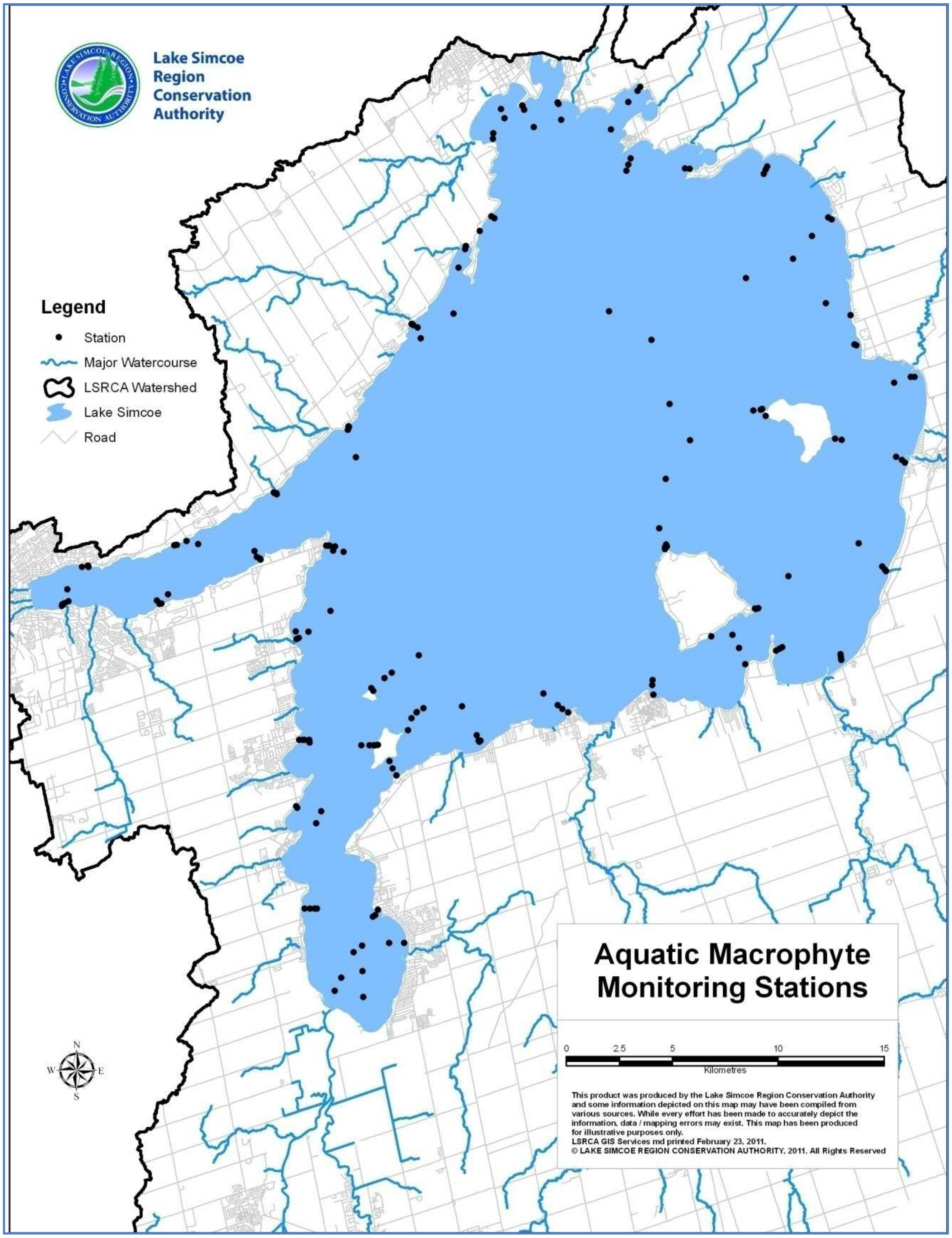
(Stantec 2007). Management concerns in this area are based on aesthetic complaints by owners of lakefront properties and the potential for plants to increase the release of sediment-bound P (see Stephen et al. 1997). Presumed increases in macrophyte biomass are likely related to increased water clarity, changes in P cycling (*cf.* Hecky et al. 2004) since the invasion of *D. polymorpha* (~1995), expansion of *M. spicatum* and other invasive species, and reductions in nutrient inputs (Winter et al. 2011).

The objectives of this study were to: examine long-term trends in macrophyte abundance and community composition in relation to trophic status and water clarity; test the utility of plants as bioindicators of lake trophic status; and present new baseline data for long-term monitoring, bioassessment, and management of Lake Simcoe.

METHODS

Sampling protocols

Submerged macrophytes were collected 17 September – 6 November 2008 from 43 transects situated perpendicular to the shoreline at 5 km intervals in Lake Simcoe (Figure 1). At each transect, five depths (1, 3, 5, 10, and 20 m) were sampled (a total of 215 sites, not all transects reached 20 m depth) using a Wildco® Lake Rake in shallow sites and a Wildco® Petite Ponar Grab in both shallow and deeper locations. As two different sampling strategies were employed, quality control efforts were taken to ensure a reasonable correlation ($r = 0.71$) between methods and redundancy in shallow sample sites. Areas sampled were normalized to 1 m^2 and the sampling protocol was selected to compare as closely as possible to the 2006 survey (Stantec 2007). At each site collected plants were placed in Ziploc® bags and kept on ice before being identified to species in the lab, weighed (wet weight biomass), dried at 105^{o}C for 24 hours in a gravity convection oven, and weighed again (dry weight biomass). Macrophyte data was expressed as percentage of total dry weight plant biomass except for comparison to previous studies which mostly relied on the less accurate wet weight biomass. Plants were identified using Newmaster et al. (1997), Crow and Hellquist (2000a, b), and Lui et al. (2008).



This product was produced by the Lake Simcoe Region Conservation Authority and some information depicted on this map may have been compiled from various sources. While every effort has been made to accurately depict the information, data / mapping errors may exist. This map has been produced for illustrative purposes only.
LSRCA GIS Services md printed February 23, 2011.

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Figure 1. Map showing the locations of 215 sample sites for aquatic plants in Lake Simcoe, September - November 2008.

Sixteen environmental variables were included in data analyses. Physical variables were: depth of sample site, substrate type (classed by particle size as silt/mud, sand, gravel, cobble, boulder, and hard substrates), surface area of catchment drained by inflow (subwatershed), and phosphorus loading of inflow (tributary). Water chemistry variables included were: water colour, specific conductance, dissolved inorganic carbon, dissolved organic carbon, total Kjeldahl nitrogen (TKN), pH, TP, turbidity, alkalinity, aluminium, and calcium. Other chemical variables (e.g. metals) were of very low levels, did not vary significantly between sites, and thus were not included in these analyses. Water chemistry analyses were carried out by Maxxam Analytics (Mississauga, Canada) which used the colourmetric technique for TP and inductively-coupled plasma mass spectrometry (ICP-MS) for metals. Latitude and longitude were included as variables to give a spatial aspect in the analyses.

