J. Great Lakes Res. 32:11–28
Internat. Assoc. Great Lakes Res., 2006

Replacement of Zebra Mussels by Quagga Mussels in the Canadian Nearshore of Lake Ontario: the Importance of Substrate, Round Goby Abundance, and Upwelling Frequency

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ABSTRACT. *The invasion of the Great Lakes by zebra mussels* (Dreissena polymorpha) *and quagga mussels* (Dreissena bugensis) *has been accompanied by tremendous ecological change. In this paper we characterize the extent to which dreissenids dominate the nearshore of the Canadian shoreline of Lake Ontario and examine mussel distribution in relation to environmental factors. We surveyed 27 5-m sites and 25 20-m sites in late August 2003. Quagga mussels dominated all sites (mean: 9,404/m^2; range 31–24,270), having almost completely replaced zebra mussels. Round gobies* (Neogobius melanostomus) *were associated with quagga populations dominated by large mussels. Quagga mussel total mass was low at 5-m sites with high upwelling frequency; we believe this is the first documentation of reduced benthic biomass in areas of upwelling in Lake Ontario. Overall, we estimated 6.32×10^{12} quagga mussels weighing 8.13×10^{11} g dry weight and carpeting ~66% of the nearshore benthic habitat. Quagga mussels are a dominant and defining feature of the Lake Ontario nearshore, and must be accounted for in management planning.*

INDEX WORDS: Dreissena, *biomass, upwelling, species replacement, substrate.*

INTRODUCTION

Lakes in North America have undergone tremendous change with the invasion of zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*). Dreissenid mussels have physically altered the lake environment by 1) increasing the availability of hard surfaces, 2) creating interstitial habitat between shells and live mussels, 3) reducing particle re-suspension, 4) changing optical conditions through filtering, and 5) increasing sediment accumulation through filtering and the production of pseudo-feces (as reviewed in Mills *et al.* 1996, Vanderploeg *et al.* 2002, Mills *et al.* 2003). In addition, recent work suggests that dreissenids have altered microbially-mediated nutrient cycling (Lavrentyev *et al.* 2000) and the nearshore phosphorus cycle (Hecky *et al.* 2004). With these changes have come the possibilities of changed benthic-pelagic linkages (Vadeboncoeur *et al.* 2002) through reductions in phytoplankton and (or) zooplankton, as well as shifts in trophic transfers that are only just becoming apparent.

From a human health perspective, dreissenid mussels are likely to alter patterns of contaminated sediment burial and bioaccumulation of contaminants (e.g., Marvin *et al.* 2002). As food webs shift to take advantage of biomass contained in dreissenid mussels, contaminant transfer to humans may occur through fish consumption. It has also been hypothesized that the proliferation of benthic algae and subsequent fouling of the shoreline is linked to

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dreissenid-mediated increases in water clarity and enhanced nutrient availability (Hecky *et al.* 2004). The likelihood of negative dreissenid effects on human health is exacerbated if high densities of dreissenids are in close proximity to urbanized areas where lakes resources are extensively used and highly valued, and where inputs of nutrients and other pollutants are likely at their highest levels. Both scenarios imply that the current approach to contaminant and nutrient management in the nearshore should be reexamined and that detailed understanding of dreissenid mussel distribution and biomass in the nearshore is critical in addressing human health issues.

Zebra mussels were discovered in Lake Ontario in 1989, followed by quagga mussels in 1990 (Griffiths *et al.* 1991, Mills *et al.* 1993). By 1991, zebra mussels were common at depths of 5 m (maximum 3,250/m^2) in the west end of the lake, and present at two sites on the eastern end of the lake (Kilgour *et al.* 2000). Observations by the Ontario Ministry of Natural Resources in 1993 found moderate to high densities of zebra mussels in the west and east ends of Lake Ontario (50–17,000 /m^2 in the west; 170–9,000/m^2 in Kingston basin), and very low numbers along the north shore of the lake (2–460/m^2); the same survey documents quagga mussels present in low numbers (max. 100/m^2) in the west and east ends of the lake but mostly absent from the northern shore (Stewart *et al.* 1994, Bailey *et al.* 1999). Zebra mussels generally were more abundant on hard substrates (Mellina and Rasmussen 1994, Nalepa *et al.* 1995), whereas quagga mussels were often found at greater proportions on deeper soft substrates (Mills *et al.* 1993). More recently, quagga mussels have colonized shallower, warmer areas of the Great Lakes.

In the Laurentian Great Lakes, it has been proposed that dreissenids have facilitated the further invasion of the Great Lakes by species associated with dreissenids in their native range (Ricciardi 2001). These new invaders include the round goby **(***Neogobius melanostomus*) which actively consumes zebra and quagga mussels (Jude *et al.* 1992) and *Echinogammarus ischnus*, an amphipod which fills a similar ecological role as the native amphipod *Gammarus* (reviewed in Vanderploeg *et al.* 2002). The invasion of dreissenids has also been accompanied by shifts in the distribution and abundance of native species including *Gammarus* (e.g., Ricciardi *et al.* 1997, Van Overdijk *et al.* 2003) and the benthic filamentous algae *Cladophora*. A solid knowledge of dreissenid mussel distribution and abundance is critical in understanding patterns of occurrence of these new invaders and native species in the nearshore.

Considerable effort by numerous researchers was directed toward quantification of the dreissenid invasion in the early and mid-1990s, but the northern shore of Lake Ontario has not been revisited in detail since that time, and most monitoring efforts have occurred offshore on soft sediments not characteristic of much of the nearshore environment. In addition, physical processes in Lake Ontario distinguish the nearshore environment of the lake from epilimnetic waters in the pelagic zone, resulting in a seasonally distinct thermal regime in the nearshore (Neilson and Stevens 1987). In the spring, the nearshore waters are warmer and are isolated from colder offshore waters by a thermal bar, and, along the north shore, intermittent coldwater upwellings during summer stratification introduce hypolimnetic waters often 10°C cooler than surface waters. Finally, lake users are most likely to interact with the nearshore regions of Lake Ontario and thus dreissenid-mediated changes in the lake will be more noticed than offshore regions of the lake.

In this paper, we quantify the spatial distribution of dreissenids along the northern shore of Lake Ontario; examine the environmental factors associated with higher abundances of dreissenid mussels, recent recruitment and the relationship between tissue and shell mass; and apply the resulting abundance model to estimate substrate and depth-specific dreissenid abundance in the Canadian nearshore of Lake Ontario. We emphasize that that a better understanding of distribution, species composition, size distribution and biomass of dreissenids in the nearshore waters will increase the scientific community's ability to accurately predict the current impact of these species on lake-wide cycles and manage nearshore water-quality issues.

METHODS

Site Description

We sampled 52 sites located along the Canadian nearshore of Lake Ontario from just west of the Niagara River in western Lake Ontario to just off Kingston, in eastern Lake Ontario (Fig. 1). Sites were stratified as much as possible by substrate type (bedrock, cobble, sand, and silt) and depth (27 sites at 5 m and 25 sites at 20 m). With the exception of two additional 5-m sites, our sites were at approximately the same locations as stations visited in 1981 (Barton 1986) and 1991 (Kilgour *et al.*

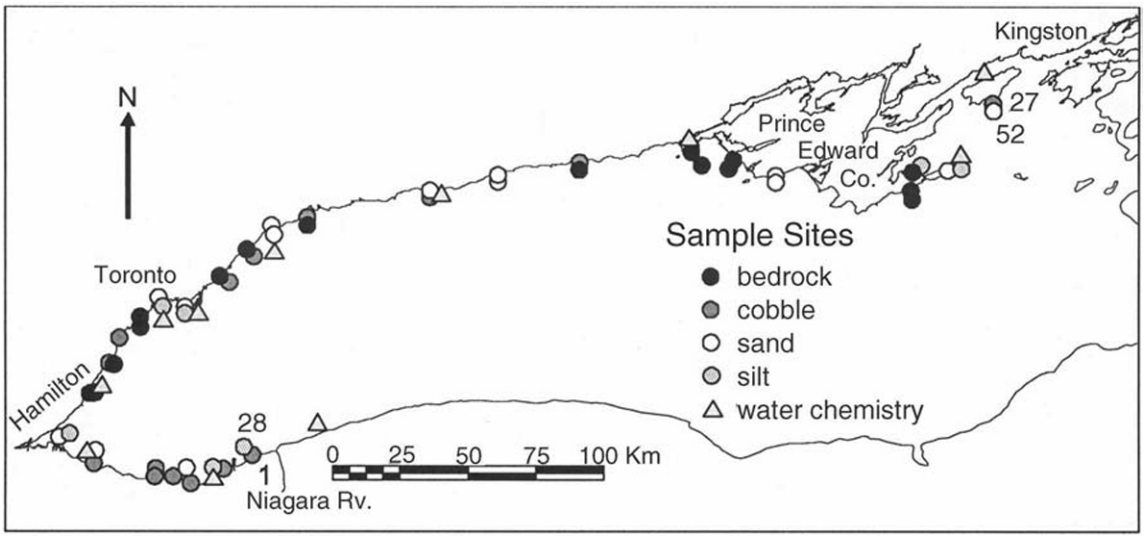

FIG. 1. Map of sample sites, coded according to substrate type. Five-meter sites are numbered 1–27 (nearshore of each pair) and 20-m sites are numbered 28–52. Sites were sampled 25 August–7 September, 2003. Ontario Ministry of the Environment index water chemistry sampling stations are indicated by a triangle.

2000) as part of previous surveys conducted for the Ontario Ministry of the Environment (MOE).

