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Quantification of Historical Changes of Submerged Aquatic Vegetation Cover in Two Bays of Lake Ontario with Three Complementary Methods

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ABSTRACT. *Submerged aquatic vegetation (SAV) distribution and coverage were quantified in two bays of Lake Ontario in 1972, 1980 (1982), and 1999–2002, using a combination of aerial photograph interpretation (API), hydroacoustics, and rake sampling. The three methods gave similar estimates of SAV presence in 2002, supporting our use of API for quantifying SAV changes across decades in bays of a large lake. The SAV coverage in Sodus Bay increased by 5% between 1972 and 1980 and by 35% between 1980 and 1999–2002 whereas the maximum depth of SAV colonization extended from 5.5 to 6.4 m during this period. In Chaumont Bay, the SAV coverage tripled while its maximum depth of occurrence increased from 5.1 to 6.1 m from 1982 to 2002. Although the difference in SAV coverage between 1972 and 1980 was not larger than the difference between consecutive years in the 2000s, the large increase in SAV coverage between the 1980s and 2000s represents a major ecosystem change in these bays. This change was likely caused by increased water clarity in Lake Ontario, which could be associated with the implementation of the Great Lakes Water Quality Agreement (GLWQA) and the dreissenid mussel invasion. Although other factors such as water level, wave exposure, bottom slope, and sediment nutrients may be important, they have not changed in a fashion that would predict local increases of SAV coverage.*

INDEX WORDS: *Submerged aquatic vegetation (SAV), dreissenid mussels, aerial photograph interpretation (API), hydroacoustics, rake sampling, water clarity, Lake Ontario.*

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INTRODUCTION

Submerged macrophytes represent the major component of submerged aquatic vegetation (SAV) in aquatic ecosystems and help shape the physical and chemical environment, as well as the biota (Jeppesen *et al.* 1998, Genkai-Kato and Carpenter 2005). For example, SAV affects nutrient dynamics, light extinction, temperature regimes, hydrodynamic cycles, and substrate characteristics as well as other primary producers including epiphytic and epipelic algae (Jeppesen *et al.* 1998, Rooney *et al.* 2003). Extensive SAV coverage in lake ecosystems also affects benthic and pelagic food web dynamics that may have cascading effects throughout the system (Scheffer *et al.* 2001). Therefore, quantifying SAV coverage and understanding how it responds to changes in environmental variables is critical to understanding ecosystem and food web responses to environmental change. In this study, we quantify historical changes in SAV coverage in coastal ecosystems of Lake Ontario using three complementary methods and we examine potential reasons for the observed changes. The methods that we present will also enable other researchers and managers to utilize existing images and data to evaluate similar habitat assessment questions elsewhere.

Past studies have revealed that the maximum depth of colonization of submerged macrophytes is strongly linked to water clarity (Chambers and Kalff 1985, Hudon *et al.* 2000, Zhu *et al.* 2006). Thus, any increase in light penetration is likely to promote SAV expansion to deeper waters (Karatayev *et al.* 2002, Lammens *et al.* 2004). Water clarity in the Great Lakes region declined with the onset of cultural eutrophication in the 1950s (e.g., Beeton 1965). In response, the Great Lakes Water Quality Agreement (GLWQA) between the United States and Canada was enacted in 1972 and led to decreased nutrient loadings and a general improvement in water transparency in Lake Ontario (Millard *et al.* 2003). In addition, the unintended introduction of filter-feeding dreissenid mussels (the zebra mussel, *Dreissena polymorpha* and the quagga mussel, *D. bugensis*) also contributed to improvement of water clarity (Mills *et al.* 1994, Zhu *et al.* 2006). The resulting increased light penetration is a key change that can affect ecosystem structure and function across entire lakes (see review by Vanderploeg *et al.* 2002).

It is expected that the increased water clarity will lead to increased coverage of SAV and corresponding ecosystem change in invaded lakes (Karatayev *et al.* 2002, Lammens *et al.* 2004). However, only a few studies have investigated the magnitude of this change in SAV coverage in the Great Lakes basin (Skubinna *et al.* 1995, Chu *et al.* 2004, Zhu *et al.* 2006). For example, Zhu *et al.* (2006) observed that submerged plants responded to increased water clarity with an extended maximum depth of colonization and increased species richness in Oneida Lake, NY. Documentation of changes in SAV distribution in the Great Lakes bays is limited, although several local studies and model predictions have been attempted (Geis and Kee 1977, Crabtree 2002, Wolter *et al.* 2005).

In addition to water clarity, the distribution of SAV in lakes is affected by bottom depth, exposure to wave action, fetch, ice scour, latitude, nutrient availability, slope, temperature, and water level fluctuations (Hudon *et al.* 2000, Rooney *et al.* 2003, Havens *et al.* 2005). For example, water level can determine the location, biomass, and annual production of aquatic plants including SAV and emergent plants (Havens *et al.* 2005). The morphometric characteristics of the littoral zone of lakes can also be a major determinant of submerged macrophyte distribution (e.g., Duarte and Kalff 1986). Nutrient enrichment in the sediments due to sedimentation and biological deposition acts to sustain SAV growth over a long time period, even though nutrient loads and nutrient concentrations in the water column have been reduced in time (Rooney *et al.* 2003). These factors may act synergistically with changes in water clarity to affect SAV distribution in lakes.

Changes in SAV distribution over time can be assessed using interpretation of historical aerial photographs taken for other purposes (Fitzgerald *et al.* 2006), which represents a time-efficient and cost-effective method for habitat assessments (Finkbeiner *et al.* 2001, Fitzgerald *et al.* 2006). However, since aerial photo interpretation (API) depends on the subjective judgment of the interpreter, the quality of photographs and water clarity (Finkbeiner *et al.* 2001, McGlone 2004), we also employed hydroacoustic mapping of SAV. Hydroacoustics uses sound waves, and is therefore not affected by water clarity and requires little subjective interpretation owing to the availability of automated classification software (Sabol *et al.* 2002). Rake sampling of plants was used to complement hydroacoustic mapping to confirm the presence of SAV and for species identification.