Statistical analyses

Multivariate statistical techniques were used to determine the relationship between aquatic plant biomass and key limnological variables. Detrended correspondence analysis (DCA) was used to determine the species turnover (i.e. gradient length) in this dataset. Canonical correspondence analysis (CCA), a unimodal direct gradient analysis technique, was used to determine the main environmental variables that were related to aquatic plant species in these sites. In the CCA, forward selection was used to select the minimum number of environmental variables that significantly ($P < 0.05$) accounted for additional variation. Fifteen of sixteen environmental variables were log transformed prior to this analysis to normalize skewed data (pH was not transformed). DCA and CCA analyses were carried out using CANOCO for Windows (version 4.5) (Lepš and Šmilauer 2007). A GIS-based kriging technique was used solely to construct a map of plant biomass distribution (no analyses using kriging) using the Geostatistical Analyst extension of ArcGIS 9.3.1.

Macrophyte Indices

In order to give an applied aspect to our study, and test the utility of macrophytes as indicators of environmental status in Lake Simcoe, wet weight plant biomass data from this study (2008) was used with wet weight plant biomass data from previous studies: 1984 (Neil et al. 1985), 1987 (Neil et al. 1991), and 2006 (Stantec 2007). Three widely used macrophyte indices were calculated: Trophic Ranking Score (TRS) (Palmer et al. 1992), Aquatic Macrophyte Community Index (AMCI) (Nichols et al. 2000), and the Macrophyte Index (MI) (Melzer 1999). TRS values were calculated using the mean cumulative trophic ranking score assigned to each species observed at each sample site (see Palmer et al. 1992). AMCI values were calculated as directed in Nichols et al. (2000) with the sum of: maximum depth of plant colonization; percentage of sites containing plants; relative frequencies of submerged, ecologically sensitive, and exotic species; Simpson's Diversity Index, and total number of species observed. MI values were calculated by summing the products of a species' indicator group value multiplied by quantity of each species, then dividing the sum of species quantities (Melzer 1999).

PART I: COMMUNITY COMPOSITION AND ECOLOGY

Sixteen species were recorded in this study of submerged aquatic plants in Lake Simcoe (Table 1) with four species (Figure 2) comprising over 86% of the total biomass: *Ceratophyllum demersum* (39% of total biomass), the invasive species *Myriophyllum spicatum* (27%), *Elodea canadensis* (11%), and the green macro-alga *Chara* spp. (10%). In several cases (i.e. *Fontinalis* sp., *Myriophyllum sibiricum / verticillatum*) definitive species-level identification was not possible due to a lack of reproductive structures. While the community composition recorded was similar to records from previous studies (Millard and Veal 1971; Neil et al. 1985, 1991; Stantec 2007), some species with short life cycles, known to be present earlier in the season (e.g. *Potamogeton crispus*) were not recorded due to the autumn sampling strategy, used to capture total (or peak) plant biomass data, and the remote sampling methods (rake and grab sampling) which are less ideal than snorkelers or SCUBA (better for recording species with encrusting or low growth

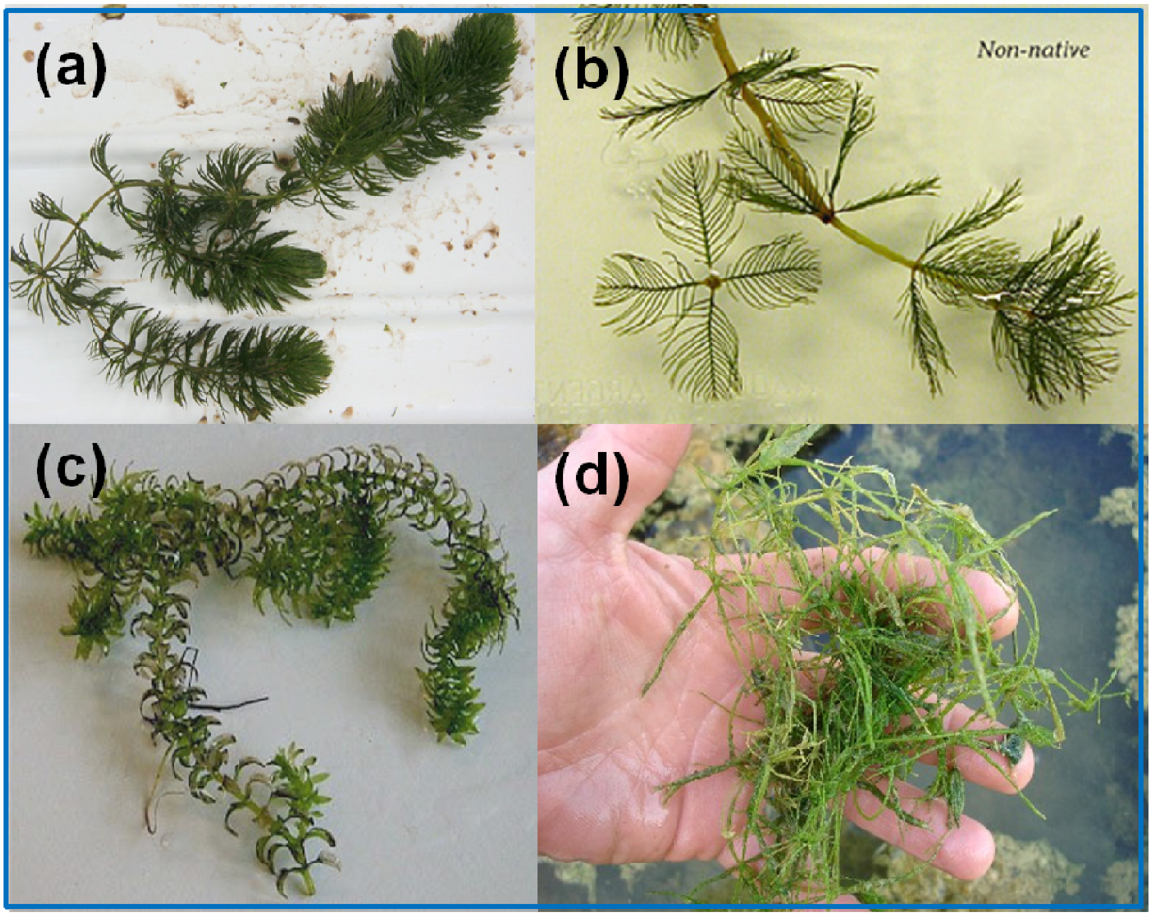

Figure 2. Photographs of the four most common aquatic plant species recorded (2008) in Lake Simcoe: (a) *Ceratophyllum demersum*, coontail (photo: Friends of Chorlton Meadows); (b) *Myriophyllum spicatum*, Eurasian watermilfoil (photo: Wisconsin Dept. Nat. Res.); (c) *Elodea canadensis*, common (or Canadian) waterweed (photo: Wisconsin Dept. Nat. Res.); (d) *Chara* spp., muskgrass (photo: Alabama Dept. Conserv. Nat. Res.)

Table 1. Submerged aquatic plant species recorded in Lake Simcoe with percentage of total macrophyte fall (September – November 2008) biomass.