Mussel Percent Cover and Collection

Dreissenid mussels were assed by divers from late August through early September, 2003. At each site, divers placed three replicate 0.15 m^2 quadrats on the substrate according to directions from surface personnel who could not see the bottom, but were in voice communication (e.g., divers were instructed to walk 1 m forward and 1 m left before dropping the quadrat). For each quadrat, the diver first estimated percent of surface area covered by dreissenids (± 5%). The diver then removed all mussels from the quadrat and placed them in a 200 µm mesh bag before sending the bag to the surface. On soft substrates the diver scooped mussels up by hand; on hard substrates the diver used a scraper to dislodge mussels and then placed them in the mesh bag. Small rocks were placed in the mesh bag and brought to the surface for mussel removal. All samples were collected within 5 m of each other. Mussels were rinsed in the mesh bag before being transferred to food-quality freezer storage bags and immediately frozen on dry ice. Benthic algae and macrophytes found within the quadrats were also harvested to collect any small attached mussels.

Mussel samples remained frozen until they were transferred to a freeze-drier and thoroughly dried for 1.5–3 weeks depending upon biomass. Dried samples were stored in airtight containers with a silica gel packet to absorb incidental moisture until processing.

Mussels were processed by Pollutech Environmental Services. For each sample, mussels were first sorted from debris, including benthic algae or macrophytes. Mussels were then counted and weighed in their entirety (shell plus soft parts). Individual mussels were then measured to obtain a length frequency distribution for the sample. Finally, mussels were dissected, and total shell weight and total soft tissue weight were measured for all mussels combined. We did not measure weights of individual mussels. In most cases, mussel numbers were so high that subsampling was required. Subsamples were selected by spreading the sorted sample evenly over a subdivided plastic sheet, and squares on the plastic sheet were used to delineate the subsamples. Technicians counted at least 20% of the sample, and, if possible, measured at least 200 individuals, and dissected at least 100 individuals. Technicians did not dissect individuals < 5 mm in length because such small mussels tended to shatter during dissection. Quagga and zebra mussels were treated in the same manner, except that zebra mussels did not require further subsampling because numbers were low.

Environmental Factors

Substrate within and surrounding the quadrats was assessed visually by the diver as percent bedrock, boulder, cobble, gravel, coarse sand, fine sand, and silt. For analyses, sites were assigned to four categories based on the dominant substrate type: bedrock, cobble, sand, and silt.

Water chemistry samples were collected by the Ontario Ministry of the Environment's Great Lakes monitoring program at 11 stations. At each sample station (Fig. 1), three replicate integrated water column samples were collected and analyzed for total nitrogen, total phosphorous, alkalinity, conductivity, and chlorophyll-*a* at the MOE's labs. Samples were collected in April–May, July–August, and December 2003; we used the mean values for all three sample periods in our analyses. Water chemistry values were assigned to multiple mussel sampling sites based on the closest water chemistry station to each mussel sampling site. Temperature and light profiles were collected during the mussel survey. Attenuation coefficients (K_d), a measure of photosynthetically available radiation, were calculated from these light profiles for each sample site.

The relative abundance of round gobies was assessed based on diver observations and underwater video. Variations in field of view resulting from differences in water clarity and substrate prevented quantification of goby numbers. Thus, goby abundance was rated 0 = not observed, 1 = rare (small numbers observed by diver but no gobies visible in video), 2 = common (commonly observed by diver and usually visible in videos), and 3 = abundant (large numbers of gobies present at the site, often so dense that in videos the substrate appears to be in constant motion). The bottom was observed with video for at least 2 min per site, and generally much longer. We used a Splashcam (model Deep Blue with a fixed 2.5 cm to ∞ focus and 3.6 mm wide angle lens) camera suspended horizontally 10 cm off the substrate.

At 5-m sites, percentage cover and height of *Cladophora*, a filamentous green algae, was assessed by the diver within five replicate 0.15 m^2 quadrats.

Upwellings are a common feature of the north nearshore of Lake Ontario, induced by prolonged winds from the west, and can result in temperature changes of > 10°C within a 24 hr period (Neilson and Stevens 1987, Simons and Schertzer 1987). Upwelling frequency for each site was estimated from geo-referenced Advanced Very High Resolution Radiometer (AVHRR) satellite images of surface temperature available from the NOAA Great Lakes CoastWatch Program. We analyzed images taken from 15 July to 15 September, when lake surface temperatures are normally ≥ 20°C, and upwelling effects (surface water < 16°C) are most likely to occur. When possible we obtained surface temperatures from one nighttime image and one daytime image per 24 hour period; however, cloud cover often limited the number of useful images, or limited the number of sites available for a given date. Over all stations and years, the number of useable images in the 2-month period averaged 58.8 images (SD = 13.0). Temperatures were obtained at the location of our sample stations using proprietary software ("cwsample.exe") available from NOAA CoastWatch. Cloud cover information provided by NOAA CoastWatch was used to eliminate samples that were influenced by cloud cover. Because the number of samples was not consistent across sites (or years), we calculated the relative frequency of images in which the surface temperature was below 16°C, and then averaged these values across five summers (1999–2003). The satellite images have a resolution of 1.8 km per pixel; to avoid "sampling" the temperature on land, we only used the temperatures at our 20-m sites to estimate upwelling frequency. This measure of upwelling should be conservative because many minor upwelling events occur during which the surface water temperatures are not affected (e.g., Rao *et al.* 2003).

Calculations and Statistical Analyses

All variables were transformed if necessary to achieve normality or an approximation of normality. Percentages and proportions were arcsine (square root(x)) transformed. We used backward stepwise multiple linear regression to model the following response variables: *Cladophora* percent cover, quagga total mass, tissue to shell mass ratios, and proportion of quagga mussels ≤ 10 or ≤ 5 mm in length. Several environmental explanatory variables (Table 1) were highly correlated (Appendix A) and discarded from the analyses; we used the following in our stepwise regressions: depth, latitude, substrate, goby relative abundance, upwelling, attenuation coefficient (k_d), total phosphorus, total nitrogen, and chlorophyll-*a*. For quagga tissue vs. shell mass comparisons, we also included proportion of mussels < 10 mm and > 20 mm. Goby relative abundance, depth and substrate were classified as categorical variables in Systat's GLM procedure

TABLE 1. Environmental variables and dreissenid statistics. Categories for nominal variables are listed. For biotic variables, values are only calculated for sites (n) at which mussels or algae were present. Mean Secchi depth is underestimated because the Secchi disk was visible on the bottom at many 5-m sites. Note that water chemistry values for the 52 sites were extrapolated from 11 water chemistry index sites. St. Dev. = 1 standard deviation.

Factor	n	Mean	St. Dev.	Minimum	Maximum
Physical and chemical					
Depth (m)	5, 20				
Latitude (decimal degrees)				43.1847	44.1022
Longitude (decimal degrees)				–79.7884	–76.7082
Substrate type	*bedrock, cobble, sand, silt*				
Upwelling frequency	52	0.107	0.047	0.015	0.175
Attenuation coefficient (kd-PAR) (/m)	52	–0.252	0.090	–0.599	–0.159
Secchi depth (m)	52	5.3	1.4	2.4	10.6
Mean alkalinity (meq/L)	52	189.49	7.13	184.21	206.35
Conductivity (µS/cm)	52	307.9	24.8	291.0	364.2
Mean chlorophyll-a (µg/L)	52	1.41	0.47	0.67	2.17
Mean total N (µM/L)	52	47.04	7.49	38.62	61.81
Mean total P (µM/L)	52	0.3197	0.1066	0.2163	0.4973
Biotic					
Mean algae thickness (cm)	25	4.7	2.2	1.0	9.5
Mean algae % cover	25	57.1	28.4	2.4	100
Mean mussel % cover	45	70.0	32.0	1.7	100
Round goby relative abundance	*absent, rare, common, abundant*				
Quagga mussels					
# ($/m^2$)	45	9404.0	7167.6	31.1	24271.1
Total mass (g/m^2)	45	998.525	662.618	5.622	2,384.622
Total tissue mass (g/m^2)	45	86.941	56.505	0.352	248.908
Total shell mass (g/m^2)	45	974.088	675.291	2.532	2,622.565
Proportion ≤ 10	45	0.44	0.27	0	0.98
Proportion > 20	45	0.18	0.23	0	0.87
Zebra mussels					
# ($/m^2$)	22	48.2	73.1	2.2	275.6
Total mass (g/m^2)	22	12.037	22.912	0.267	105.074
Total shell mass (g/m^2)	22	11.728	19.378	0.246	87.606
Total tissue mass (g/m^2)	22	0.941	1.394	0.007	5.813

(Systat 2000). To avoid the statistical complications associated with ratios (Jackson *et al.* 1990), we modeled the relationship between quagga tissue mass and shell mass as a linear regression, and then examined the residuals in relation to our environmental variables. Here the residuals represent deviations from the modeled relationship between tissues and shell mass; a positive residual indicates more tissue than expected based on observed shell mass, conversely, a negative residual indicates less tissue than expected based on observed shell mass.