In this paper, we first compared the estimates of

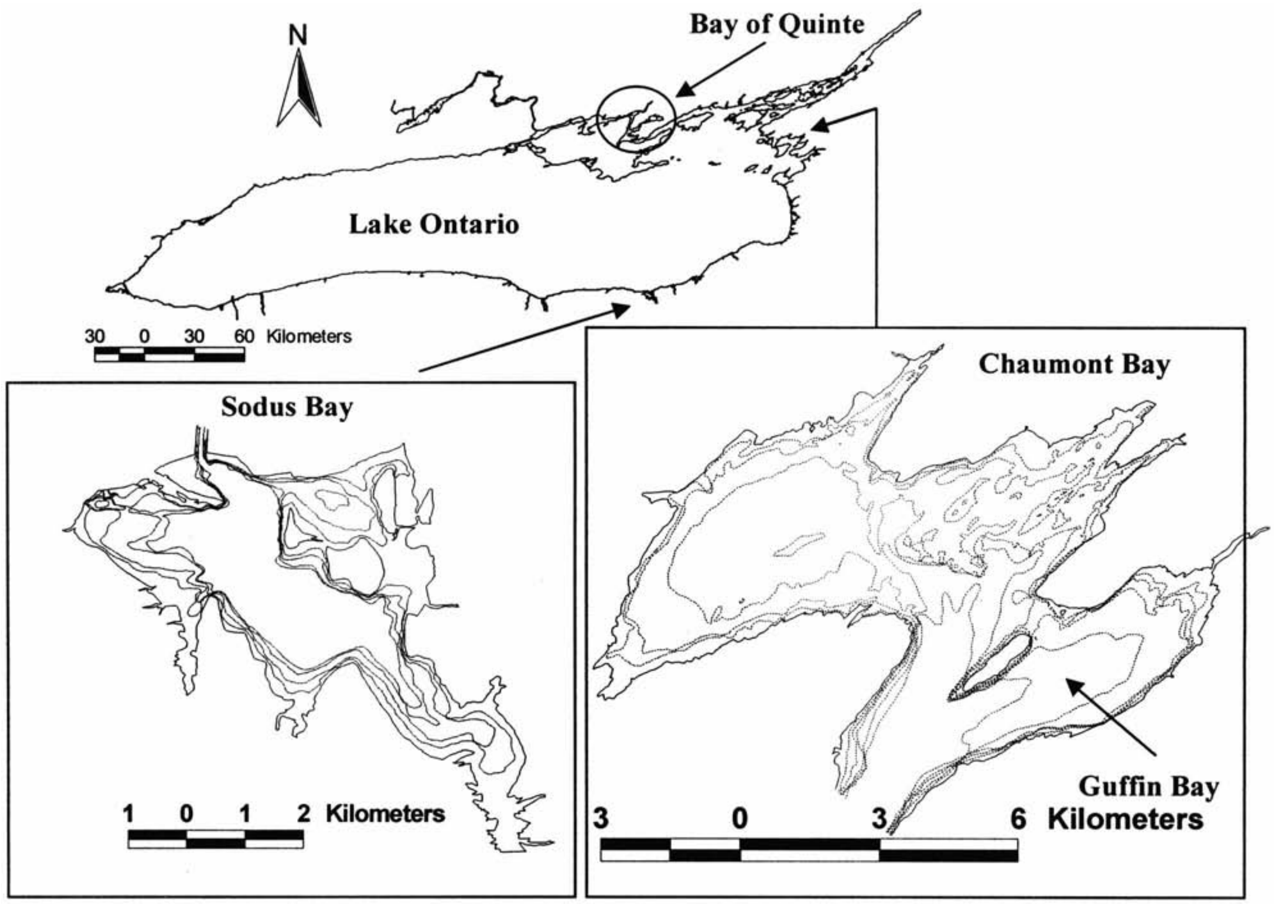

FIG. 1. Map of study locations: Sodus Bay and Chaumont Bay (including Guffin Bay) of Lake Ontario. Dashed lines in Sodus Bay indicates bathymetry of 1.8 m (6 feet), 3.7 m (12 feet), 5.5 m (18 feet) and 6.4 m (21 feet); Dashed line in Chaumont Bay indicates bathymetry of 2 m, 4 m, 6 m, 8 m, and 10 m.

SAV distribution obtained with API, hydroacoustics, and rake sampling in 2002 in two bays (Sodus Bay and Chaumont Bay) of Lake Ontario. Then we interpreted historical photographs to assess SAV coverage in 1972, 1980 (1982), and 1999-2002. Finally we compared changes of SAV in coastal Lake Ontario with changes in factors that could cause the observed expansion of SAV coverage. Our objectives were: 1) to test the measurement accuracy of API relative to hydroacoustic surveys and rake sampling; 2) to quantify the historical changes of SAV in Sodus Bay and Chaumont Bay with API; and 3) to investigate the likely causes for changes of SAV distribution by comparisons with measured and inferred ecosystem changes in Lake Ontario.

METHODS

Study Sites

Sodus Bay, with a surface area of 14.1 km^2, mean depth of 4.9 m, and maximum depth of 14.6 m, is located on the south shore of Lake Ontario (N 43°15′ W 76°57′, Fig. 1, Gilman and Smith 1988, Klumb 2003). The bay is generally shallow and sheltered, especially around the Le Roy, Newark and Eagle islands, the northwestern shore, and the southern inland portion. By contrast, the central-eastern and -western shores are more exposed and have a narrow shelf with a very steep slope. Chaumont Bay, with a surface area of 62.2 km^2, mean depth of 5.4 m, and maximum depth of 20.0 m, is located on the east shore of Lake Ontario (N 44°03′

W 76°12′, Fig. 1, Klumb 2003). In this study, "Chaumont Bay" includes both Chaumont Bay and Guffin Bay, which is a natural extension of Chaumont Bay toward Lake Ontario. The northern part of Chaumont Bay has gentle sloping bottom and low exposure to wind whereas the southern shore has steeper bottom slope and high wind exposure. This bay also has rocky shores, varying water depths, macrophyte and rock-covered substrates, and shoals well suited for fish spawning (Klumb 2003). In both Chaumont and Sodus bays, nuisance aquatic vegetation has been a great public concern, leading to herbicide applications and mechanical harvest of SAV in Sodus Bay since 1988 (R. Williams, Wayne County Soil & Water Conservation District, Lyons, New York, personal communication).

Aerial Photograph Interpretation

Aerial photographs used in this study were obtained from different sources. All recent images (1999–2002) of Sodus Bay and Chaumont Bay were available as 35 mm color slides from the Farm Service Agency county offices of the U.S. Department of Agriculture (USDA), who contracted low elevation, land-use inventory flights that also included lake shorelines. Slides with a clear view of the SAV and/or water were printed at a scale of 1:10,000 for Sodus Bay (15–31 August 1999–2002) and of Chaumont Bay (early September to late October 1999–2002).

Historical images representing the period of cultural eutrophication (1972) and the early period of nutrient abatement (1980 or 1982) were available as 1:30,000 scale color photographs collected by the National Ocean Service of the National Oceanic and Atmospheric Administration (NOAA) on 20 August 1972 and 29 September 1980 for Sodus Bay and 25 October 1982 for Chaumont Bay. SAV distribution was mapped for each year and site; in Chaumont Bay, the unsatisfactory quality of slides for 1999–2002 required the assemblage of a composite SAV map.