Common Name	**Species scientific name**	**Percentage of total fall biomass**
Coontail (rigid hornwort)	*Ceratophyllum demersum*	39.1
Eurasian watermilfoil	*Myriophyllum spicatum*	27.4
Canadian (common) waterweed	*Elodea canadensis*	10.7
Muskgrass (skunkweed)	*Chara* spp.	9.7
Star duckweed	*Lemna trisulca*	6.3
Water stargrass	*Zosterella dubia*	4.1
Wild celery	*Vallisneria americana*	0.01
Flatstem pondweed	*Potamogeton zosteriformis*	0.01
Northern watermilfoil / whorled watermilfoil	*Myriophyllum sibiricum / verticillatum*	0.01
Slender naiad	*Najas flexilis*	0.001
Richardson’s pondweed	*Potamogeton richardsonii*	0.001
Horned pondweed	*Zannichellia palustris*	0.001
Sago pondweed	*Stuckenia pectinata*	0.001
Robbins’ spikerush	*Eleocharis robbinsii*	< 0.001
Aquatic moss	*Fontinalis* sp.	< 0.001
Broad-leaved (large leaf) pondweed	*Potamogeton amplifolius*	< 0.001

morphologies). The dominant species recorded (*C. demersum* and *M. spicatum*) are typical of eutrophic systems (Lacoul and Freedman 2006) and are often associated with *Lemna* spp. which, while only comprising 6.3% of the biomass in this study, is a floating macrophyte and recorded here as a “by-catch” of sampling; although it is frequently observed floating in large mats, especially in Cook’s Bay and the Holland River.

DCA results suggest macrophyte species changed across the limnological gradients included in this study and the gradient length (3.2 units of standard deviation, DCA λ axis-1 = 0.7) was sufficient to use unimodal direct gradient statistical methods. In this study CCA was used to determine the variation in species that could be ‘directly’ related to the measured environmental variables. In the CCA, forward selection determined four of the 16 environmental variables were significant: depth of sample site ($p = 0.001$), P load from tributary ($p = 0.003$), substrate type ($p = 0.01$), and subwatershed area ($p = 0.02$). Eigenvalues associated with the canonical axes are relatively high (λ axis-1 = 0.37; λ axis-2 = 0.13). It is not surprising that several of these significant variables are correlated as the amount of P exported from a subwatershed is related to the surface area of the subwatershed, and fine-grained substrates (e.g. mud or silt) are found in areas of higher sedimentation / P loading. The four significant limnological variables (depth, substrate type, phosphorus loading, and tributary drainage area) were similar to those reported by other studies (Chambers et al. 1999, Lacoul and Freeman 2006) and reflect well-studied attributes of aquatic plant ecology: depth likely incorporates water clarity or available light, which can govern plant distribution, depth of colonization, and depth of maximum biomass (Chambers and Kalff 1985, Istvánovics et al. 2008); substrate type would account for stability of attachment, nutrient availability, and shelter from wave action (Anderson and Kalff 1988, French and Chambers 1996); phosphorus loading and size of drainage area are evidence of potential nutrient availability and deposition of fine sediments near the shoreline, an ideal environment for a large biomass of canopy-forming macrophytes (Chambers and Kalff 1987).

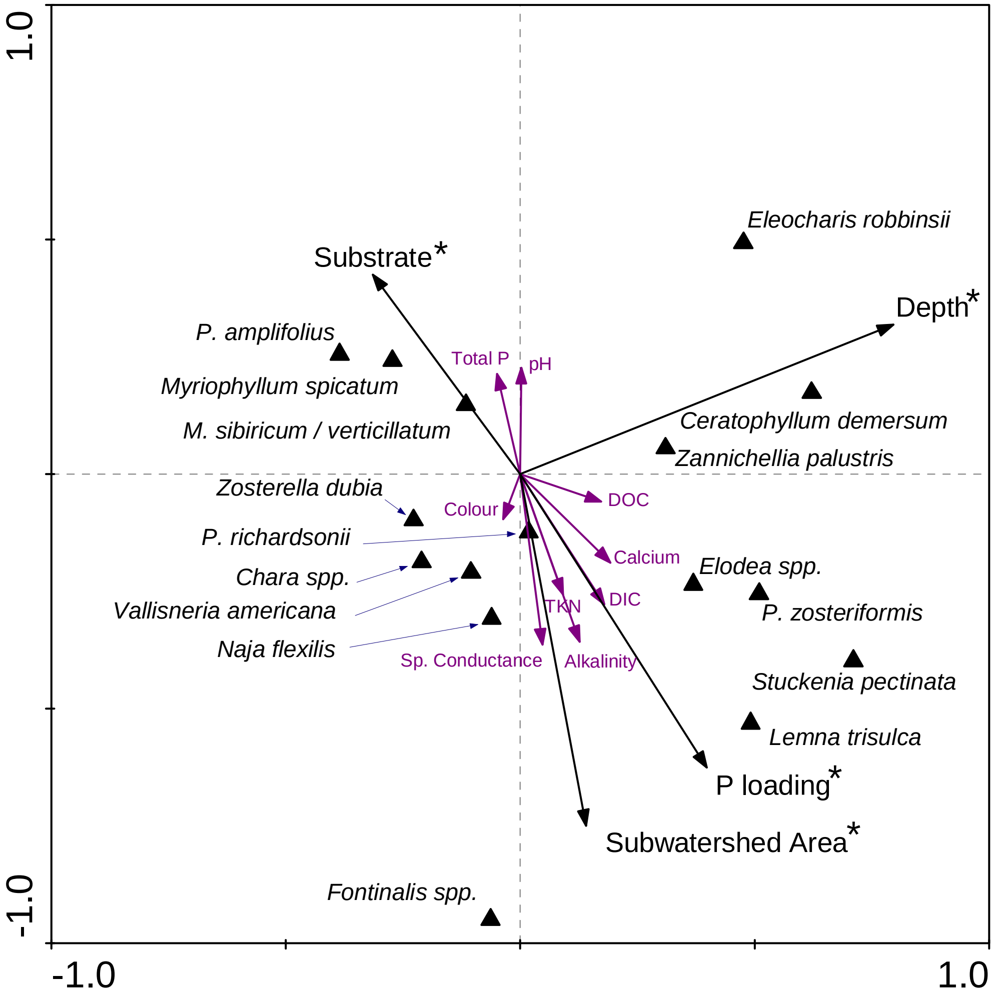

Figure 3. Canonical Correspondence Analysis (CCA) ordination showing distribution of 16 aquatic plant species (triangle symbols) recorded in Lake Simcoe in relation to environmental variables (indicated by black and purple arrows). Asterix (*) and black arrows identify the four statistically significant variables.

