Abundance of *Dreissena polymorpha* and *Dreissena bugensis* in a warmwater plume: effects of depth and temperature

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Abstract: The generalization that quagga mussel (*Dreissena bugensis*) and zebra mussel (*Dreissena polymorpha*) occur in deep–cold water and shallow–warm water, respectively, is inappropriate. We estimated dreissenid densities at sites affected by warmwater discharges into Lake Erie (Nanticoke, Ontario) to separate the effects of depth and temperature. Both species' densities increased with depth. After controlling for depth, quagga mussel were more abundant at thermally enriched sites than at sites unaffected by the discharge. This suggests that quagga mussel may occur in deep water not because such sites are cooler in summer, but because they are warmer over winter because of the inverse stratification in the range 0–4°C. Zebra mussels were unaffected by the warmwater plume at a broad scale, but were almost entirely absent from a site at the mouth of the discharge canal. This is inconsistent with previous indications that zebra mussel can tolerate higher temperatures than quagga mussel. Even in shallow water unaffected by the discharge, quagga mussel were more abundant than zebra mussel. Because Nanticoke was among the first places in North America to be colonized by quagga mussel, their numerical dominance at Nanticoke may be followed by similar changes in other nearshore areas of the lower Great Lakes.

Résumé : La généralisation selon laquelle la moule quagga (*Dreissena bugensis*) et la moule zébrée (*Dreissena polymorpha*) se retrouvent dans des eaux froides et profondes et dans des eaux chaudes et peu profondes, respectivement, ne tient pas. Afin de distinguer les effets de la température de ceux de la profondeur, nous avons estimé la densité des dreissénidés dans des stations du lac Érié soumises à des rejets d'eaux chaudes, à Nanticoke (Ontario). Pour les deux espèces, la densité augmentait avec la profondeur. Une fois éliminé l'effet de la profondeur, la moule quagga était plus abondante dans les stations enrichies par la chaleur que dans celles non soumises au rejets. Il est donc possible que ce mollusque se retrouve dans les eaux profondes non pas parce que celles-ci sont plus froides en été, mais parce qu'elles sont plus chaudes en hiver à cause de la stratification inverse des eaux de 0 à 4°C. Le panache d'eaux chaudes n'avait aucun effet à grande échelle sur la moule zébrée, mais cette espèce était presque complètement absente d'une station située à l'embouchure de l'émissaire. Ces constatations contredisent les indications antérieures selon lesquelles la moule zébrée pourrait tolérer des températures plus élevées que la moule quagga. Même dans les eaux peu profondes non touchées par les rejets, la moule quagga était plus abondante que la moule zébrée. Comme Nanticoke est une des premières localités nord-américaines à être envahie par la moule quagga, la dominance numérique de cette espèce à Nanticoke risque d'être suivie d'une évolution semblable dans d'autres zones côtières des Grands Lacs inférieurs.
[Traduit par la Rédaction]

Introduction

Dreissenid mussels are now prominent members of benthic communities in the southern Laurentian Great Lakes and St. Lawrence River and have colonized several other drainage basins in North America. Two dreissenid species are present. Zebra mussel, *Dreissena polymorpha*, were first identified in Lake St. Clair in 1988 (Hebert et al. 1989). Quagga mussel, *Dreissena bugensis*, were first distinguished in Lake Ontario in 1991 (May and Marsden 1992) and identified as *D. bugensis* in 1994 (Rosenberg and Ludyanskiy 1994; Spidle et al. 1994).

Zebra mussel generally reach their highest densities in warm, shallow water, whereas quagga mussel occur in colder, deeper water (Dermott and Munawar 1993; Mills et al. 1993). These patterns of occurrence may reflect different species habitat preferences. However, because depth and temperature tend to be correlated within a lake, especially during the ice-free season, it is difficult to distinguish patterns of abundance associated with depth from those of temperature. For example, Mills et al. (1993) found that quagga mussel numbers in Lake Ontario increased linearly with increasing depth and declined linearly with increasing bottom temperature, which also declined with increasing depth.

Examination of mussel populations in areas affected by heated water discharges from industrial plants and power stations solves this difficulty. The discharges form warmwater plumes, partially uncoupling depth and temperature and providing an opportunity to look at their independent effects.

Such an analysis is possible at Nanticoke, Ontario, where Ontario Hydro operates a coal-fired generating station (Wiancko 1981). Heated water from the station's condenser

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cooling system empties into the northeastern end of Long Point's outer bay, in the eastern basin of Lake Erie. The resulting plume generally flows eastward from the station towards Peacock Point, although its extent and location vary with winds, currents, and the water discharge rate from the station. Ontario Hydro has conducted studies to determine the extent and behaviour of the Nanticoke warmwater plume (summarized in Burchat 1984): winds and currents push the plume eastward along the shoreline 56% of the time, offshore 22%, westward along the shoreline 16%, and split onshore 6%. Eastward, the affected area can extend past Peacock Point. In the summer, the plume floats on the surface; when ambient lake temperature drops below 4°C, the plume sinks and runs across the lake bottom.