Calculations of nearshore mussel total mass and coverage were based on the importance of depth, upwelling frequency, substrate, and chlorophyll-*a* as factors describing quagga total mass in a multiple regression (see results). In a GIS, we split substrate maps digitized from Rukavina (1969, 1970) first by depth (0–10 m and 10–20 m), then by shore regions (5) that roughly corresponded to areas of high and low upwelling frequency and chlorophyll-*a* concentration. We used samples located within each depth-shore region to estimate total mass and coverage of mussels for each substrate type; if there was more than one sample of a given substrate type for that depth and region, we used the average value. If no corresponding sample was available for

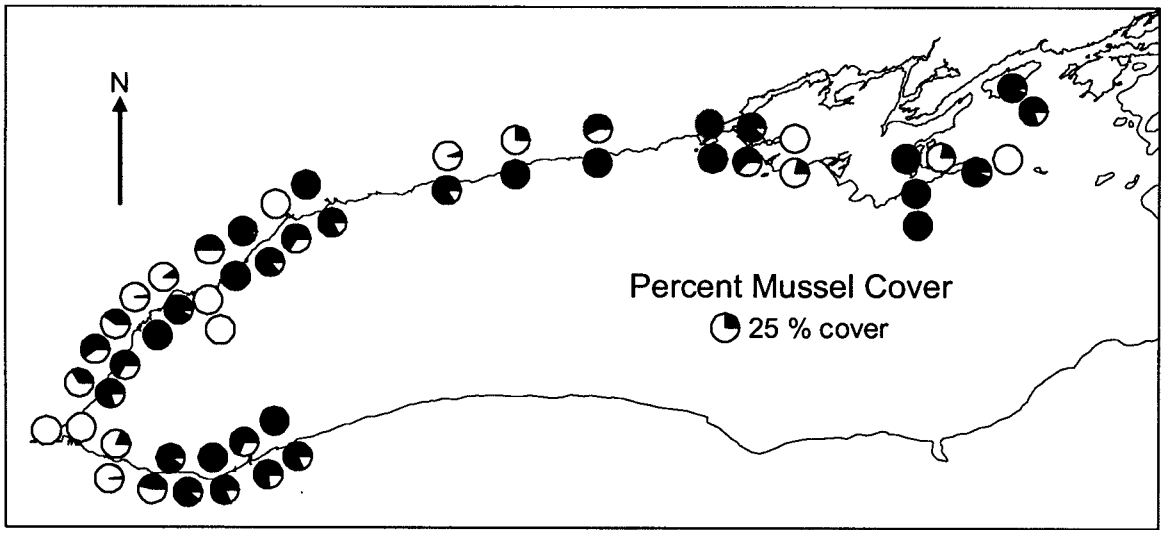

FIG. 2. Dreissenid mussel mean percent cover as observed by divers. Symbols have been shifted from actual site locations to avoid overlap; inshore = 5-m sites, offshore = 20-m sites.

a substrate type, we used a value (or average if available) from other depth-shore regions with similar upwelling frequency and chlorophyll-a concentrations. We did not sample any 5-m silt sites, but because silt sites often contained no mussels at 20 m, we assumed that any mapped shallow silt sites would also not contain dreissenids.

Length Frequency Analysis

For the purposes of this analysis we summed all three replicates from each site to increase the number of individuals in each length class. Length-frequency differences among sites were compared by calculating the proportion of individuals in seven 5-mm length classes (0 to 5, 6 to ≤ 10, 11 to ≤ 15, 16 to ≤ 20, 21 to ≤ 25, 26 to ≤ 30, and >30). Individuals ≤ 5 mm represent recent recruitment; individuals ≤ 10 mm are most likely less than one year old (Baldwin *et al.* 2002). These length classes also encompassed abundant lengths in the data at 10, 15, and 20 mm. Patterns in length frequency classes relative to environmental factors were examined using direct gradient analysis (canonical correspondence analysis (CCA)) with CANOCO (ter Braak and Similauer 1998). Categorical environmental factors were coded as binomial dummy variables and appear as points in the biplots (rather than gradients). Highly correlated environmental factors were discarded as were any factors with CCA inflation factor values > 20.

RESULTS

Distribution and Abundance of Dreissenid Mussels

We found no mussels at seven sites, four of which were 5-m sand sites (7, 13, 16, and 23) and three of which were 20-m silt sites (33, 38, and 50). On average, dreissenid mussels covered 60.5% of the bottom (± 38.3 SD; Fig. 2), and percent cover varied by substrate type: bedrock 78.6 (± 29.0 SD), cobble 72.6 (± 27.0 SD), sand 37.1 (± 40.9 SD), and silt 40.2 (± 45.1 SD). Some sand and silt sites did have high coverage of mussels; if the seven sites with no mussels are excluded, mean cover increases to 52 ± 39.5 SD for sand (n = 10) and 70.4 ± 35.2 SD for silt (n = 4). Quagga mussels dominated at all stations in both numbers and total mass (Table 1, Fig. 3a). Zebra mussels were found at only eight 20-m and fourteen 5-m sites and in low numbers and total mass (Table 1, Fig. 3b). Zebra mussels ranged from 0 to 6.7% of the total dreissenid numbers, and averaged 1.5% at the sites with both mussel species.

Measures of mussel abundance (percent cover, numbers, total mass, total tissue mass, and total shell mass) were strongly correlated within each species (n = 45, Pearson's $r > 0.66$), but zebra mussel measures were uncorrelated with quagga mussel measures (n = 45, Pearson's $r = -0.19$–0.16), even when sites with no zebra mussels were removed from the analysis (n = 22, Pearson's $r < 0.44$) . We

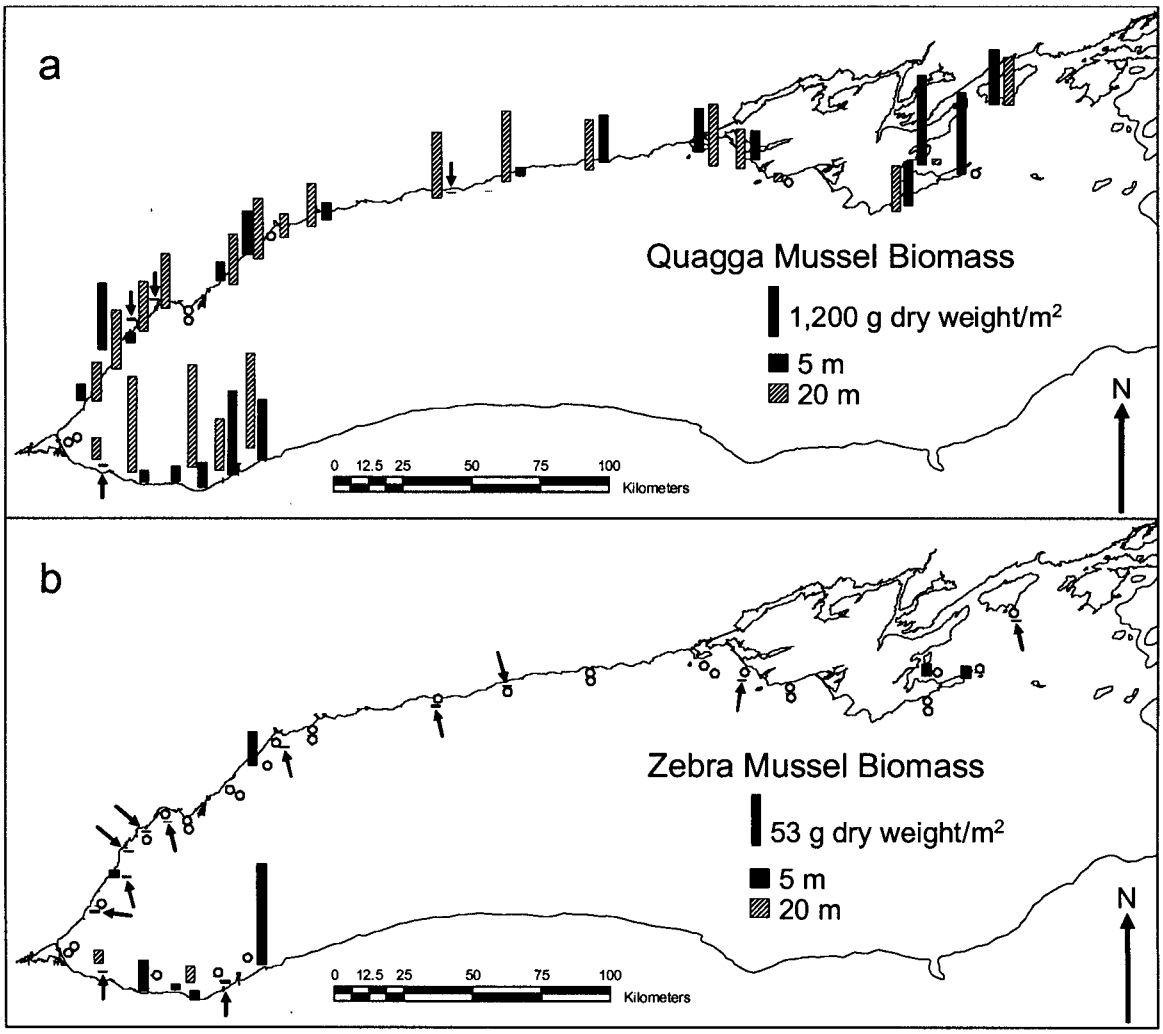

FIG. 3. Dreissenid whole mussel mass. Note that the scale of panel a is almost 23 times greater than panel b as indicated by the vertical bars in each legend. Solid bars = 5-m sites; hatched bars = 20-m sites. a) Quagga mussels. Arrows point to sites with ≤ 30 g mussels/m^2. b) Zebra mussels. Zebra mussels were present at only 22 sites, often in very low numbers. Arrows point to sites with ≤ 3 g mussels/m^2.

used total mass of each species to represent the suite of mussel abundance measures in most analyses because all variables were highly correlated, and we felt total mass would be the easiest measure to obtain for future comparisons.