We followed the guidelines for monitoring coastal land use and land cover with API according to the Coastal-Change Analysis Program (C-CAP) of NOAA (Finkbeiner *et al.* 2001). Slides were scanned and visually enhanced prior to printing or were directly enhanced by the commercial developer. Photographs produced from either method were suitable for interpretation of SAV distribution by examining differences in color, contrast, shade, glare, and tint with the consideration of the local micro-topography and bathymetry (e.g., Finkbeiner *et al.* 2001). The interpretation was delineated on acetate overlays (0.5 mm, Steiner Paper Corporation, Irvington, NJ) and then scaled onto Mylar™ overlays (Charette ProPrint film 9104 Charrette Corp. Woburn, MA) registered to U.S. Geological Survey 7.5′ (1:24,000) topographic quadrangle maps using landmark ground control points. The Mylar™ overlays were digitized with a large format scanner (Scangraphics CF 1000/44, monochrome) and then vectorized using ArcGIS software (Version 9.0, ESRI, Inc., Redland, CA).

Hydroacoustic Survey

Hydroacoustic surveys, coupled with global positioning systems (GPS), were conducted in Sodus Bay on 9 September 2002 and in Chaumont Bay on 19 September 2002 with most data collected over the plant beds near shore (Fig. 2 A and B). Data were collected with a 420-kHz single-beam digital echo sounder (DT-4000) (BioSonics, Inc., transducer beam angle 6°, pulse length 0.1 ms, pulse rate 5 ping·s^{-1}) and analyzed with Visual Analyzer software and EcoSAV software (BioSonics 2001, Sabol *et al.* 2002). EcoSAV gave location, bottom depth, plant height and plant cover at each sampling point determined by GPS (every 10–14 pings). Echograms were also inspected with Visual Analyzer for depth adjustment and plant identification. We defined plant beds on the echograms where echoes extend distinctly from the bottom toward the surface and were elongated (Sabol *et al.* 2002). As a result, we only accepted EcoSAV's classification of plants when both of the following criteria were met: 1) plant height was higher than 0.2 m, and 2) plant cover was greater than 50%. Observations of rare plant-like echoes in deep water were excluded as they may represent plant material that was uprooted and transported there. Plants were also not considered to be present in water deeper than nine meters because they are generally not able to tolerate high water pressure below this depth in lakes (Wetzel 1983).

Maximum depths (Z_{max}) of plant beds from hydroacoustics were identified as the depth of the deepest plant echo continuous with a SAV bed. For each such measure, we drew a line perpendicular from the location of Z_{max} to the shoreline. The point where this line intersected the outer edge of SAV using API image was considered the Z_{max}

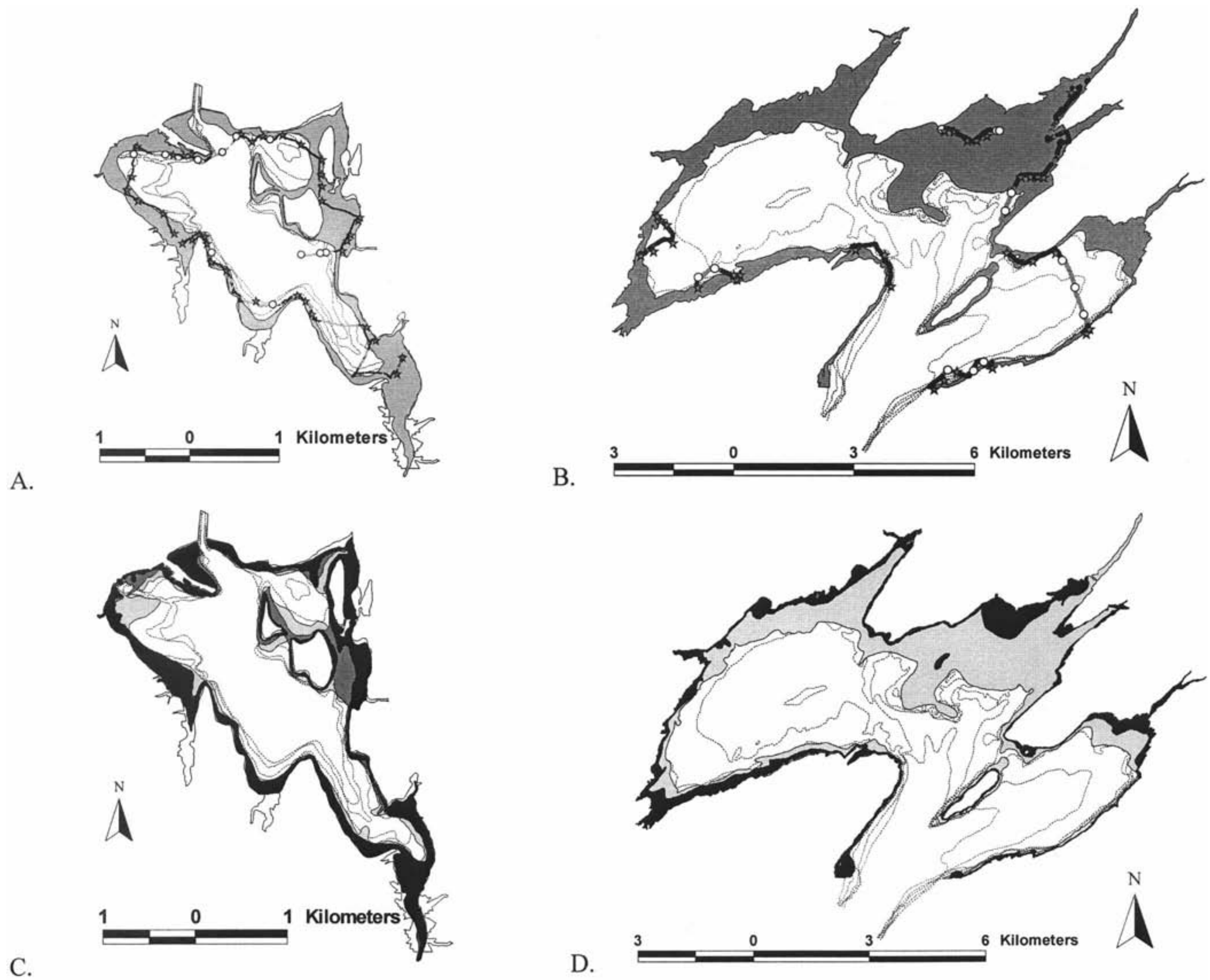

FIG. 2. Distribution of submerged aquatic vegetation (SAV) and comparisons of aerial photograph interpretation (API), hydroacoustics, and rake sampling in Sodus Bay and Chaumont Bay. A. Comparisons of three methods in Sodus Bay. Distribution of SAV from API is shown in the shaded area, hydroacoustic survey is represented as black line (plant presence) and light gray line (plant absence), and rake sampling locations are indicated as stars (plant presence) and circles (plant absence); B. Comparisons of three methods in Chaumont Bay—(see A for the legend); C. Distribution of SAV in Sodus Bay in 1972 (black), 1980 (gray), and 1999 (light gray); D. Distribution of SAV in Chaumont Bay in 1982 (black) and 1999–2002 (light gray).

from API corresponding to the Z_{max} from hydroacoustics. This depth was then estimated from bathymetric maps.