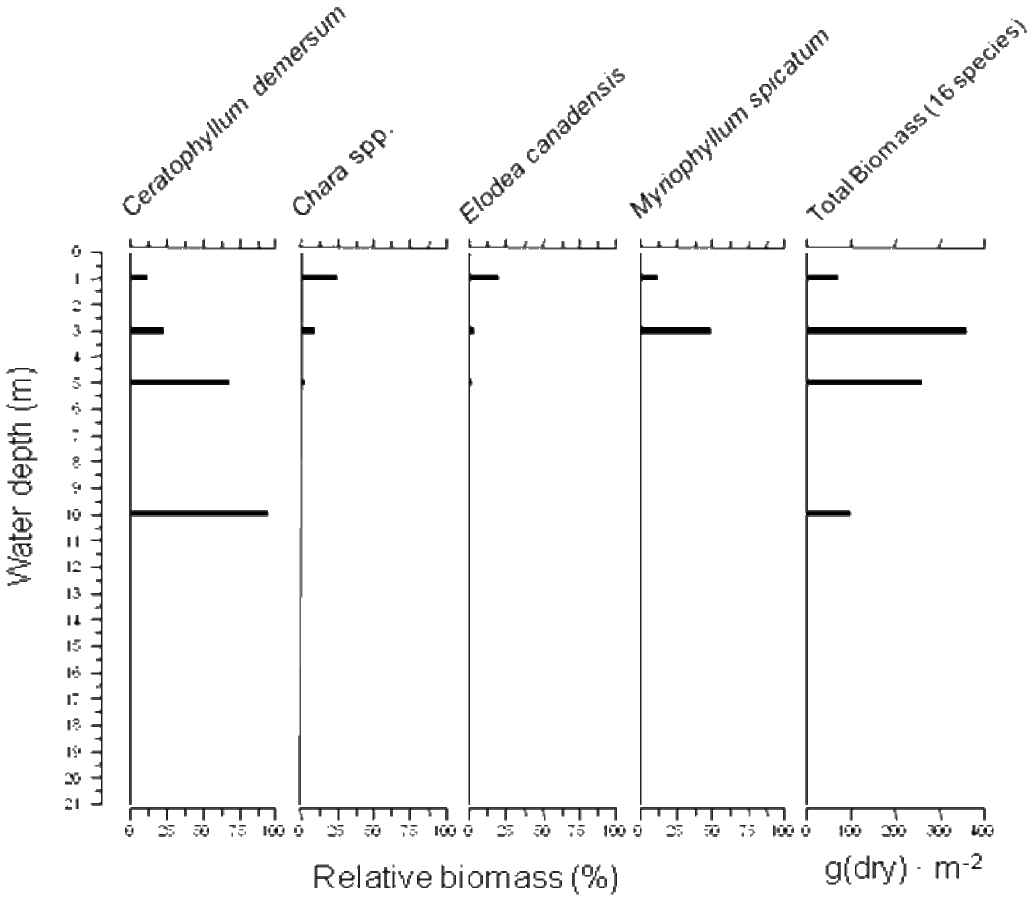

Figure 4. Frequency diagram showing change in relative abundance of four most common recorded aquatic plant species in Lake Simcoe, along with total aquatic plant biomass with respect to depth.

Distribution of aquatic plant species with respect to environmental variables (Figure 3) indicate *C. demersum* tends to occupy deeper sites and was dominant below ~ 3.5 m depth (Figure 4), whereas *M. spicatum* and *Chara* spp. were dominant at shallower (1 -3 m depth) sites (Figure 4). Currently in Lake Simcoe, shallow (e.g. < 3.5 m) depths are dominated by *M. spicatum* (silt substrates) or a combination of *M. spicatum* and *Chara* spp. (sand substrates), likely due to *M. spicatum*'s its high light requirement, high photosynthetic and growth rates, rapid dispersal through fragmentation, and ability to outcompete other shallow-water species by shading the substrate with thick canopies and quickly using sediment nutrients (Smith and Adams 1986; Madsen et al. 1991a, 1991b). Likely as a result of this high light requirement, *M. spicatum* is replaced at deeper sites (below ~3 m) in Lake Simcoe by *C. demersum*, a species more tolerant of lower light levels. No aquatic plants were recorded below a depth of 10.5 m – currently the 1% light level in Lake Simcoe is ~14 m.

PART II: MACROPHYTE DISTRIBUTION IN LAKE SIMCOE

In addition to describing the current Lake Simcoe macrophyte community and key limnological drivers, baselines for future monitoring studies (i.e. how will these plant communities change at 5-year intervals?) require information on locations of high plant biomass and populations of invasive species. Such information enables lake managers to evaluate restoration targets and focus their efforts on the most environmentally impacted areas. As such, the total (all species combined) biomass of macrophytes was plotted for each of the 215 sample sites in Lake Simcoe (Figure 5), identified by contour lines of mean total biomass, and a gradient of green colour. Southern areas of Cook's Bay (outlet of the East and West Holland rivers) had the highest plant biomass (mean: 1118.5 g(dry) $\cdot$ m^{-2}; range: 45.1 – 11262.7 g(dry) $\cdot$ m^{-2}), followed by northern Cook's Bay (mean: 307.0 g(dry) $\cdot$ m^{-2}; range: 21.4 – 2304.3 g(dry) $\cdot$ m^{-2}).

Previous studies of aquatic plants in Lake Simcoe were limited to Cook's Bay (Neil et al. 1985, 1991; Stantec 2007), which has the highest nutrient loading (combined annual P-loading 16,923 kg $\cdot$ y^{-1}), sheltered location, and silt substrates. This study, for the first time, recorded other areas of high plant biomass: south of Georgina Island at the outlet of the Black River (50.0