Environmental Variables

Round gobies were present at 17 sites (Fig. 4a) and ranged in relative abundance from only a few individuals noted by the divers to such high abundances that the bottom appeared to shift and move in video footage. Because gobies appeared to be attracted to the video camera when it was initially lowered to the bottom, we assumed that if gobies were noted by the diver but not seen in the video footage then they were present but in very low numbers. Sculpins (*Cottus* spp.), native bottom-dwelling fishes, were also seen on video, but were only common at sites not occupied by gobies, mostly along the north shore of the lake. Gobies were most abundant in shallow cobble sites near the Niagara River and at two isolated sites on the east end of the lake. In at least two instances, gobies were seen to gather at areas disturbed by the camera frame or diver and consume attached dreissenid

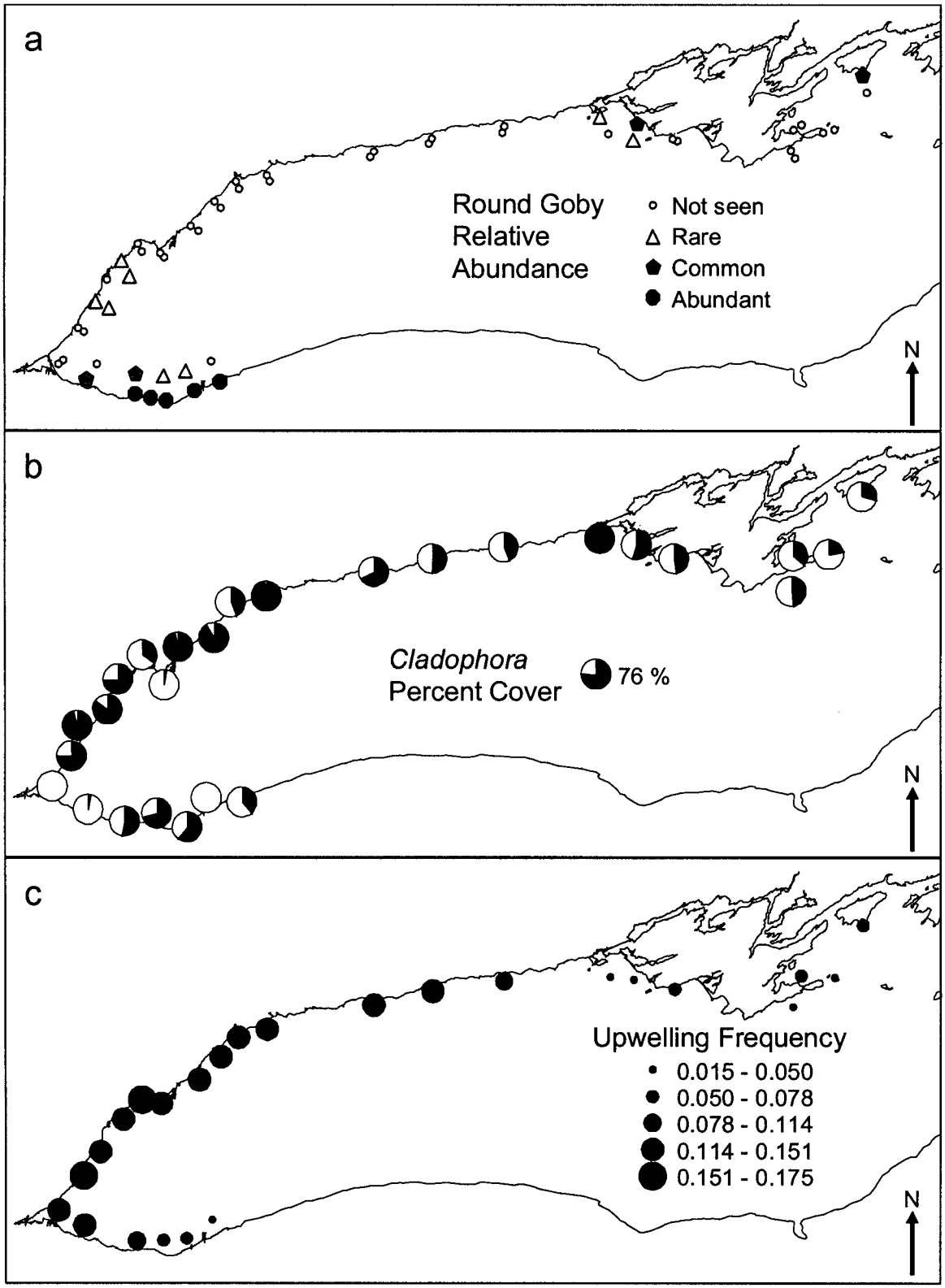

FIG. 4. Spatial distribution of selected environmental variables. a) Round goby relative abundance determined from video and diver observations, b) Cladophora percent cover at 5-m sites as observed by divers, c) upwelling frequency from 15 July to 15 Sept. averaged for 5 years (1999–2003). The values represent the proportion of satellite temperature images of which surface water temperature was < 16°C.

mussels, often by grabbing and twisting to loosen individual mussels.

Cladophora percent cover was positively associated with mussel percent cover ($p < 0.001$), upwelling frequency ($p = 0.02$) and negatively associated with goby relative abundance ($p = 0.048$, multiple $R^2 = 0.55$, n = 27). At the 25 5-m sites at which *Cladophora* was present, it covered, on average, 57.1% of the substrate and averaged 4.7 cm thick (Table1, Fig. 4b). We occasionally observed *Cladophora* growing attached to mussel shells at 20-m stations, although at lower density than at 5 m. Macrophytes were rarely encountered. *Potamogeton* spp. were sparse at seven sites and only one site (25) had abundant macrophytes.

Upwelling frequency ranged from 0.175 along the north shore, to 0.015 near Prince Edward County and 0.050 near the Niagara River mouth (Fig. 4c). In a comparison of real-time AVHRR satellite data for the days we sampled, the satellite information was a good predictor for measured bottom temperature at the 5-m sites ($r^2 = 0.65$, $p < 0.001$) but not at 20-m sites ($r^2 = 0.04$, $p = 0.33$). Of the nine 5-m sites with bottom temperatures < 16°C (our upwelling criteria), all had calculated upwelling frequencies > 0.134, which is well over the mean upwelling value (Table 1), suggesting that satellite-derived upwelling frequency is a good measure of benthic temperatures. The poor correlation between upwelling frequency and bottom temperature (or the real-time AVHRR satellite data) for the 20-m sites is primarily due to six sites along the western shore (sites 28–34) at which bottom temperatures were near 5°C but surface temperatures were near 20°C, potential evidence of a minor upwelling event affecting the deeper sites without changing surface water temperature.

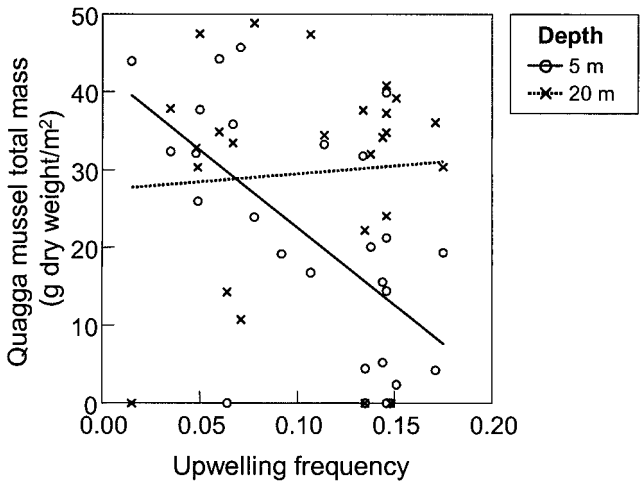

FIG. 5. Quagga mussel total mass vs. upwelling frequency. Quagga total mass decreased significantly with increasing upwelling frequency at 5-m sites ($r^2 = 0.37$, $p = 0.001$; solid line), but not at 20-m sites ($r^2 = 0.005$, $p = 0.74$; dotted line). Quagga total mass is square-root transformed.

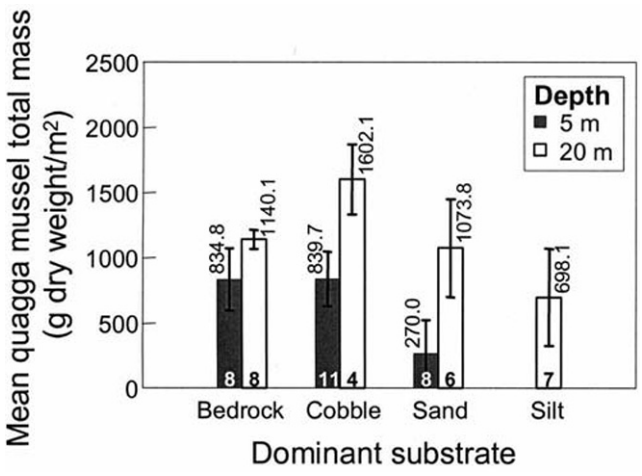

FIG. 6. Mean quagga total mass by depth and substrate type. Mean value for each substrate type is above each bar and the number of sites is written within the bar. Notice that there were no silt sites at 5 m. Error bars = 1 standard error, n = 52.

Associations between Environmental Factors and Quagga Mussel Total Mass

Quagga total mass was best explained by depth ($p = 0.001$), upwelling frequency ($p = 0.001$), substrate ($p = 0.001$) and chlorophyll-*a* concentration ($p = 0.025$, multiple $R^2 = 0.48$, n = 52). If sites with no quagga mussels were excluded from the analysis (n = 45, multiple $R^2 = 0.27$), chlorophyll-*a* and substrate were no longer significant, in part because several silt and sand sites were excluded. Quagga total mass was negatively related to upwelling frequency at 5 m but not 20 m depth (Fig. 5). Quagga total mass was greatest on bedrock and cobble substrates at 20 m depth (Fig. 6). Zebra total mass was negatively related to upwelling frequency ($p = 0.04$) and latitude ($p = 0.05$, multiple $R^2 = 0.32$, n = 22).

Environmental Factors Influencing Tissue and Shell Mass

The regression of quagga tissue mass vs. shell mass was highly significant ($r^2 = 0.86$, $p < 0.001$).

A multiple linear backward stepwise regression found that the tissue-shell residuals were best explained by the proportion of quagga mussels > 20 mm ($p = 0.003$) and chlorophyll-*a* concentration ($p = 0.017$, multiple $R^2 = 0.23$, n = 45). Sites dominated by smaller mussels had more positive residuals, suggesting that small mussels devote proportionately more mass to tissue than shell. Higher chlorophyll-*a* values were associated with more negative residuals suggesting that mussels at sites with higher chlorophyll-a levels devote proportionally less mass to tissue than shell.

In contrast, the regression of zebra mussel tissue vs. shell mass was less significant ($p = 0.001$, $r^2 = 0.46$), and tissue-shell residuals were significantly associated with the attenuation coefficient (k_d) ($p = 0.008$) and upwelling frequency ($p = 0.04$). Generally, tissue vs. shell mass residuals were negative at low k_d values, and positive at high k_d values. Most high k_d values were recorded at 5-m sites where wave action had resuspended bottom sediments, increasing light attenuation rates. Thus, at these "high energy sites" zebra mussels devoted more mass to tissues that shells, whereas at sites with low k_d values (mostly 20-m sites) mussels devoted proportionally less mass to tissue than shells. Patterns in relation to upwelling most likely related to the spatial distribution of zebra mussels.