Coverage of SAV from API was calculated directly from ArcGIS software and the potential SAV beds were estimated from the Z_{max} and the relationships between depth (Z) and area (A) that covers from that depth to shore from USGS bathymetry maps:

$$A = 0.134^{*} Z^3 - 1.446^{*}Z^2 + 5.687^{*}Z - 0.959$$
$$(1 \leq Z \leq 7,\ R^2 = 0.978) \text{ for Sodus Bay, and}$$

$$A = -0.106^{*} Z^3 + 1.998^{*}Z^2 - 4.443^{*}Z + 7.185$$
$$(1 \leq Z \leq 12,\ R^2 = 0.982) \text{ for Chaumont Bay.}$$

Rake Sampling

Hydroacoustic identification of SAV was confirmed by the simultaneous sampling submerged plants with a double-headed rake (Weaver *et al.* 1997). Triplicate samples, oriented in different directions, were collected at 49 (Sodus Bay) and 44 (Chaumont Bay) locations along the hydroacoustic survey paths. All submerged plants collected were identified to genus or species. Frequency of occurrence of each species was calculated as the proportion of samples taken that contained a species (Skubinna *et al.* 1995). Plant presence/absence was compared with classifications from API and hydroacoustics.

API and Hydroacoustics Comparison

We compared API and hydroacoustics using two approaches. First, we determined the regression between maximum depths as detected by API and hydroacoustics (N = 53) and tested if the relationships in two bays were different using ANCOVA (Zar 1999). We further determined whether the slope of the regression line differed from one and the intercept of this line differed from zero using *t*-test (Zar 1999). A slope of one and intercept of zero for the relationship between maximum depth as determined by API and hydroacoustics would indicate that these methods produce equivalent results. These analyses were conducted using the GLM procedure of SAS 9.0 (SAS Institute, Cary, NC). Second, we classified each point along each transect for which we had hydroacoustic data (N = 11,050) using both hydroacoustics and API. Four categories were used to determine agreement between the two methods 1) both API and hydroacoustics indicate plant presence (P/P), 2) API indicates plant presence and acoustics indicates absence (API-P/Hydro-A), 3) both API and acoustics indicate plant absence (A/A), or 4) API indicates plant absence and acoustics indicates presence (API-A/Hydro-P). The proportion of points in each category was calculated for every 0.5 m in depth.

Water Clarity and Water Level

Historical data on water clarity since 1972 in Sodus Bay and Chaumont Bay are not available. In order to place the available contemporary data from these two embayments into a long-term context, we examined data on light extinction coefficient of the lower Bay of Quinte, Lake Ontario from 1972 to 2003. The Bay of Quinte is a Z-shaped bay on the northeastern shore of Lake Ontario with a total area of 257.4 km^2 (Fig. 1, Chu *et al.* 2004). The bay is divided into three sections and the lower bay, with an area of 71.8 km^2, connects with Lake Ontario and is therefore similar to Sodus Bay and Chaumont Bay in this respect. Data from the lower Bay of Quinte were re-analyzed and revised from Chu *et al.* (2004). Data for 4 years closest to the studied years were used in our analysis (i.e., 1972–1975, 1979–1982, and 1999–2002). Contemporary data on water clarity in Sodus Bay and Chaumont Bay were Secchi depth readings and collected biweekly from May to October, 1995 to 2004 (Mills *et al.* 2006). Water level data of Lake Ontario from 1971 to 2004 were acquired from the U. S. Army Corps of Engineers (Detroit District, Engineering and Technical Services, Great Lakes Hydraulics and Hydrology Office). Only data from April to September in the studied years were used because these months are of particular importance for the growth of SAV (Spence 1982, Wetzel 1983). We used ANOVA to compare light extinction coefficients for the three periods, followed by pair-wise contrast statements to compare any two periods (SAS 9.0, SAS Institute, Cary, NC).

RESULTS

Comparison of API, Hydroacoustics, and Rake Sampling in 2002

Rake sampling identified a total of nine submerged macrophytes as well as one macroalgae – muskgrass (*Chara* sp.) in the two bays (seven species in Sodus Bay and eight in Chaumont Bay). The nine submerged macrophytes were: claspingleaf pondweed (*Potamogeton richardsonii*), common waterweed (*Elodea canadensis*), coontail (*Ceratophyllum demersum*), Eurasian water milfoil (*Myriophyllum spicatum*), slender naiad (*Najas flexilis*), small pondweed (*P. pusillus*), variable pondweed (*P. gramineus*), water stargrass (*Zosterella dubia*), and wild celery (*Vallisneria americana*) (Fig. 3). The most frequently occurring plant was an invasive plant—Eurasian water milfoil (frequency of occurrence was 82% in Sodus Bay and 47% in Chaumont Bay), followed by wild celery and coontail in both bays. *Cladophora glomerata* was the dominant filamentous algae found attached to SAV.

Classification of SAV presence/absence with rake sampling was similar to the classification based on hydroacoustics and API. Concordance of results was generally high between hydroacoustics and rake sampling, whereas the agreement between API and rake sampling was lower. Hydroacoustics and

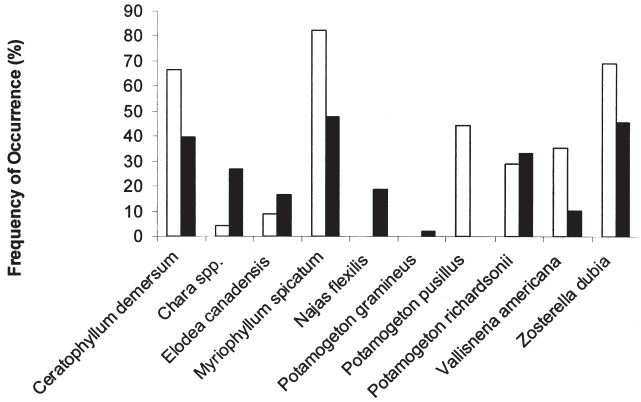

FIG. 3. The submerged aquatic vegetation (SAV) species and their frequency of occurrence in Sodus Bay (white columns) and Chaumont Bay (black column) from rake sampling in 2002.