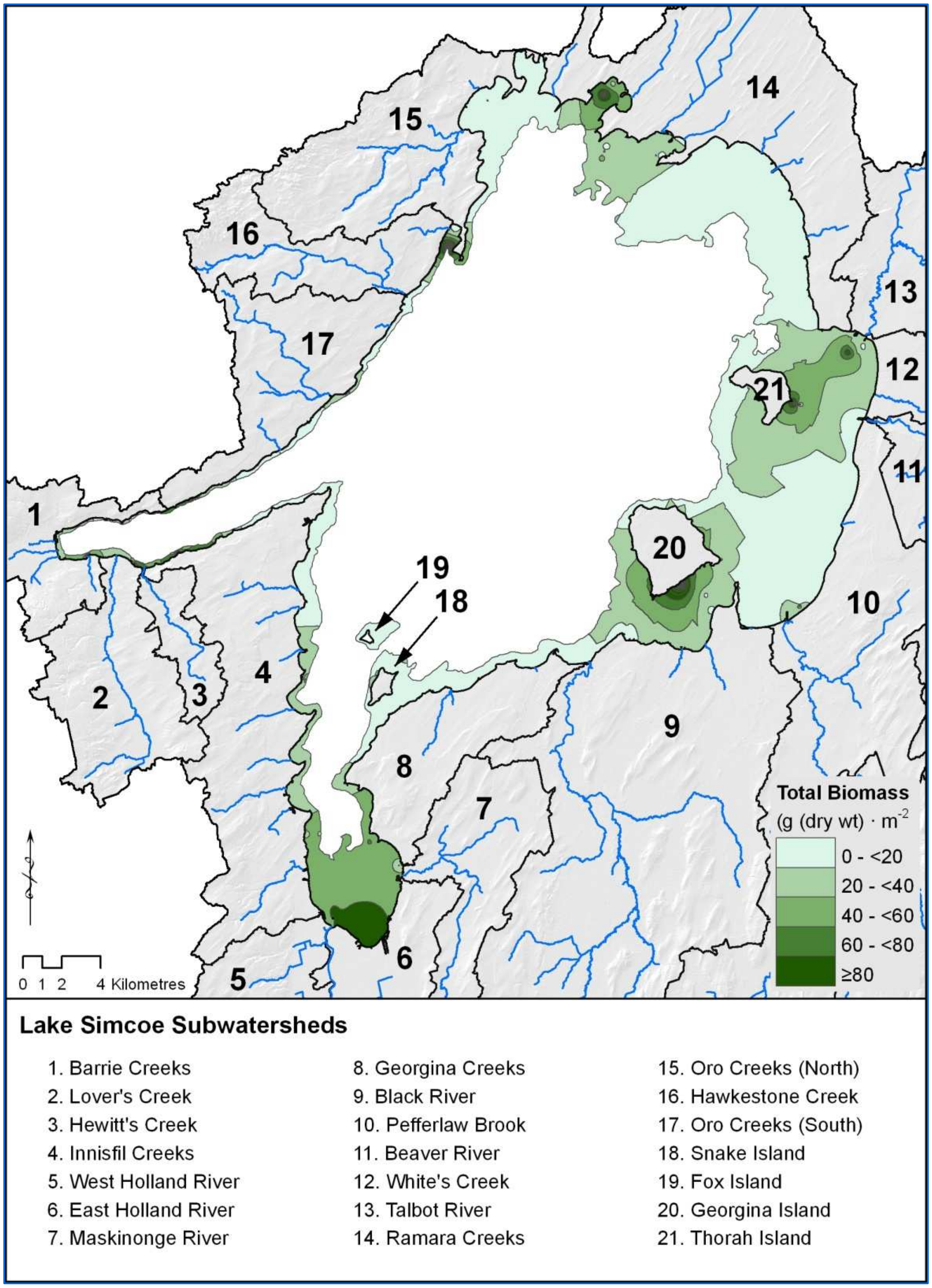

Figure 5. Map showing mean biomass (g (dry wt) · m^{-2}) of submerged aquatic plants in Lake Simcoe, Fall 2008. Subwatersheds (tributaries) are identified by numbers.

Table 2. Surface area and mean annual phosphorus load (2004-2007) from tributaries entering Lake Simcoe (data courtesy of E. O'Connor and J. Winter, unpublished). Numbers (1 – 21) refer to tributary / subwatersheds labeled on Figure 5.

	Tributary	Surface Area (km^2)	Phosphorus Export ($kg \cdot yr^{-1}$)
1	Barrie Creeks	37.5	8059
2	Lover's Creek	60.0	813
3	Hewitt's Creek	17.5	398
4	Innisfil Creeks	107.2	3760
5	West Holland River	351.9	7917
6	East Holland River	247.2	9006
7	Maskinonge River	63.5	1118
8	Georgina Creeks	49.3	2477
9	Black River	375.4	4428
10	Pefferlaw Brook	446.2	3550
11	Beaver River	327.2	3293
12	White's Creek	105.0	1075
13	Talbot River	367.8	2091
14	Ramara Creeks	143.5	1931
15	Oro Creeks (North)	75.3	4261
16	Hawkestone Creek	47.8	505
17	Oro Creeks (South)	57.4	1061
18	Snake Island	1.4	9
19	Fox Island	0.2	1
20	Georgina Island	12.9	86
21	Thorah Island	4.4	45

g(dry) · m^{-2}; range: 2.7 – 274.6 g(dry) · m^{-2}), at the outlet of the Talbot River (44.2 g(dry) · m^{-2}; range: 10.9 – 154.0 g(dry) · m^{-2}), the Ramara shoreline, particularly at McPhee Bay (60.0 g(dry) · m^{-2}; range: 20.1 – 174.8 g(dry) · m^{-2}), the Oro shoreline at Carhew Bay (88.3 g(dry) · m^{-2}; range: 4.4 – 247.6 g(dry) · m^{-2}), and at Barrie near Minet's Point (mean = 77.7 g(dry) · m^{-2}; range: 25.8 – 319.3 g (dry) · m^{-2}) (Figure 5). No plants were recorded below a depth of 10.5 m (white area on Figure 5). All areas of high macrophyte biomass correspond to sheltered shorelines with soft substrates (silt, mud, or sand) and high P exports from tributaries which drain the largest or most urbanized subwatersheds (Table 2).

Most of Lake Simcoe's sediments have a very high TP load (mean 855 µg · g^{-1}; range 875-1400 µg · g^{-1}), but high macrophyte biomass correspond to areas of reduced sediment TP (e.g. ~340 µg · g^{-1} in southern Cook's Bay) likely indicating high P uptake by plants. Carignan and Kalff (1980) concluded macrophytes obtain ~75% of their nutrient requirements from sediments. Other locations of relatively high plant biomass, although with recorded values greatly lower than Cook's Bay, correspond to P inputs from rivers (Black, Pefferlaw, Talbot), increased surface run- off from land clearance and development (Ramara and Oro shorelines), or urban run-off and outputs from water pollution control facilities (Barrie).

PART III: HISTORICAL CHANGES IN COOK'S BAY

In order to track temporal changes to the submerged macrophyte community, the results of the current study from Cook's Bay were compared with previous investigations from 1971 (Millard and Veal 1971); 1984, which include the first biomass records of *M. spicatum* in Lake Simcoe (Neil et al. 1985); 1987 (Neil et al. 1991); and 2006 (Stantec 2007). Unfortunately the initial plant survey on Lake Simcoe (Millard and Veal 1971) did not contain biomass data, instead using "density classifications" (e.g. heavy, moderate, or scattered growth based on estimated areal coverage) so direct comparison was not possible. However, the authors do describe southern Cook's Bay as having up to 80% areal coverage by plants with other "abundant" to "heavy" areas being Barrie (up to 80%) and the Ramara and Oro shorelines (up to 51.4 % cover)