Both zebra and quagga mussels occur at Nanticoke. Zebra mussel were first observed at Nanticoke in 1989 (Griffiths et al. 1991). Quagga mussel had settled at the station by 1992 (Mills et al. 1993), and may have been present at Nanticoke as early as 1987 (Domm et al. 1993). Both species are now abundant along the Nanticoke shoreline, attached to loose cobble and rubble overlying bedrock in shallow water, and on cobble and clam shells on silt–clay in deeper water.

In this study, we sampled mussels at sites varying in depth, both inside and outside of the area influenced by the Nanticoke warmwater plume. We examined the variation with depth in each species' abundance. Then, having controlled for depth, we looked at the pattern of the residual variation in relation to the warmwater plume.

Methods

In June 1993, we sampled 38 sites between Stelco Pier and Peacock Point, a stretch of shoreline approximately 8 km long centered on the Nanticoke Generating Station (see Fig. 2*a*). Sites were 100–2000 m offshore. Depth, bottom temperature, underlying substrate type, and the extent of algal cover at each site were recorded.

Mussels were sampled by collecting rocks or other hard objects from the lake bottom and then scraping the attached mussels from them. (Although the particles collected were sometimes clam shells, we refer to all particles as rocks.) Three rocks were collected by divers at each site. The diver placed a plastic bag over his hand, picked up the rock, then inverted the bag over it. Rocks collected were selected randomly using quadrats and randomly preselected grid coordinates. At the surface, water was drained from the bag and replaced with sufficient ethanol (95%) to immerse the rock.

For each rock, we recorded the number of mussels present and its size. Mussels were scraped from each rock, separated by species, and counted. Species identification proved difficult for newly settled (very small) mussels, so only mussels longer than 1 mm were counted. Surface areas of rocks were determined by wrapping the rocks in aluminum foil, weighing the foil, and then comparing that weight to the weight of a known area of foil (Reice 1980).

Large rocks are expected to have more mussels attached to them than small rocks. However, the relationship between rock size and mussel number need not be isometric, so crude mussel density (i.e., number of mussels per rock surface area) is not an appropriate measure of abundance. Previous workers have found that variation in mussel number with particle size is best described using an allometric function (Hamilton 1992; Wisenden 1993). Therefore, in our analyses, we log-transformed both mussel number and rock surface area. We then controlled for rock surface area in statistical analyses by using it as a separate predictor in our models.

Separate multiple regressions were performed for quagga and zebra mussels to examine, for each species, the relationship between the number of mussels and water depth, while controlling for rock surface area. Because the depth relationships were potentially nonlinear, polynomial regressions were used (a depth^2 term was included as a predictor). Two-way interactions between rock surface area and both depth terms were also included in the models.

The location of the warmwater plume is not fixed, so sites could not be assigned fixed temperatures or temperature profiles. This meant that the effect of temperature could not be examined directly. Instead, residuals from the previously described regressions were examined to see whether percent deviation from the predicted number of mussels was consistent with each sample's general proximity to the warmwater plume. The residual from a regression of mussel number against depth is the component of total variation that is unexplained by depth. The Nanticoke warmwater plume runs either eastward along shore or else offshore 80% of the time in the same direction and can extend past Peacock Point (Burchat 1984). Therefore, in our analyses, we considered all sites east of the discharge canal mouth to be affected by the plume. For each species, we compared the median percent deviations inside and outside the plume using Mann–Whitney *U* tests.

Results

Shallow sites were generally warmer and often had a bedrock substrate. Concentrations of filamentous algae were dense at some shallow sites. Deep sites were cooler, algal growth was less evident, and the substrate was often silt or clay (Table 1). At the shallowest site sampled, MA1, few mussels were attached to the rocks collected, but there were many byssal scars where mussels had previously been attached. Temperature at most sites varied between 10 and 17°C. An exception was the site at the mouth of the discharge canal (PL), where the bottom temperature was 27°C.

Both species were present at all sites and quagga mussel outnumbered zebra mussel at each. Mussels occurred in high densities only on loose, overlying particles. Small mussels were occasionally seen attached to bedrock at shallow sites, and outcrops and crevices were often heavily colonized. Mussels occurred singly or in small druses lying on silt–clay in deeper water. These mussels were not sampled, but in neither case did densities appear to approach those on cobble and rubble.

Depth

Depth and rock surface area were both significant predictors of quagga mussel abundance (Fig. 1*a*; Table 2). Depth explained 34.9% of variation in quagga mussel counts among rocks. Rock surface area explained 10.7%, and the interaction between rock surface area and depth explained a further 1.5%. In shallow water, the rock surface area coefficient was greater than one, so that the number of mussels per unit area increased with rock size. In water deeper than 6.2 m, the coefficient dropped below one, and densities were greatest on smaller rocks. Quagga mussel density increased with depth but as a decreasing function. Extrapolating from our model, quagga mussel densities would reach a maximum at 15 m for rocks 30 cm^2 in surface area, and at 9 m for rocks 610 cm^2 in surface area (the range of rock sizes sampled in this study).