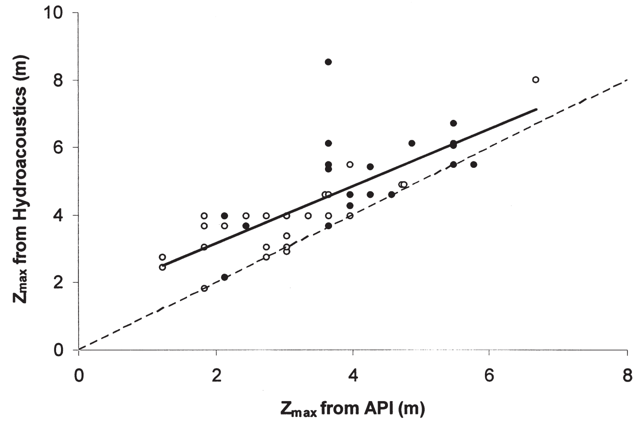

FIG. 4. Comparison of the maximum depth of submerged aquatic vegetation (SAV) colonization in Sodus Bay and Chaumont Bay. The regression is $Depth_{Hydro}$ = 0.84* $Depth_{API}$ + 1.48 (P < 0.001). Empty circles denote data from Sodus Bay and solid circles denote data from Chaumont Bay. The solid line is the regression line for all data and the dashed line is the 1:1 line.

rake sampling coincided in 43 of 49 locations (88%) in Sodus Bay and 42 of 44 (96%) in Chaumont Bay. API and rake sampling agreed in 42 of 49 locations (86%) in Sodus Bay and 32 of 44 (73%) in Chaumont Bay. At most sites where the classification differed between the two methods, rake sampling indicated plant presence and API indicated plant absence (7 of 7 such locations in Sodus Bay and 9 of 12 such locations in Chaumont Bay). These sites were located at the edge of the SAV beds (Figs. 2 A and B).

Because of the large spatial coverage of both API and hydroacoustics, we had over 5000 data points in each bay for comparison of these two methods. Generally hydroacoustics detected deeper SAV than did API in both Sodus Bay and Chaumont Bay in 2002 (Figs. 2 A and B). Based on 53 locations in the hydroacoustic survey paths, the maximum depth obtained with the two methods was correlated in both bays and the regressions did not significantly differ from each other (ANCOVA, df = 1, F = 2.71, P = 0.106). The regression for all data was: $Depth_{Hydro}$ = 0.84* $Depth_{API}$ + 1.48 (Fig. 4, P < 0.001). The slope of this regression did not differ significantly from 1.00 (*t* test, N = 53, t = –1.72, P = 0.091). However the intercept was significantly different from zero (*t* test, N = 53, t = 4.35, P < 0.001), indicating consistently deeper SAV detection with hydroacoustics than with API. The maximum depth of SAV was 6.7 m using API and 8.0 m using hydroacoustics in Sodus Bay and 6.1 m using API and 8.5 m using hydroacoustics in Chaumont Bay. Of the 53 locations where we measured the maximum SAV depth with both hydroacoustics and API (Fig. 4), nine (17%) gave the same maximum depth, 34% showed a difference of less than 0.3 m, and 87% showed a difference less than 1.5 m. All but two locations showed deeper depth in hydroacoustic measurement than in API. The locations with the same or similar maximum depth with the two methods occurred mostly in the northwest portion of Sodus Bay and the northeast proportion of Chaumont Bay. Differences were most pronounced in the northeastern and southeastern shores of Sodus Bay and the southern and western shores of Chaumont Bay.

Of the over 11,000 data points classified, hydroacoustics and API agreed on 63.2%: 60.0% in Sodus Bay and 66.2% in Chaumont Bay (Table 1). API failed to detect SAV in 27–32% of points where hydroacoustics detected plants. Conversely, hydroacoustics did not reveal plant presence in 7–8% of points in which API detected plants. The correctly classified data points occurred primarily in water depth above 4 m for plant presence and below 7.5 m for plant absence, indicating higher concordance of API and hydroacoustics in shallow and deep water than at medium depths. This was expected given that hydroacoustics detects plants in deeper water than API. Disagreement between methods primarily occurred at depths between 4.0 and 7.5 m, where API underestimated plant occurrence by 20–60% in comparison with hydroacoustics. Con-

TABLE 1. Comparison of aerial photograph interpretation (API) with hydroacoustics in Sodus Bay and Chaumont Bay in 2002 (numbers in parentheses are proportion to the all sampling points).

		Hydroacoustics			
		Sodus Bay		Chaumont Bay	
Unit (Points)		Presence	Absence	Presence	Absence
API	Presence	1924 (35%)	429 (8%)	2954 (53%)	373 (7%)
	Absence	1759 (32%)	1361 (25%)	1510 (27%)	740 (13%)
Overall Concordance (%)		60.0		66.2	

versely, hydroacoustics failed to report plant presence in 20–25% of points located at some shallow areas between 0.5 and 2.5 m bottom depth. This is due to our method of identifying the outer edge of the SAV beds with API and assuming continuous coverage from that edge to shore. These areas probably represent those where wave action, fetch or bottom substrates are unsuitable for SAV (Hudon *et al.* 2000, Crabtree 2002).

Changes in SAV during Recent Consecutive Years 1999–2002

To assess the likelihood that observed changes in SAV since the 1970s and 1980s represent responses to long-term ecosystem changes, we need to assess how much measured SAV coverage to vary from one year to the next. Therefore, we compared the SAV coverage measured with API for four consecutive years, 1999-2002, in Sodus Bay. For these years, the SAV coverage increased from 5.00 km^2 in 1999 to 5.37 km^2 in 2001 and then decreased to 4.77 km^2 in 2002 (Table 2). The percentage changes between every 2 consecutive years ranged from 3.6% to 11.2% with an average of 6.2%. Most of the changes were associated with changes in the area around the three islands, the southern end of the bay, and the northwestern shores. In addition, we estimated the maximum depth of SAV from API according to bathymetry. The maximum depth had a similar trend as the SAV coverage: increasing from 5.5 m in 1999 to 7.0 m in 2001 and decreasing to 6.4 m in 2002. The potential SAV coverage estimated from depth-area relationships and maximum depth of the plants increased from 8.9 to 14.0 km^2 from 1999 to 2001 and decreased to 12.5 km^2 in 2002. These values were much larger than coverage estimated from API, mainly because plant beds seldom reached the maximum depth observed in the bay. In addition, the extent of the SAV beds did not coincide with any particular isobath.

Changes in SAV across Three Decades

Significant increases in depth and coverage of SAV were observed from 1972 to 1980 (1982), and

TABLE 2. Water level, water clarity, coverage and the maximum depth (Z_{max}) of submerged aquatic vegetation (SAV) in Sodus Bay and Chaumont Bay, Lake Ontario in 1972, 1980 (1982), and 1999–2002.