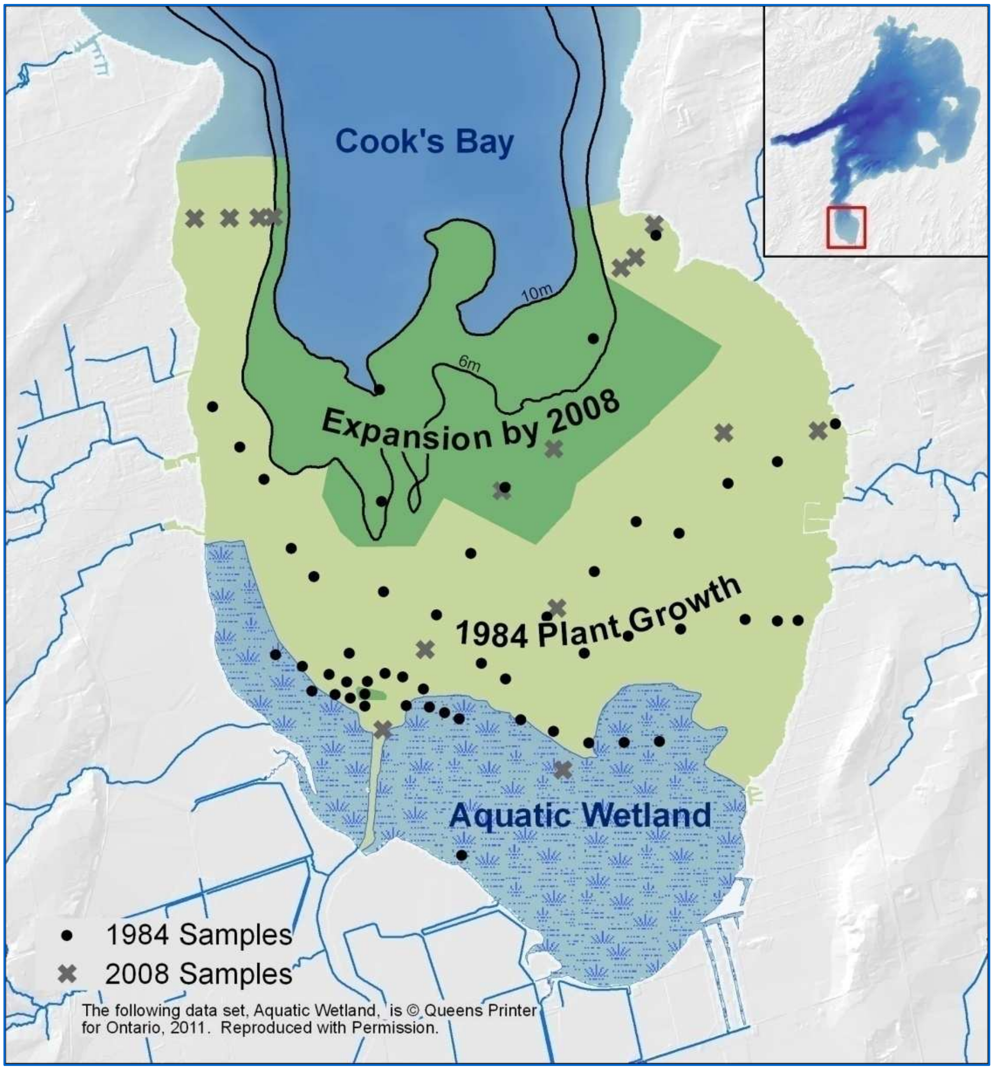

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Figure 6. Map comparing aquatic plant coverage in Cook's Bay (Lake Simcoe) between the 1984 (Neil et al. 1985) and 2008 studies.

Table 3. Comparsion of aquatic plant studies in Cook's Bay, Lake Simcoe for 1984 (Neil et al. 1985), 1987 (Neil et al. 1991), 2006 (Stantec 2007), and 2008 (current study).

Variable	**1984**	**1987**	**2006**	**2008**
Total Number of Species	11	14	14	13
Maximum depth of plants (m)	6.0	6.0	8.5	10.5
Maximum wet weight (kg (wet) · m^{-2})	1.2	2.4	1.4	3.1
% of sites with:				
Myriophyllum spicatum	11.9	40.5	39.4	60.7
Chara spp.	69.0	52.4	29.4	32.1
Ceratophyllum demersum	38.1	42.9	68.8	85.7

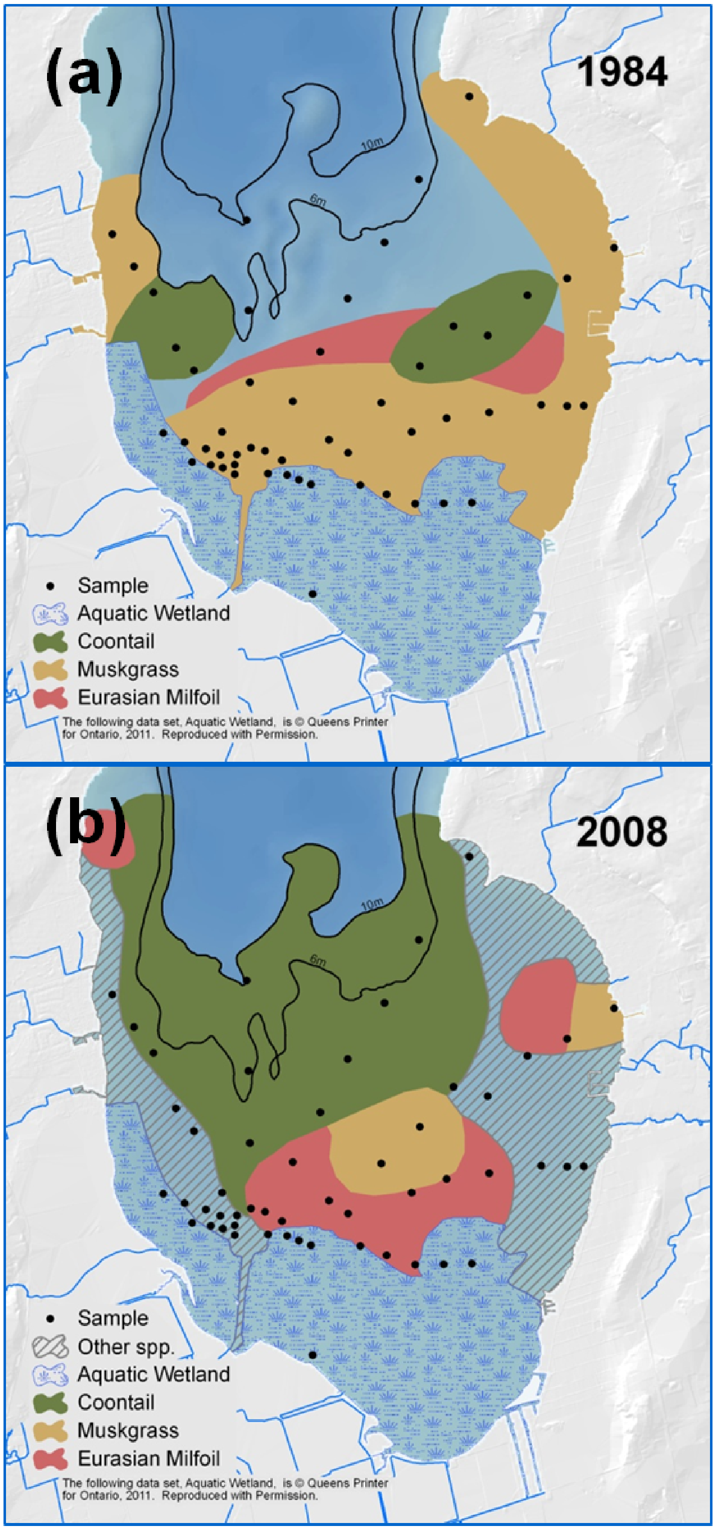

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Figure 7. Map comparing the distribution of most common plant species in Cook’s Bay (Lake Simcoe) between (a) 1984 (modified after Neil et al. 1985) and (b) 2008. Note that in 2008, the “Other spp.” designation represents co-dominance of habitat by *M. spicatum* and *V. americana*.

near the outflow of the lake at Atherley Narrows, sites which correspond to current (2008) areas of high plant biomass.

Since 1984, the maximum depth of colonization has increased from 6.5 m to a current 10.5 m (Figure 6, Table 3), resulting in a large increase in potential habitat, demonstrated by a doubling in areal coverage by macrophytes (9.5 km^2 in 1984 to 18.1 km^2 in 2008) (Depew et al. 2011). Mean wet weight biomass has also increased from 1.2 kg · m^{-2} (1984) to 3.1 kg · m^{-2} (2008) (Table 3). The 1984 data reports *Chara* spp. was the dominant shallow-water species (Figure 7a, Table 3) and *C. demersum* in deeper waters (below 3.7 m depth). *M. spicatum* was recorded in only 5 samples from a small area on the eastern side of the Cook's Bay (Figure 7a). By 2008 (Figure 7b), *Chara* sp., has been displaced and is dominant only in a small, sand substrate, shallow water area of northern Cook's Bay. The invasive species *M. spicatum* is currently the dominant shallow-water species in the southern, mud and silt substrate, sites. Large areas of *M. spicatum* and *V. americana* are co-dominant in much of the former *Chara* spp. habitat. *C. demersum*, in both 1984 and 2008, occupied the deeper habitats, and has expanded its area of colonization, likely due to an increased depth of colonization compared to 1984.