Mussel Length-frequency Analyses

Of the 260 zebra mussels found in the portion of samples examined, lengths ranged from 5 to 26 mm, with a mean length of 15.7 mm (SD = 4.2). Although our small sample size complicates interpretation of the length-distributions, most sites showed little evidence of recent recruitment: only nine of 22 sites had individuals ≤ 10 mm, and only Site 25 had more than four individuals ≤ 10 mm. Large (> 20 mm) empty zebra mussel shells were often observed at sites with or without live zebra mussels.

In contrast, quagga mussel length-frequency distributions showed abundant recent recruitment, with an average of 14% of the mussels ≤ 5 mm in length, and 44% of mussels ≤ 10 mm in length; 77% of sites had mussels ≤ 5 mm. The proportion of quagga mussels ≤ 5 mm (new recruits) was positively related to latitude ($p = 0.009$) and attenuation coefficient (k_d) ($p = 0.04$), and negatively related to goby relative abundance ($p = 0.02$; multiple $R^2 = 0.49$, n = 45). The proportion of quagga mussels ≤ 10 mm was related to latitude ($p = 0.006$), depth ($p = 0.02$) and goby relative abundance ($p = 0.006$, multiple $R^2 = 0.57$, n = 45). The proportion of mussels ≤ 10 mm was greater at 5-m sites, low at sites with high relative abundance of gobies, and increased with increasing latitude. Latitudinal patterns were driven by sites in the Niagara-Hamilton region (low latitude) that had high goby abundance. Sites with high relative abundance of gobies had low numbers of quagga mussels but not unusually low total mass suggesting that biomass was concentrated in fewer but larger individuals (Fig. 7).

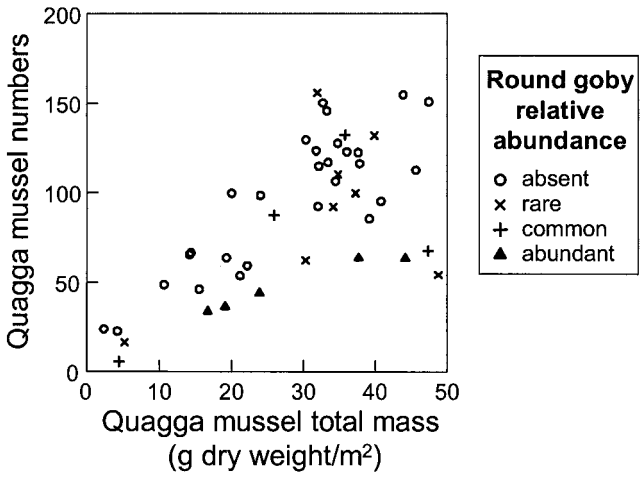

FIG. 7. Quagga number vs. total mass coded by round goby relative abundance. Quagga numbers are low relative to total mass for sites with high goby abundance. Both axes are square root transformed.

A CCA ordination of length classes for all sites containing quagga mussels was highly significant (Fig. 8, Table 2a). Sites with sand substrates and no gobies had large numbers of small individuals (≤ 10 mm; Sites 18, 12, 19, 25, 48, 52); cobble sites with high abundances of gobies were dominated by mussels in the 16 to 25 mm range (Fig. 8). Sites 30, 31, and 32, where gobies were rare or common but not abundant in the videos, were unusual in that they were dominated by very large mussels (> 25 mm in length). Fig. 9 presents representative length-distributions suggested by the ordination.

A CCA ordination of the 5-m sites containing quagga mussels was also significant (Fig. 10, Table 2b). High *Cladophora* percent cover was associated with sites dominated by mussels 6 to 10 mm in length (21, 27, 26, 10, 15, etc.); these sites were also associated with higher levels of total phosphorus. Otherwise, environmental factors were associ-

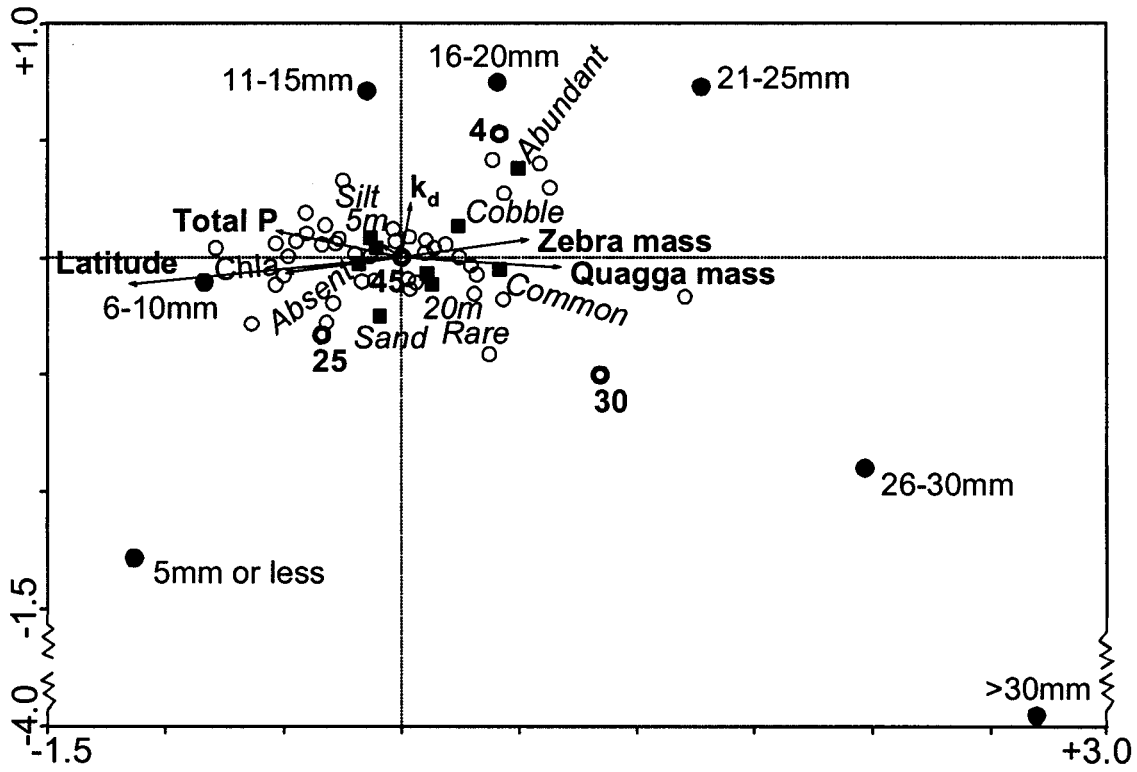

FIG. 8. CCA ordination of quagga mussel length-frequencies at all 52 sites. Substrate type, depth, and goby abundance are categorical variables and represented by centroids (squares). Large solid circles represent length-frequency classes. The lengths of the arrows represent the relative importance of the associated environmental variable. Absent, rare, common, and abundant refer to relative abundance of round gobies. Length-frequencies of highlighted sites (bold circles with site numbers) are illustrated in Figure 9.

ated with sites much in the same patterns as the full data set.

Estimates of Total Quagga Numbers, Total Mass and Percent Cover

Based on substrate type coverage, and an estimated nearshore area of 810.9 km^2 extending from the mouth of the Niagara River to the western shore of Prince Edward County, we calculated a total of 6.32×10^{12} quagga mussels weighing 8.13×10^{11} g dry weight. Using a conversion factor of 0.0269 dry tissue to whole wet mussel (Marvin *et al.* 2000), whole wet mussel mass was approximately 3.02×10^{13} g. Dreissenid mussels completely covered approximately 65.6% of the bottom (531.7 km^2) based on substrate type coverage, similar to the mean percent cover of all sample sites (60.5%).

DISCUSSION

The lasting impression of this work should be of the enormity of change that has occurred in the Lake Ontario nearshore zone from the invasion first of zebra mussels, to the near complete displacement of zebra mussels by quagga mussels. Although dreissenid densities have subsided somewhat from those measured in the early to mid-1990s, the shear magnitude of the effect on bottom habitat is staggering, both on terms of the mussel biomass present (813,000 metric tonnes) and the amount of substrate modified by the presence of mussels (from 60 to 65% of the substrate in the Canadian nearshore alone). Currently, dreissenid mussels are the defining feature of the Lake Ontario benthos.

Evidence of quagga mussel recruitment within the last year (mussels ≤ 10 mm) was common throughout our sampling sites, and most prevalent at 5-m sites with no round gobies present. However,

TABLE 2 a and b. Ordinations of quagga length distributions where the "species" are proportion of individuals in each of seven length categories. A) All sites. DCA environmental gradient = 2.395. The first canonical axis (eigenvalue = 0.168, F = 22.069, p < 0.001) and all canonical axes (Trace = 0.229, F = 2.961, p < 0.001) were significant. Upwelling frequency was an environmental variable, but was removed from the plot because it contributed very little.

A) Axes	1	2	3	4	Total inertia
Eigenvalues	0.168	0.042	0.013	0.004	0.395
Species-environment correlations	0.831	0.715	0.550	0.472	
Cumulative percentage variance					
of species data	42.4	53.1	56.4	57.4	
of species-environment relation	73.1	91.5	97.2	98.9	
Sum of all unconstrained eigenvalues					0.395
Sum of all canonical eigenvalues					0.229

B) Ordination of 5-m sites only. DCA gradient length: 2.531. The first canonical axis (eigenvalue = 0.295, F = 15.309, p = 0.007) and all canonical axes (Trace = 0.385, F = 3.204, p = 0.003) were significant.