		Sodus Bay			Chaumont Bay		
Year	Water Level (m)	Secchi Depth (m)	Z_{max} (m) from API	API Coverage (km^2)	Secchi Depth (m)	Z_{max} (m) from API	API Coverage (km^2)
1972	75.2	—	5.5	3.57	—	—	
1980	75.1	—	5.5	3.75			
1982	74.9				—	5.1	7.16
1999	74.7	2.22	5.5	5.00	5.43		
2000	75.0	3.06	6.4	5.18	5.92		
2001	74.9	3.78	7.0	5.37	4.82	6.1	21.3
2002	75.0	2.62	6.7	4.77	5.33		

to 1999–2002 in both embayments (Figs. 2 C and D). To represent this trend, we used the 1999 SAV map of Sodus Bay as being typical of the SAV distribution in recent years. The maximum depth of SAV in Sodus Bay did not change until 2000 but the potential SAV bed increased from 8.9 to 11.3 km^2 across three decades. The SAV coverage from API increased 5.0% from 3.56 km^2 in 1972 to 3.75 km^2 in 1980, and further increased 35.5% to 5.08 km^2 in 1999–2002 (Table 2), with expansion particularly around the three island areas in the northeast where the water is shallow and less exposed to wind (Fig. 2C). In Chaumont Bay, the maximum depth of SAV increased about 20% from 5.1 m to 6.1 m and the potential SAV bed increased about 9% from 22.4 to 30.4 km^2. The SAV coverage from API almost tripled from the period after 1982 to the period 1999-2002 (i.e., 198% areal increase) and SAV expanded to deeper areas at almost every location along the shoreline; the most extreme increases took place at the northern shorelines, where water depths are shallow (Fig. 2D).

Changes in Water Clarity and Water Level

Changes in water clarity and water level in Lake Ontario were studied in order to explain the historical changes of SAV. Water clarity has likely increased through 1972–2002. Light extinction coefficient in the lower Bay of Quinte showed a continuous decline from 0.64 in 1972 to 0.32 in 2003 and suggests that a similar trend of increased water clarity occurred in other embayments of Lake Ontario during this period (Fig. 5). When the time series was divided into shorter periods corresponding to our SAV data for Sodus Bay and Chaumont Bay, water clarity was significantly different in 1972–1975, 1979–1982, and 1999–2002 (ANOVA, df = 2, F = 63.8, $P < 0.001$). Water clarity increased slightly, but not significantly between the 1972–1975 and 1979–1982 periods; as light extinction coefficient decreased from 0.67 ± 0.02 (mean ± 1 SE) to 0.61 ± 0.02 (ANOVA, contrast, df = 1, F = 4.48, P = 0.064). By contrast, between the 1979–1982 and 1999–2002 periods there was a relatively large and statistically significant decrease in light extinction, which declined to 0.37 ± 0.02 (ANOVA, contrast, df = 1, F = 113.8, $P < 0.001$). Recent Secchi depth data from Sodus Bay also showed a trend of increase in water clarity, increasing from 2.9 m in 1995 to 4.0 m in 2004 (Fig. 5). Water clarity in Chaumont Bay varied between 4.5 and 5.9 m with no significant time trend from 1995 to 2004 (Fig. 5, P = 0.349). These data suggest that relatively small increases in water clarity occurred between 1972 and 1980, but that large increases occurred between 1980 and 1999–2002.

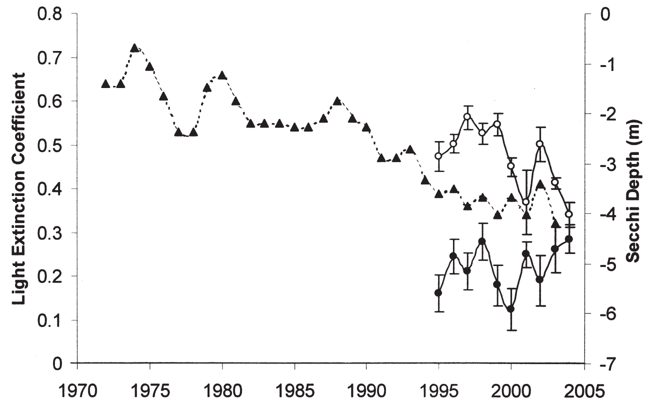

FIG. 5. Changes in water clarity in the Bay of Quinte, Sodus Bay and Chaumont Bay of Lake Ontario. Change in the Bay of Quinte is measured by light extinction coefficient from 1972 to 2003 (—▲—); changes in Sodus Bay (—○—) and Chaumont Bay (—●—) are measured by Secchi depth from 1995 to 2004. Error bars represent ± 1SE.

Water level (April–September mean) showed no overall trend in the past 30 years in Lake Ontario (Fig. 6, P = 0.060). The average water level was 75.03 ± 0.03 m above mean sea level from 1971 to 2004. In the 7 years for which we also have SAV data, mean water levels were similar but the ranges varied slightly (Fig. 6). Water level in 1972 was the highest (75.17 m, range 0.39 m) among the 7 years, whereas 1999 exhibited the lowest mean level and narrowest range (mean 74.70 m, range 0.23 m). The highest range occurred in 2002 (range 0.68 m) with a mean water level of 75.05 m.

Correlations between SAV Z_{max} / Coverage and Water Clarity / Water Level

The increase in maximum depth of SAV was marginally correlated with increase of Secchi depth from 1999-2002 in Sodus Bay (Fig. 7A, df = 3, ρ = 0.924, P = 0.075). However there was no significant correlation between Secchi depth and the SAV coverage during this period (df = 3, ρ = 0.806, P = 0.194) while the correlation from 1999 to 2001 was significant (Fig. 7A, df = 2, ρ = 0.998, P = 0.041). The lack of correlation from 1999 to 2002

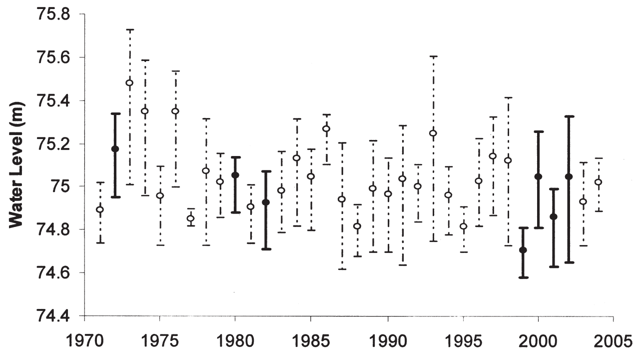

FIG. 6. Mean (dots) and range (bars) of water levels (April–September) in Lake Ontario from 1971 to 2004. The seven studied years (1972, 1980, 1982, 1999, 2000, 2001, and 2002) are shown as solid symbols.

may be due to the unusual decrease of the SAV coverage caused by mechanical harvesting and chemical control or the highly variable water levels in 2002. Yet the expansion in SAV coverage was correlated with the increase in water clarity over the longer period (Fig. 7B). Light extinction from the Bay of Quinte and SAV coverage from Sodus Bay in 1972, 1980, 1999, 2000, 2001, and 2002 were highly correlated (df = 5, $\rho = 0.968$, $P < 0.001$). Our analysis also revealed no significant correlation between the SAV coverage and either water levels (data not shown, df = 5, $\rho = -0.641$, $P = 0.17$) or water level fluctuations (data not shown, df = 5, $\rho = 0.174$, $P = 0.742$).