The information gained from this current study, when compared to previous studies, allows key management questions in macrophyte ecology to be addressed, such as long-term trends in the community related to lake trophic status and the potential to use macrophytes as bioindicators of environmental change. Comparison of this study with previous investigations record southern Cook's Bay as highest in plant biomass, but over 25-year period, *M. spicatum* had expanded (1984 mean: 44.5 g (wet) · m^{-2}; 2008 mean: 272.5 g (wet) · m^{-2}) mainly, as in other areas (see Madsen et al. 1991b), at the expense of other shallow water species, particularly *Chara* spp. (1984 mean: 123.3 g (wet) · m^{-2}; 2008 mean: 7.9 g (wet) · m^{-2}). Changing environmental conditions since 1984 have also resulted in increased biomass of other species common in eutrophic lakes (e.g. *C. demersum*, *Vallisneria americana*, *E. canadensis*). These macrophyte increases have likely resulted from increased water clarity due to P-loading reductions (Winter et al. 2011) and removal of algae and suspended particles by dreissenid filtering capacity (Evans et al. 2011), changes which are observed in other lakes across the Laurentian – Great Lakes Region (Skubinna et al. 1995, Zhu et al. 2006). Evidence of increased water clarity and light penetration, allowing an increase in potential habitat for macrophyte colonization is demonstrated by a large increase in Secchi depth. In 1972-1985 (pre-dreissenid invasion, P-loading ~100 t · y^{-1}) Secchi depth was 1.0 – 3.5 m in Cook's Bay, 1.8 – 4.5 m in other areas of the lake (Eimers et al. 2005). Currently (2008 – 2011), with reduced P-loading and dreissenid populations, the Secchi depth is 2.5 – 5.7 m in Cook's Bay and 6.3 – 8.0 m in other areas (B.K. Ginn, unpublished). Current Secchi depths are similar to records of 7.0 m from 1926 (Rawson 1928).

PART IV: UTILITY OF MACROPHYTE INDICES OF LAKE TROPHIC STATUS

In order to assess the applicability of macrophytes as indicators of lake trophic status, and more fully compare environmental trends for a lake management perspective, biomass data from three previous studies 1984 (Neil et al. 1985), 1987 (Neil et al. 1991), and 2006 (Stantec 2007) were used with the current (2008) data to determine index values from three macrophyte indices: the Trophic Ranking Score (TRS) developed by Palmer et al. (1992) for British waters; the Macrophyte Index (MI) for Europe (Melzer 1999); and the Aquatic Macrophyte Community Index (AMCI) for Wisconsin, USA lakes (Nichols et al. 2000). In addition, the scores were compared to measured TP and Secchi depth values to test the accuracy of index scores calculated. In general, all three models failed to capture recorded trends in either phosphorus concentration or water clarity (Table 4), but there may be several reasons for this inaccuracy that may enable future use of plants as biological indicators.

The AMCI was the only model developed for North American species and was also the most comprehensive, accounting for: maximum plant depth; percentage of sites vegetated; frequency of submerged, sensitive, and invasive species, and included the Simpson Diversity Index. While it was the only index to include all 16 species recorded by this study, and account for macrophyte biomass and influence of invasive species, it poorly followed the trend in water column TP through time (*r* = -0.66) but was more accurate with water clarity (*r* = 0.58). Rather

Table 4. Comparison of recorded mean annual total phosphorus (TP), mean annual Secchi depth, and three macrophytes indices: Trophic Ranking Score, or TRS (Palmer et al. 1992); Macrophyte Index, MI (Melzer 1999), and Aquatic Macrophyte Community Index, AMCI (Nichols et al. 2000) for Cook's Bay (Lake Simcoe) calculated using data from surveys in 1984 (Neil et al. 1985), 1987 (Neil et al. 1991), 2006 (Stantec 2007), and 2008 (current study).

	TP **($\mu g \cdot L^{-1}$)**	**Secchi** **(m)**	**TRS**	**MI**	**AMCI**
1984	23.4	2.2	9.03	2.90	42
1987	15.7	2.6	8.58	3.36	43
2006	22.6	4.3	9.25	3.01	43
2008	16.4	3.8	8.76	4.07	45
Scale			1 – 10	1 – 5	7 – 70
"Good" value			1	1	7
"Poor" value			10	5	70

than following the trends in distinct limnological variables, AMCI likely takes into account the overall impacts of plants to environmental status, diversity of the macrophyte community, and the impacts of exotic species. AMCI records increases of invasive *M. spicatum* biomass (such as in Cook's Bay) and the loss of native species and diversity as a decline in ecological status (Nichols et al. 2000).

The MI model also performed poorly for reconstructing water column TP (r = -0.79) but most closely followed the trend in clarity (r = 0.95). In fact, MI inferred a change from "low" nutrient enrichment in 1984 to "massive" nutrient enrichment in 2008 (Melzer 1999), an opposite trend from measured TP. MI may be responding to relatively high nearshore phosphorus concentrations (up to 48 $\mu g \cdot L^{-1}$). While MI, like AMCI, does account for changes in macrophyte biomass, it is based on 45 European species lumped into nine subjective indicator groups, does not account for exotic species (*M. spicatum* is indicative of high nutrients but is native to European waters) and ignores some prominent species in the Lake Simcoe community (e.g. *Vallisneria americana* and *Zosterella dubia*).

The TRS model performed best of the three tested in terms of water column TP (r = 0.91) and reasonably well for water clarity (r = 0.41). The adequate performance of this model may be linked to its simplicity as it relies on species presence or absence (not accounting for biomass) combines species into four broad trophic categories, and the final index is a mean of individual species trophic scores.

The unreliability of these macrophyte indices as environmental indicators in Lake Simcoe is likely related to macrophyte biomass and diversity being driven by non-nutrient variables (e.g. depth, wave exposure, substrate stability) (suggested by Thiebault et al. 2002), and the dramatic ecosystem changes (increased water clarity and decreased TP) following the establishment of *D. polymorpha* ~1995 (which have a high filtering rate and very effective suspended particle removal efficiency), as well as concurrent P-loading reductions as part of lake management strategies. In addition, it should be noted that macrophytes obtain most of their phosphorus from sediments. In Cook's Bay, a previous study of sediment phosphorus (Johnson and Nicholls 1989) report sediment TP ~ 1040 µg · g^{-1} compared with a (2008) mean value of 518 µg · g^{-1} (~300 µg · g^{-1} in area of highest plant biomass in southern Cook's Bay). This reduced sediment TP is likely the result of macrophyte biomass increases between studies.