(B) Axes	1	2	3	4	Total inertia
Eigenvalues	0.295	0.053	0.024	0.009	0.468
Species-environment correlations	0.946	0.838	0.854	0.640	
Cumulative percentage variance					
of species data	63.0	74.3	79.5	81.4	
of species-environment relation	76.6	90.4	96.7	98.9	
Sum of all unconstrained eigenvalues					0.468
Sum of all canonical eigenvalues					0.385

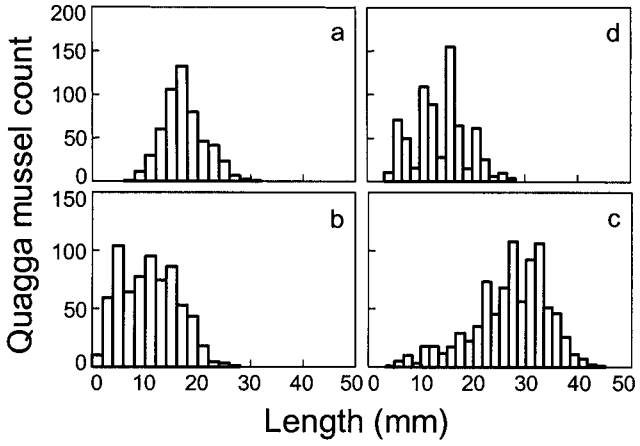

FIG. 9. Representative quagga length distributions suggested by the CCA ordination in Figure 8. Histogram bars represent data counted over 2 mm bins. a) Site 4 (5 m) was dominated by cobble with high relative abundance of round gobies; b) Site 25 (5 m) was dominated by sand with no gobies present; c) Site 30 (20 m) was dominated by sand with gobies rare; d) site 45 (20 m) was dominated by bedrock with no gobies present. Note that the y-axis scale differs between the top and bottom panels.

our sampling dates may have been too early to detect some recruitment events in 2003; Chase and Bailey (1999) reported that zebra mussel spawning at Port Dalhousie, near our sample Site 2, occurred between mid-August and the end of October, indicating that new recruits would be smaller (≤ 5 mm), if present at all, at our sites. We found mussels < 5 mm at 40 of 52 sites suggesting that, although we may have missed later settlement, most sites received new recruitment in 2003. In fact there may have been more sites with new recruitment than we measured because small mussels (< 5 mm) may have been overlooked by divers collecting mussels by hand.

Although zebra mussels are nearly gone from the nearshore of Lake Ontario, quagga mussel densities are in many areas very similar to zebra mussel densities documented during the early to mid 1990s. For instance, zebra mussel abundance near Port Dalhousie in western Lake Ontario at 6 m peaked in 1993 (14,494/m^2) and dropped to 7,916/m^2 in 1994 (Chase and Bailey 1999). In 2003, we found quagga mussels at densities of 3,984/m^2 nearby on similar substrate. In May 1995, Marvin *et al.* (2000) found

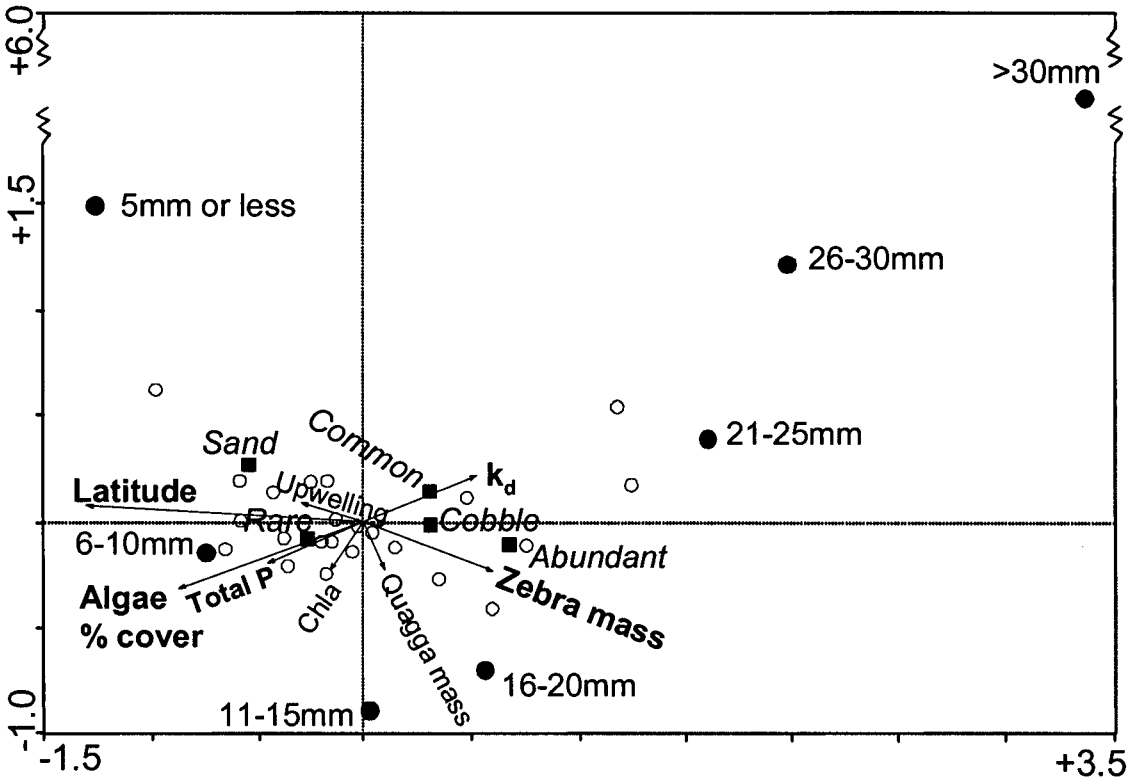

FIG. 10. CCA ordination of quagga mussel length-frequencies at 5-m sites only to show contribution of percent* Cladophora *cover (algae % cover). Substrate type and goby abundance are categorical variables and represented by centroids (squares). Large solid circles represent length-frequency classes. The lengths of the arrows represent the relative importance of the associated environmental variable. Rare, common, and abundant refer to relative abundance of round gobies.

dreissenids at densities of 11,800/m^2 at a depth of 12 m (48% zebra mussels and 52% quagga mussels). We found 12,111/m^2 at our nearby 20-m site on similar substrate (silt). There are, however, few data for nearshore sites with hard underlying substrates because ponar grabs and other ship-board sampling devices frequently used in monitoring efforts do not sample hard surfaces. Thus we must assume that the same process of replacement observed on soft sediments is likely to have occurred on hard substrates.

Our estimates of total numbers and mass of dreissenids in the Canadian nearshore of Lake Ontario are the most complete of which we are aware. These estimates account for substrate type, depth, and spatial variations in mussel mass and numbers. Our estimate is rough in other respects, however; for instance, 5-m mussel densities are likely to over-estimate mussel abundance at 1 or 2 m because shallow-water mussels are often dislodged by waves and ice during winter and the substrate is re-colonized each spring (e.g., Bially and MacIsaac 2000). Likewise, 5-m samples likely underestimate mussel abundances at 9 or 10 meters. In addition, we may have underestimated small (< 5 mm) mussels by collecting mussels by hand. This could lead to a significant underestimation of mussel numbers (but not mass) at high energy sites where mussels might re-colonize each year (i.e., 5 m sand sites). Our values are within the same order of magnitude as those calculated by Bailey *et al.* (1999) for all dreissenids in all of Lake Ontario in 1993 (3.0×10^{10} to 8.7×10^{12} mussels). This discrepancy between estimates may have resulted from different methods of estimation, but most likely demonstrate the significant increase in dreissenid abundance since 1993 concurrent with the replacement of zebra mussels by quagga mussels.

This survey demonstrates that the majority of substrate (with the exception of 5-m sand and 20-m

silt areas) has high coverage of mussels forming extensive patches of a substrate type that did not exist prior to 1990. We found that the underlying substrate type influenced mussel percent cover and total mussel mass, with the greatest numbers found on consolidated substrates (boulder and cobble) and lower numbers on unconsolidated substrates (sand and silt). These results mirror those of Mellina and Rasmussen (1994), who found that substrate size most consistently explained zebra mussel density, and may reflect ease of attachment and substrate stability.

Impact due to site occupation by dreissenid mussels on the habitat once provided by these underlying substrates differs in both magnitude and mechanism. For instance, on flat stretches of bedrock, the physical structure of the mussel beds retains fine particulate matter (Marvin *et al.* 2000) and mussel faeces and pseudo-faeces (Stewart *et al.* 1998), leading to the accumulation of organic and inorganic materials and associated nutrients that otherwise would be deposited in deeper areas of the lake. These materials are utilized by detritivores such as *Gammarus* and the non-native amphipod *Echinogammarus ischnus* (Stewart *et al.* 1998), which consistently increase in abundance with increases in dreissenids (Stewart *et al.* 1998, Haynes *et al.* 1999, Kuhns and Berg 1999). This effect maybe less significant in cobble areas where preexisting interstitial habitat existed for organic matter to accumulate. Sites with underlying unconsolidated substrates (sand and silt) have likely undergone the most dramatic transformation. For instance, at one 20-m silt site, we found 100% mussel cover, and densities averaging 22,744/m^2 in an area that prior to the 1990s would have contained no hard substrate. In addition to changes induced by hard substrate, dense beds of dreissenid mussels alter underlying sediments by reducing dissolved oxygen and modifying nutrient cycling (Frischer *et al.* 2000, Burks *et al.* 2002).