DISCUSSION

Effects of eutrophication on the Great Lakes have been widely described since the 1970s (e.g., Crowder and Bristow 1986), conversely, potential consequences of oligotrophication caused by decreased nutrient levels and the dreissenid mussel invasion have not been as well documented. SAV influences a range of ecosystem processes (Jeppesen *et al.* 1998, Havens *et al.* 2005). Therefore changes in SAV maximum depth and coverage in response to ecosystem change are of particular interest to both scientists and managers. Crowder and Painter (1991) stressed the significance of SAV in Lake Ontario and urged the development of comprehensive SAV maps that would allow for a quantitative assessment of the response of SAV to ecological changes. Our study is among the first to provide comprehensive maps of SAV coverage for whole

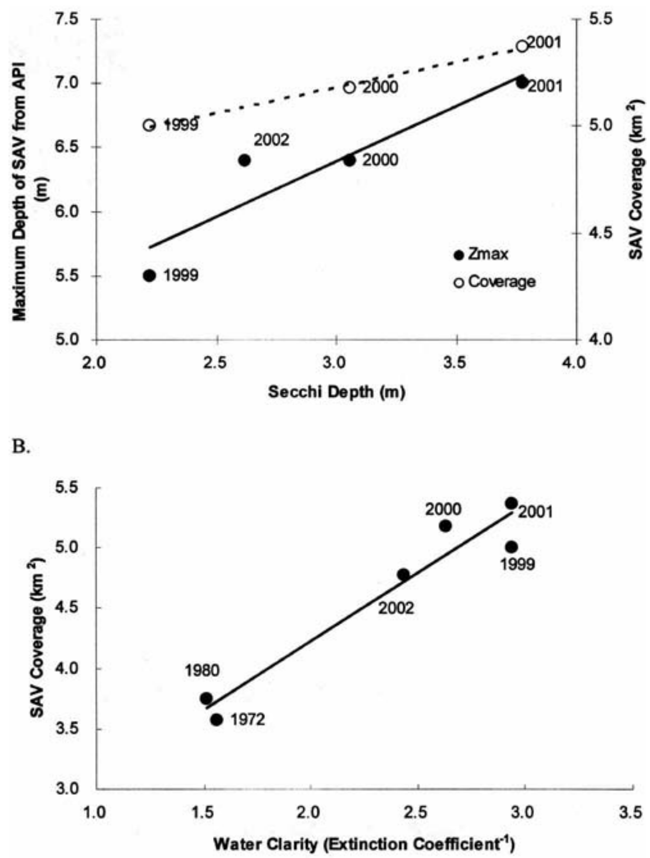

FIG. 7. Correlation between water clarity and maximum depth / coverage of submerged aquatic vegetation (SAV) in Sodus Bay. A. Correlation in Sodus Bay. SAV maximum depth was marginally correlated with Secchi depth (df = 3, $\rho = 0.924$, $P = 0.076$) from 1999 to 2002 and SAV coverage was highly correlated with Secchi depth from 1999 to 2001 (df = 2, $\rho = 0.998$, $P = 0.041$). B. Correlation between light extinction coefficient (from Bay of Quinte) and SAV coverage in 1972, 1980, 1999, 2000, 2001, and 2002. The correlation was significant (df = 5, $\rho = -0.975$, $P < 0.001$). Data from Chaumont Bay is not shown because only two points were available.

bays. These findings identify a large increase in SAV coverage and maximum depth between the early 1980s and the 1999–2002 time period but less extreme changes from 1972 to the early 1980s.

Our approach of aerial photo interpretation from accessible sources is a low-cost method allowing to map SAV over large geographic areas, such as Lake Ontario embayments (Fitzgerald *et al.* 2006). Our study also revealed a good correspondence between rake sampling and hydroacoustics, as > 88% of the sites were classified identically by the two methods. This supports previous comparisons between hydroacoustics and field sampling or diver surveys (Sabol *et al.* 2002). However, our comparisons of API with hydroacoustics and rake sampling indicate that API underestimates the extent of SAV coverage in deeper water by about 0.8 m on average. Whereas API adequately quantifies the SAV reaching the surface or forming dense beds, SAV located at the edge of the beds, in deep water or representing less than 50% cover are not included in the assessment. Although hydroacoustics assessment is not affected by water clarity or subjectivity in the interpretation, we consider that API does nevertheless provides a useful, albeit conservative, estimate of SAV coverage, and further allows to evaluate historical changes (see also Fitzgerald *et al.* 2006). Most importantly, API provides better spatial coverage of SAV distributions than hydroacoustics. Consequently researchers have started to apply API to studies in estuary, river, and lake ecosystems (McGlone 2004, Wolter *et al.* 2005, Fitzgerald *et al.* 2006). The combination of these two methods may be ideal for detecting long-term changes in SAV distribution.

We demonstrated increases in SAV depth and coverage as well as increases in water clarity in bays of Lake Ontario. These results are consistent with the fact that underwater light penetration has been identified as the primary factor controlling SAV distribution (Spence 1982, Wetzel 1983). The observed increase in water clarity after 1980s is mostly likely associated with dreissenid mussels (Mills *et al.* 2003) and this study demonstrated a temporal association of SAV expansion to suitable habitat and dreissenid invasion (Fig. 7). Similarly, SAV expanded to deeper water after the dreissenid mussel invasions in Oneida Lake, New York, Saginaw Bay of Lake Huron, the Bay of Quinte of Lake Ontario, and Lake Veluwe in the Netherlands (Skubinna *et al.* 1995, Chu *et al.* 2004, Lammens *et al.* 2004, Zhu *et al.* 2006). These studies suggest that increased light penetration sufficiently explains the observed increase in depth range of SAV (Chambers and Kalff 1985, Genkai-Kato and Carpenter 2005). Further, the observed year-to-year changes in SAV coverage and maximum depth between 1999 and 2002 in Sodus Bay followed the same trends as water clarity (Fig. 7A), suggesting that the response of SAV to improvements in water clarity can occur from one year to the next. The expected effect of water clarity is also similar to predictions from the relationship between Secchi depth and the SAV maximum depth listed by Hudon *et al.* 2000, although we observed plants deeper than these predictions. This is likely due to differences in lake and river systems and other local factors. Thus, we suggest that water clarity is the major factor determining increases in SAV depth and coverage Lake Ontario embayments and that the *Dreissena* –driven increase in lake-wide water clarity is an example of ecosystem engineering (Jones *et al.* 1997, Karatayev *et al.* 2002, Mayer *et al.* 2002, Zhu *et al.* 2006).