OVERVIEW ECOLOGICAL PROCESSES AFFECTING MACROPHYTES

In Lake Simcoe, the distribution of the plant community was driven by several key environmental variables (Figure 8). Available light and the increase in transmission through the water column due to increased water clarity following zebra mussel (*D. polymorpha*) invasion enables plants to grow deeper, thus providing more habitat for expansion and increases in plant biomass. These changes in water clarity point to two regime shifts in Lake Simcoe as a lake with high water clarity (7.0 m Secchi depth in 1926) (Rawson 1928) changed to the alternative ecological state of an algal-dominated, turbid lake due to increasing P-loading by the 1970-80's (Secchi depth 1.0 – 4.5 m) (Eimers et al. 2005). With P-reduction and invasive dreissenids resulting in less algae and suspended particles in the water column, the lake shifted to a dreissenid-supported clearwater state which enabled increases in macrophyte depth of colonization and areal coverage, similar to that observed in other nutrient-rich lakes in the Laurentian Great Lakes Region with significant dreissenid populations (Scheffer et al. 1993, Zhu et al. 2006, Scheffer and Jeppesen 2007).

In terms of substrate, plants are typically found on mud or silt substrates which hold large amounts of bioavailable P, enable stable attachment for shallow water species (e.g. *M. spicatum*) and are found in locations sheltered from wind and wave exposure. Sand and shell substrates are found in slightly more exposed locations and have lower macrophyte biomass due to wind and waves which can fragment large branching forms (*M. spicatum*), substrate movement provides less stability for attachment, and less P is contained in sediment. Cobble, boulder, and hard substrates have the least plant biomass due to little attachment (except my aquatic moss) and have the highest amount of physical exposure.

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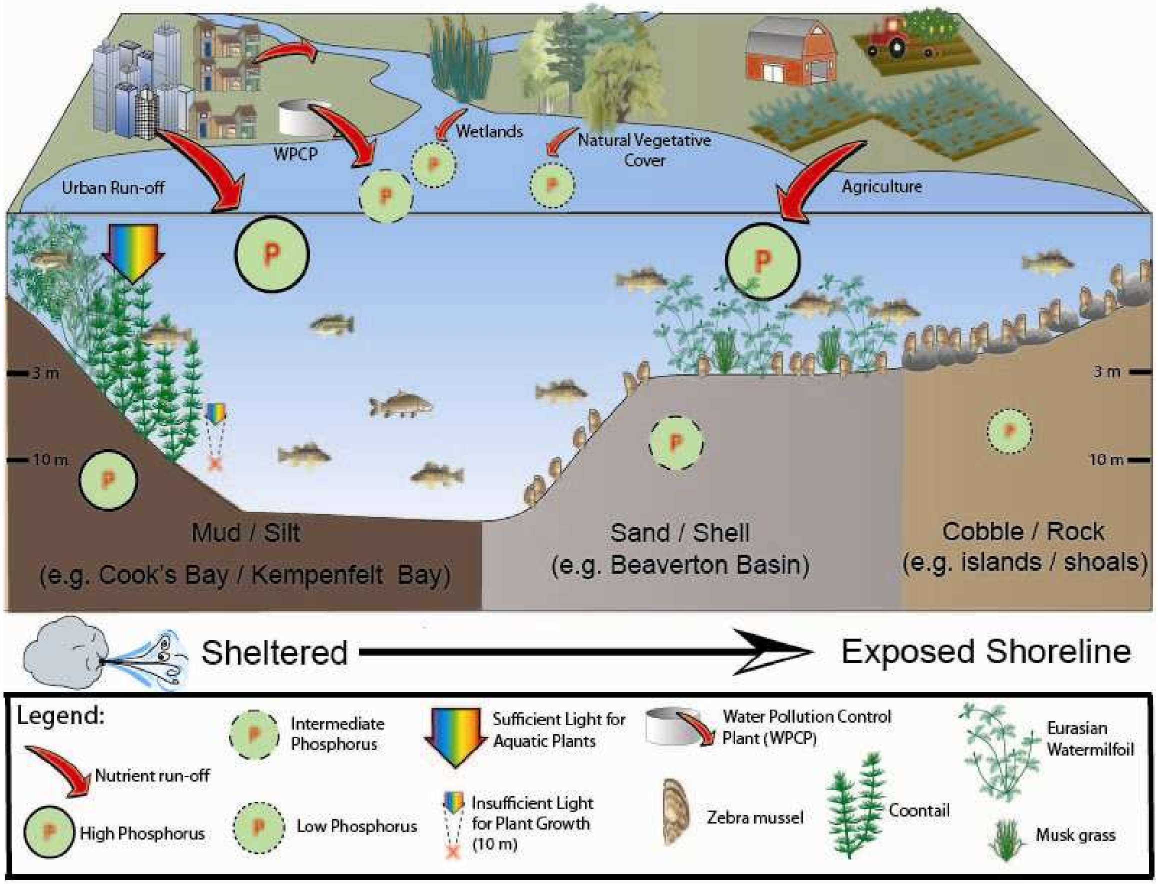

Figure 8. Conceptual diagram illustrating how aquatic plant distribution in Lake Simcoe is connected to phosphorus inputs, substrate type, available light, as well as amount of wind and wave exposure.

Phosphorus loading and subwatershed size have a role in influencing plant biomass in the larger subwatershed typically have a higher percentage of cleared land (i.e. less natural vegetative cover) and allow the release of P into receiving waters. Wetland and natural vegetation typically retain nutrient-rich runoff, whereas hard surfaces (urban areas), cleared terrain (agriculture, construction, and quarries) facilitate surface run-off or the uptake and deposition of nutrient-rich dust. In addition, P from offshore areas are pulled inshore by dreissenid beds resulting the deposition of P-rich flocs in shallow areas with soft substrates

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This investigation of macrophyte community changes in a nutrient-rich, dreissenid colonized lake presents an examination of long-term trends in macrophyte abundance and community composition. Despite modest nutrient reductions, the increase in water clarity and a high loading of sediment-phosphorus presents an environment which can support a large increase in macrophyte biomass. In such cases, likely repeated in nutrient-rich lakes across the Laurentian Great Lakes Region, macrophytes may not be sufficient bioindicators of trophic status as they receive up to 72 % of their phosphorus requirements from sediment and as such changing environmental conditions are not reflected in common plant-based index values. Macrophytes are, however, an important and often criticized aspect of an aquatic ecosystem and baseline data collected in studies such as this are vital to monitoring the progress of lake management plans (e.g. the Lake Simcoe Protection Plan) for recovery to sustainable states.

RECOMMENDATIONS

In order to assess the environmental impact of macrophytes in Lake Simcoe, and assess critical changes, a monitoring program should include the following records: change in maximum depth of colonization, changes in sediment nutrient concentrations, increases in plant abundance / biomass, critical shifts in plant distribution and species composition of the community. A full survey of Lake Simcoe should be undertaken at five-year intervals with a sampling strategy to target depth changes and expansion of habitat area, as well as introduction and changing role of invasive species. In addition, seasonal sampling should be carried out a five key areas across

Lake Simcoe to account for seasonal /annual changes in biomass, species composition, and invasive species.

ACKNOWLEDGEMENTS

I wish to thank those who have assisted in carrying out this project: T. French, E. O’Connor, and B. Longstaff for their helpful and insightful comments; the assistance of L. Bennett, D. Lembcke, and R. Wilson with field sampling; and D. Campbell and M. Dennis with kriging analysis for maps. This project was funded by Environment Canada’s Lake Simcoe Clean-up Fund with contributions from the Lake Simcoe Region Conservation Authority, it’s municipal partners, as well as the Lake Simcoe Conservation Foundation and it’s donors.

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