Benthic habitat is changed indirectly by dreissenids through shifts in the distribution of native organisms. We found substantial growths of *Cladophora* at almost all 5-m sites. At hard substrate sites, *Cladophora* grew attached to both the underlying substrate and mussel shells, at times so thickly that the *Cladophora* had to be pushed aside to observe mussels underneath. The facilitating effect of hard substrate provided by the mussels was most apparent at shallow, high-energy sandy sites, where *Cladophora* grew on the mussels but not on unconsolidated sand. Observed occurrences of *Cladophora* represent a substantial increase in coverage since 1981, when *Cladophora* was present in 56% of the 5-m sites (Barton 1986) and 1991, when *Cladophora* was present at 48% of the 5-m sites (Kilgour *et al.* 1995). We commonly observed low densities of *Cladophora* attached to quagga mussels at the 20-m sites, where it was absent in 1981 and 1991 (OMOE unpublished data, Barton 1986). This response is consistent with increases in water clarity observed in the presence of dreissenids (e.g., Howell *et al.* 1996). Hecky *et al.* (2004) have suggested that by filtering the water column and releasing nutrients directly into the water or to the sediments as faeces and pseudo-faeces, quagga mussels shunt nutrients to nearshore areas, making these nutrients readily available for *Cladophora* (Hecky *et al.* 2004). *Cladophora* thus potentially benefits from the hard substrate provided by mussel shell, the increased water clarity from mussel filtering, and the relocation of nutrients from water column to the benthic environment through mussel excretions (Hecky *et al.* 2004).

Persistent populations of dreissenid mussels have the potential to affect contaminant cycling in the nearshore, and these contributions will change over time as quagga mussels are further integrated into the food web. By filtering particulate matter from tributary discharge before these enriched and often contaminated waters mix with lake water, quagga mussels may hold contaminants in the nearshore where they may be more easily incorporated in the food web (Hecky *et al.* 2004). The amphipods *Gammarus* and *Echinogammarus* both scavenge mussel faeces and pseudo-faeces, and are in turn eaten by fish (Vanderploeg *et al.* 2002). Nearshore populations of quagga mussels are directly consumed by waterfowl such as lesser and greater scaup and bufflehead (Petrie and Knapton 1999), and newspapers have recently reported the consumption of dreissenids by yellow perch in the St. Lawrence River. A more recent development involves the invasion of the round goby, which readily consumes quagga and zebra mussels, as well as the invertebrates that live in association with dreissenid colonies. The round goby itself is readily consumed by predatory fish and diving birds (e.g., Somers *et al.* 2003) and may provide a direct link between dreissenids and higher trophic levels.

The replacement of zebra mussels by quagga mussels in the Great Lakes (Mills *et al.* 1999) has mirrored changes that occurred in reservoirs in the Dneiper River basin in the Ukraine from 1960–1970s (Mills *et al.* 1996). Quagga and zebra

mussels arrived in Lake Ontario within a few years of each other (Mills *et al.* 1993), but initially zebra mussels colonized the shallow nearshore and quagga mussels colonized the deeper (profundal) areas (Mills *et al.* 1993). Baldwin *et al.* (2002) found that juvenile zebra and quagga mussels had similar growth rates at high levels of food, but quagga mussels grew marginally in cold, low food scenarios (i.e., profundal conditions at 6°C) whereas zebra mussels lost weight. These results are similar to those of MacIsaac (1994) for juvenile mussels grown in eastern Lake Erie. It has been suggested that zebra mussels facilitated (e.g., Ricciardi 2001) the quagga mussel population expansion by reducing food availability to levels at which the quagga mussel was a superior competitor (Baldwin *et al.* 2002). Other factors that may contribute to the replacement of zebra mussels by quagga mussels include lower respiration rates in quagga mussels and lower allocation of energy towards reproduction, allowing for greater growth and, presumably, energy reserves for stress situations (Stoeckmann 2003). Our data give little insight into these possible mechanisms, although, intriguingly, we found zebra mussels most abundant in the area where they first colonized (from the outflow of the Niagara River) around 1989 (Griffiths *et al.* 1991) and at the tip of Prince Edward County where zebra mussels were located as early as 1991 (Kilgour *et al.* 2000). This suggests that these areas are in some way better for zebra mussels and so these local populations are self-sustaining. Alternatively, these sites may receive propagules from "up river" but this scenario is unlikely given quagga mussel dominance of both the Niagara River (ASE-Group-Project-E20473 2004) and eastern Lake Erie (Mills *et al.* 1999). These small concentrations of zebra mussels may also represent periodic re-introductions from transoceanic vessels; the areas near the Niagara River and eastern Prince Edward County intersect shipping lanes at the 20 m contour, and these same areas were the first to receive other invasive organisms (e.g., *Potamopyrgus antipodarum* (Zaranko *et al.* 1997) and the round goby, this study).

The role of coldwater upwellings in structuring benthic communities in the Great Lakes is likely more important than generally assumed. In Lake Ontario, the area subjected to extreme upwelling events was the last to be colonized by zebra mussels in the early 1990s (Stewart *et al.* 1994, Kilgour *et al.* 2000), and has few zebra mussels today. We also found lower total mass of quagga mussels at 5-m sites in this area. To our knowledge, this is the first reported instance in which coldwater upwellings have been associated with reduced levels of benthic biomass in the Great Lakes. There is, however, evidence from sampling done at approximately the same sites in 1981 and 1991, that upwellings influence benthic invertebrate community composition (Barton 1986, Kilgour *et al.* 2000) and a suggestion that upwellings along Lake Ontario's north shore may be responsible for the paucity of benthic invertebrate species in shallow water (0 to 2 m) relative to other Great Lakes (Barton and Hynes 1978). Water temperature fluctuations associated with upwelling events can be extreme for nearshore environments: during the upwelling event that occurred during our 2003 sampling, bottom water temperatures at 5 m averaged 20.3°C along the southwest shore (and northeast shoreline), and 9.7°C only kilometers away along the north shore. We feel that our measure of upwelling frequency is, if anything, conservative, because it only measured cold water events that reached the surface, and would have missed ecologically important upwelling events such as one in Georgian Bay, Lake Huron, where divers observed benthic fish and crayfish deaths after a rapid cold water intrusion that did not reach the surface (Emery 1970). This may be one explanation as to why we did not see an association with upwelling on our 20-m sites which likely experience lower (< 16°C) temperatures on a more regular basis during the summer stratification period.

Results from several studies including this one suggest that round gobies will shift dreissenid mussel length-frequency distributions by preferentially consuming smaller mussels (Ray and Corkum 1997). It is unlikely that high densities of round gobies will significantly impact recruitment in future years by eliminating cohorts because small mussels survive goby predation when they are located beneath rocks or wedged between larger mussels (Djuricich and Janssen 2001). However, there may be other indirect effects mediated by round gobies. Shifts in length-frequency distributions may alter rates of filtration and pseudo-faeces production (Young *et al.* 1996). The physical structure of mussel beds may also change as a result of goby foraging, with greater patchiness in mussel cover and an increase in shell fragments. Round gobies continue to rapidly expand their range in Lake Ontario and the other Great Lakes, ensuring that the structure and function of the mussel beds will remain dynamic in future years.

Driessenid mussels have now been an important feature of the Lake Ontario nearshore since the early 1990s, and are associated with shifts in both habitat (e.g., increases in hard substrate and light) and biotic interactions. By the summer of 2003, quagga mussels had nearly replaced zebra mussels along the north shore of Lake Ontario and covered an estimated 65.6% of the substrate between the shore and 20 m in depth. We are now faced with a new, rather ironic, risk: disturbance to the extensive mussel beds, due to predation, disease, or recruitment failure, may result in the release of nutrients, contaminants, and fine sediments currently associated with the mussel beds, leading to adverse effects on water quality and food webs in the nearshore of Lake Ontario.

ACKNOWLEDGMENTS

We would like to thank the efforts of Ontario Ministry of the Environment staff (V. Kopalle, R. Duval, G. Stronghill) with help with GIS applications and G. Hobson and R. Dolliver for their help in the field. We also would like to thank the divers for POLLUTECH EnviroQuatics Limited who did the field collections. We greatly appreciated the access and assistance with the AVHRR images used in calculating upwelling frequency (G. Leshkevich and the NOAA Great Lakes CoastWatch program). Finally, two anonymous reviewers and D. Barton contributed greatly to the paper. K.A.W. was supported through a postdoctoral fellowship funded through the Ontario Ministry of the Environment and the Canada Ontario Agreement program.

REFERENCES

ASE-Group-Project-E20473. 2004. *Enhanced bio-monitoring program on the Niagara River—Final Report for the Ontario Ministry of the Environment.* OMOE contact: L. Richman.

Bailey, R.C., Grapentine, L., Stewart, T.J., Schaner, T., Chase, M.E., Mitchell, J.S., and Coulas, R.A. 1999. Dreissenidae in Lake Ontario: Impact assessment at the whole lake and Bay of Quinte spatial scales. *J. Great Lakes Res.* 25:482–491.

Baldwin, B.S., Mayer, M.S., Dayton, J., Pau, N., Mendilla, J., Sullivan, M., Moore, A., Ma, A., and Mills, E.L. 2002. Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes. *Can. J. Fish. Aquat. Sci.* 59:680–694.

Barton, D.R. 1986. Nearshore benthic invertebrates of the Ontario waters of Lake Ontario. *J. Great Lakes Res.* 12:270–280.

———, and Hynes, H.B.N. 1978. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. *J. Great Lakes Res.* 4:27–45.

Bially, A., and MacIsaac, H.J. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshw. Biol.* 43:85–97.

Burks, R.L., Tuchman, N.C., Call, C.A., and Marsden, J.E. 2002. Colonial aggregates: effects of spatial position on zebra mussel responses to vertical gradients in interstitial water quality. *J. N. Am. Benthol. Soc.* 21:64–75.

Chase, M.E., and Bailey, R.C. 1999. The ecology of the zebra mussel (*Dreissena polymorpha*) in the lower Great Lakes of North America: I. Population dynamics and growth. *J. Great Lakes Res.* 25:107–121.

Djuricich, P., and Janssen, J. 2001. Impact of round goby predation on zebra mussel size distribution at Calumet Harbor, Lake Michigan. *J. Great Lakes Res.* 27:312–318.

Emery, A.R. 1970. Fish and crayfish mortalities due to an internal seiche in Georgian Bay, Lake Huron. *J. Fish. Res. Board Can.* 27:1165–1168.

Frischer, M.E., Nierzwicki-Bauer, S.A., Parsons, R.H., Vathanodorn, K., and Waitkus, K.R. 2000. Interactions between zebra mussels (*Dreissena polymorpha*) and microbial communities. *Can. J. Fish. Aquat. Sci.* 57:591–599.