In addition to dreissenid grazing, phosphorus reduction can cause an increase in water clarity, leading to expansion of SAV distribution. For example, plant biomass and coverage in the shallow upper portion of Bay of Quinte increased from 1972 to 1979 (Crowder and Bristow 1986) following total phosphorus reduction (from 22 to 15 $\mu g.L^{-1}$) in Lake Ontario (Millard *et al.* 2003). However, water clarity may have been only marginally affected by phosphorus control as light extinction in the Bay of Quinte only decreased from 0.67 to 0.61 in the same years. Assuming a similar pattern of water clarity change for Sodus Bay, it is not surprising that SAV coverage only increased 5% from 1972 to 1980. This variation is similar to observed annual variation (in the order of 6%) of SAV coverage in recent consecutive years (1999–2002). Although this annual variation can be due to difference in quality of the aerial photographs, human error, or real differences in SAV coverage, we believe these differences are real as the increase from 1999 to 2002 is mirrored by changes in water clarity.

Factors other than water clarity, such as water level, nutrient availability, exposure, and bottom slope can affect SAV distribution (Hudon *et al.* 2000, Crabtree 2002, Vis *et al.* 2003, Havens *et al.* 2005). Water level can determine the location, biomass and annual production of both SAV and emergent plants (Vis *et al.* 2003, Havens *et al.* 2005). The water level fluctuations observed in our study may have affected SAV distribution; for example, the largest fluctuation occurred in 2002 when there was an 11% decrease in SAV coverage in Sodus Bay. Additionally, water level fluctuations may have influenced estimation of SAV depth and coverage because the shorelines varied with water levels among years but our estimation of shoreline from API did not, possibly leading to deeper SAV maximum depth and larger areal coverage with low water. However, water levels did not change dramatically between our studied years and there were no significant correlations between water level or its fluctuation and the SAV coverage. Therefore, water level changes appear to have minimal effect on SAV coverage in Lake Ontario during the study period.

Nutrient enrichment in the sediments may also contribute to submerged macrophyte distribution (Rooney *et al.* 2003). Even though nutrient loadings have been limited and nutrient concentrations have decreased in the water column after the implementation of the GLWQA, the temporal sequence of changes in nutrient loading to bays and littoral area is probably more complex and heterogeneous from site to site than in the central part of lakes. The accumulative nutrient storage in the sediment in the littoral zone can sustain macrophyte growth for a long period. In addition, SAV distribution could also be affected by an episodic disturbance, such as Hurricane Agnes, which increased sedimentation associated with storm flows and presumably nutrient additions (Hoopes 1974).

Exposure to wind and the bottom slope may also be major determinants of SAV presence (Spence 1982). The role of exposure in controlling the distributions of aquatic macrophytes is well established (Hudon *et al.* 2000, Vis *et al.* 2003): waves may remove biomass, uproot seedlings, and transport propagules; waves also indirectly affect SAV through the erosion, transport, and deposition of sediment (Wetzel 1983). In addition, the steepness of the bottom is decisive for the sediment stability along slope gradients and influences the establishment and extent of the vegetation. For example, Duarte and Kalff (1986) reported the shoreline slope can account for up to 72% of the observed variability in maximum submerged macrophyte biomass. The lower exposure to wind and the shallow bottom slope may explain why there were significant increases in SAV coverage in the regions of three islands in Sodus Bay and the northern part of Chaumont Bay but not at other sites. Other periodic factors, such as weed control, can affect the estimation of SAV coverage as well. Part of the decrease of SAV coverage from 2001 to 2002 in Sodus Bay could be due to the success of chemical control in summer 2001 and earlier mechanical harvest in 2002 (R. Williams, Wayne County Soil & Water Conservation District, Lyons, New York, personal communication). All these factors may act synergistically with changes in water clarity to determine the extent of SAV distribution in lakes. However, exposure and bottom slope has not changed much since 1972 and these factors are therefore not likely the major causes of the observed changes in SAV coverage since that time.

The increase of SAV distribution is part of a suite of changes in ecosystem and food web function in lakes. The Lake Ontario benthic and pelagic food webs have changed from 1970–2000, a period of nutrient reduction and expansion of dreissenid mussels (Mills *et al.* 2003). In other systems similar changes have been reported (Mayer *et al.* 2002, Zhu *et al.* 2006). Fish populations are also likely affected by the increase of SAV—we expect benthic fish species to increase and pelagic species to decline (Mills *et al.* 2003, Strayer *et al.* 2004). While some of the above change may be perceived as positive, the consequences of expanding macrophyte distributions may not be uniformly perceived as positive by lake users. Dense stands of aquatic vegetation reduce the aesthetic appeal of the water as well as some desirable fish species. For example, walleye numbers have been declining since the mid-1990s as water clarity and SAV increased in the Bay of Quinte, Lake Ontario (Chu *et al.* 2004). This increase in SAV has also been commensurate with an increase in attached algae like *Cladophora glomerata*, which contribute to the shift in phosphorus balance that is likely enhancing conditions for the growth and expansion of SAV (Higgins *et al.* 2005), thereby instituting a positive feedback supporting further expansion of SAV. Improvement of water quality can also facilitate successful colonization of non-native species, such as Eurasian water milfoil—which became the most frequently occurring species in both bays and may suppress and displace native plants (e.g., Madsen *et al.* 1991).

Documentation of the changes in the SAV distribution with complementary methods in two bays of Lake Ontario identified large-scale changes over time, which is most likely caused by increased water clarity modified by the bathymetry, exposure, bottom slope, and nutrient availability. Improvements in water clarity in Lake Ontario have increased the importance of benthic production over pelagic production in the food web, thereby representing an overall alteration of ecosystem function—a process we refer to as benthification (Mills *et al.* 2003, Zhu *et al.* 2006). Expansion of SAV coverage from 1972 to 2002 represents one significant aspect of the process. A similar process of a shift to benthic production in aquatic ecosystems following invasions by dreissenid mussels has been observed other aquatic ecosystems (Strayer *et al.* 2004, Havens *et al.* 2005). Mapping and quantifying the historical changes of SAV by using low-cost technologies like API will help understand the magnitude of SAV response to environmental changes, improve understanding of the corresponding system-wide response, and predict future environmental changes and needs for management.

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