Griffiths, R.W., Schloesser, D.W., Leach, J.H., and Kovalak, W.P. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 48:1381–1388.

Haynes, J.M., Stewart, T.W., and Cook, G.E. 1999. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena*: Continuing change. *J. Great Lakes Res.* 25:828–838.

Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N., and Howell, T. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61:1285–1293.

Howell, E.T., Marvin, C.H., Bilyea, R.W., Kauss, P.B., and Somers, K. 1996. Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. *J. Great Lakes Res.* 22:744–756.

Jackson, D.A., Harvey, H.H., and Somers, K.M. 1990. Ratios in aquatic sciences—statistical shortcomings with mean depth and the morphoedaphic index. *Can. J. Fish. Aquat. Sci.* 47:1788–1795.

Jude, D.J., Reider, R.H., and Smith, G.R. 1992. Establishment of Gobiidae in the Great-Lakes Basin. *Can. J. Fish. Aquat. Sci.* 49:416–421.

Kilgour, B.W., Bailey, R.C., Howell, E.T., and Morton, W.M. 1995. *Nearshore benthos of Lake Ontario 1981 and 1991, Volume 1—Main Findings.* Final Report

prepared by Water Systems Analysts for the Ontario Ministry of the Environment and Energy.

_____, Bailey, R.C., and Howell, E.T. 2000. Factors influencing changes in the nearshore benthic community on the Canadian side of Lake Ontario. *J. Great Lakes Res.* 26:272–286.

Kuhns, L.A., and Berg, M.B. 1999. Benthic invertebrate community responses to round goby (*Neogobius melanostomus*) and zebra mussel (*Dreissena polymorpha*) invasion in southern Lake Michigan. *J. Great Lakes Res.* 25:910–917.

Lavrentyev, P.J., Gardner, W.S., and Yang, L.Y. 2000. Effects of the zebra mussel on nitrogen dynamics and the microbial community at the sediment-water interface. *Aquat. Microb. Ecol.* 21:187–194.

MacIsaac, H.J. 1994. Comparative growth and survival of *Dreissena polymorpha* and *Dreissena bugensis*, exotic mollusks introduced to the Great Lakes. *J. Great Lakes Res.* 20:783–790.

Marvin, C.H., Howell, E.T., and Reiner, E.J. 2000. Polychlorinated dioxins and furans in sediments at a site colonized by *Dreissena* in western Lake Ontario, Canada. *Environ. Toxicol. Chem.* 19:344–351.

_____, M.T., Howell, E.T., Kolic, T.M., and Reiner, E.J. 2002. Polychlorinated dibenzo-*p*-dioxins and bibenzofurans and dioxinlike polychlorinated biphenyls in sediments and mussels at three sites in the lower Great Lakes, North America. *Environ. Toxicol. Chem.* 21:1908–1921.

Mellina, E., and Rasmussen, J.B. 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physicochemical factors. *Can. J. Fish. Aquat. Sci.* 51:1024–1036.

Mills, E.L., Dermott, R.M., Roseman, E.F., Dustin, D., Mellina, E., Conn, D.B., and Spidle, A.P. 1993. Colonization, ecology, and population-structure of the quagga mussel (Bivalvia, Dreissenidae) in the lower Great-Lakes. Can. *J. Fish. Aquat. Sci.* 50:2305–2314.

_____, Rosenberg, G., Spidle, A.P., Ludyanskiy, M., Pligin, Y., and May, B. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. *American Zoologist* 36:271–286.

_____, Chrisman, J.R., Baldwin, B., Owens, R.W., O'Gorman, R., Howell, T., Roseman, E.F., and Raths, M.K. 1999. Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *J. Great Lakes Res.* 25:187–197.

_____, Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Holeck, K.T., Hoyle, J.A., Johannsson, O.E., Lantry, B.F., and Makarewicz, J.C. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). *Can. J. Fish. Aquat. Sci.* 60:471–490.

Nalepa, T.F., Wojcik, J.A., Fanslow, D.L., and Lang, G.A. 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: Population recruitment, density, and size structure. *J. Great Lakes Res.* 21:417–434.

Neilson, M.A., and Stevens, R.J.J. 1987. Spatial heterogeneity of nutrients and organic-matter in Lake-Ontario. *Can. J. Fish. Aquat. Sci.* 44:2192–2203.

Petrie, S.A., and Knapton, R.W. 1999. Rapid increase and subsequent decline of zebra and quagga mussels in Long Point Bay, Lake Erie: Possible influence of waterfowl predation. *J. Great Lakes Res.* 25:772–782.

Rao, Y.R., Skafel, M.G., Howell, T., and Murthy, R.C. 2003. Physical processes controlling taste and odor episodes in Lake Ontario drinking water. *J. Great Lakes Res.* 29:70–78.

Ray, W.J., and Corkum, L.D. 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus. Environ. Biol. Fishes* 50:267–273.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? *Can J. Fish. Aquat. Sci.* 58:2513–2525.

_____, Whoriskey, F.G., and Rasmussen, J.B. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Can. J. Fish. Aquat. Sci.* 54:2596–2608.

Rukavina, N.A. 1969. Nearshore sediment survey of western Lake Ontario, methods and preliminary results. In *Proc. 12th Conf. Great Lakes Res. Part 1*, pp. 317–324. Internat. Assoc. Great Lakes Res.

_____. 1970. Lake Ontario nearshore sediments, Whitby to Wellington, Ontario. In *Proc. 13th Conf. Great Lakes Res. Part 1*, pp. 266–273. Internat. Assoc. Great Lakes Res.

Simons, T.J., and Schertzer, W.M. 1987. Stratification, currents, and upwelling in Lake-Ontario, summer 1982. *Can. J. Fish. Aquat. Sci.* 44:2047–2058.

Somers, C.M., Lozer, M.N., Kjoss, V.A., and Quinn, J.S. 2003. The invasive round goby (*Neogobius melanostomus*) in the diet of nestling double-crested cormorants (*Phalacrocorax auritus*) in Hamilton Harbour, Lake Ontario. *J. Great Lakes Res.* 29:392–399.

Stewart, T., Hoyle, J., and Schaner, T. 1994. *Lake Ontario Fisheries Unit—1993 Annual Report (Chapter 6: Zebra mussel studies)*. ISSN 0838-5653, Ontario Ministry of Natural Resources.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. *J. N. Am. Benthol. Soc.* 17:81–94.

Stoeckmann, A. 2003. Physiological energetics of Lake Erie dreissenid mussels: a basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. *Can. J. Fish. Aquat. Sci.* 60:126–134.

Systat. 2000. Version 10, SPSS Inc., Chicago.

ter Braak, C.J.F., and Similauer, P. 1998. CANOCO for Windows Version 4.02, Centre for Biometry

Wageningen, CPRO-DLO, Wageningen, The Netherlands.

Vadeboncoeur, Y., Vander Zanden, M.J., and Lodge, D.M. 2002. Putting the lake back together: reinventing benthic pathways into lake food web models. *BioScience* 52:44–54.

Van Overdijk, C.D.A., Grigorovich, I.A., Mabee, T., Ray, W.J., Ciborowski, J.J.H., and MacIsaac, H.J. 2003. Microhabitat selection by the invasive amphipod *Echinogammarus ischnus* and native *Gammarus fasciatus* in laboratory experiments and in Lake Erie. *Freshw. Biol.* 48:567–578.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 59:1209–1228.

Young, B.L., Padilla, D.K., Schneider, D.W., and Hewett, S.W. 1996. The importance of size-frequency relationships for predicting ecological impact of zebra mussel populations. *Hydrobiologia* 332:151–158.

Zaranko, D.T., Farara, D.G., and Thompson, F.G. 1997. Another exotic mollusc in the Laurentian Great Lakes: The New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). *Can. J. Fish. Aquat. Sci.* 54:809–814.

Submitted: 9 March 2005
Accepted: 22 October 2005
Editorial handling: David R. Barton

APPENDIX A. Pearson correlations of environmental variables (n = 52). Bolded values are significant at alpha = 0.05 (Bonferoni corrected). Values for algae thickness and algae % cover are calculated for 5-m sites only (n = 27). Measurement units are listed in Table 1.

	Latitude	Longitude	Upwelling	Attenuation coef.	Secchi depth	Alkalinity	Conductivity	Chlorophyll-*a*	Total nitrogen	Total phosphorus	Quagga mass	Zebra mass	Algae thickness	Algae % cover
Lat.	1.00													
Long.	**0.80**	1.00												
Upwelling	–0.23	**–0.70**	1.00											
Atten. Coef.	–0.31	–0.17	–0.10	1.00										
Secchi	0.37	0.24	0.09	**–0.61**	1.00									
Alkal.	0.31	0.19	–0.20	–0.13	0.00	1.00								
Cond.	–0.10	–0.44	**0.56**	0.02	–0.14	0.25	1.00							
Chl–*a*	0.33	**0.61**	**–0.64**	–0.09	–0.06	**0.56**	–0.07	1.00						
Total N	–0.26	**–0.62**	**0.62**	0.03	–0.19	0.31	**0.95**	–0.14	1.00					
Total P	0.25	–0.04	0.13	–0.09	–0.07	**0.77**	**0.74**	0.37	**0.75**	1.00				
Quagga mass	0.00	0.14	–0.28	–0.18	0.24	–0.17	–0.27	–0.04	–0.30	–0.25	1.00			
Zebra mass	–0.40	–0.18	–0.12	0.39	–0.15	–0.31	–0.22	–0.12	–0.17	–0.32	0.28	1.00		
Algae thickness	0.39	0.09	0.06	–0.24	0.46	0.42	0.11	0.02	0.14	0.39	0.01	–0.03	1.00	
Algae % cover	0.24	–0.03	0.15	–0.12	0.39	0.25	0.10	–0.03	0.12	0.25	0.14	0.06	**0.74**	1.00