Both depth and rock surface area were also significant predictors of zebra mussel density (Fig. 1*b*; Table 1). Unlike the situation for quagga mussel, the effect of depth on zebra mussel was linear and there was no interaction between depth and rock surface area. Rock surface area explained 13% of the

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Table 1. Characteristics of the 38 point samples (Fig. 2*a*) taken between Stelco Pier and Peacock Point in June, 1993.

Site	Latitude (N)	Longitude (W)	Depth (m)	Temperature (°C)	Algae	Substrate
ST1	42°47.384′	80°04.819′	3.2	14.0	1	Bedrock
ST2	42°47.162′	80°04.720′	3.3	13.5	15	Bedrock
ST3	42°46.865′	80°04.597′	10.3	11.0	None	Sand–clay
ST4	42°46.551′	80°04.566′	11.0	11.2	Sparse	Silt–clay
ST5	42°46.242′	80°04.429′	11.9	10.0	Sparse	Silt–clay
MA1	42°47.749′	80°04.138′	1.8	14.5	1	Bedrock
MA2	42°47.494′	80°03.976′	6.4	12.0	Sparse	Bedrock
MA3	42°47.246′	80°03.906′	7.3	12.1	5	Bedrock
MA4	42°46.907′	80°03.920′	11.0	11.2	Sparse	Silt–clay
MA5	42°46.624′	80°03.893′	11.6	11.1	None	Silt–clay
NW1	42°47.612′	80°03.236′	3.7	14.5	10	Bedrock
NW2	42°47.255′	80°03.096′	9.4	11.1	None	Bedrock
NW3	42°47.070′	80°03.001′	10.7	11.1	None	Silt–clay
NW4	42°46.680′	80°03.538′	11.3	12.0	None	Silt–clay
NW5	42°46.379′	80°03.500′	11.6	12.2	1	Silt–clay
NE4	42°46.719′	80°02.153′	7.9	12.5	8	Bedrock
NE5	42°46.385′	80°02.033′	8.8	12.2	5	Bedrock
PL	—	—	3.7	28.9	None	Bedrock
NB1	42°48.367′	80°01.996′	2.1	17.0	15–20	Bedrock
NB2	42°48.096′	80°01.953′	6.1	14.0	10	Silt
NB3	42°47.762′	80°01.902′	9.1	12.0	5	Silt–clay
NB4	42°47.427′	80°01.977′	10.1	12.0	5	Silt–clay
NB5	42°47.109′	80°02.135′	10.4	11.0	1	Silt–clay
LA1	42°48.342′	80°01.341′	3.0	17.0	2–10	Sand–clay
LA2	42°48.129′	80°01.464′	6.1	15.1	5	Sand–clay
LA3	42°47.900′	80°01.476′	7.3	13.1	10–12	Sand–clay
LA4	42°47.410′	80°01.570′	8.8	13.2	None	Silt–clay
LA5	42°47.219′	80°01.376′	9.1	13.5	5	Silt–clay
EL1	42°48.035′	80°00.504′	2.7	15.9	15	Bedrock
EL2	42°47.808′	80°00.607′	4.6	13.0	15	Bedrock
EL3	42°47.566′	80°00.686′		12.8	15	Bedrock
EL4	42°47.310′	80°00.693′	7.3	12.5	10	Bedrock
EL5	42°46.985′	80°00.675′	7.9	12.9	5	Sand
PW1	42°47.801′	79°59.632′	4.3	16.2	None	Silt–clay
PW2	42°47.682′	79°59.714′	6.4	14.0	2	Silt–clay
PW3	42°47.422′	79°59.717′	7.0	13.8	None	Silt–clay
PW4	42°46.857′	80°00.013′	6.1	11.0	15	Bedrock
PW5	42°46.553′	79°59.941′	6.7	12.0	15	Bedrock

Note: Algae refers to the amount (approximate length in centimetres) of filamentous attached algae at the site. Substrate refers to the predominant underlying substrate type.

variation in zebra mussel numbers. Depth explained a further 18.5%.

Temperature

Median percent residuals from the quagga mussel regression differed with location (east or west of the discharge canal mouth) (Mann–Whitney U test, $n = 65,44$, $U = 1850$, $p = 0.01$) (Fig. 2*a*). Quagga mussel were more abundant in the plume (medium percent deviation 107%, IQR 94–113%) than outside it (median percent deviation 101%, IQR 88–104%).

Residuals from the zebra mussel regression were evenly distributed with respect to the warmwater plume (Mann–Whitney U test, $n = 65,44$, $U = 1432$, $p = 0.99$) (Fig. 2*b*). The median percent deviations were 104% (IQR 80–120%) within the plume and 109% (IQR 80–123%) outside it.

The difference in the plume's effect between species was most apparent at the PL site, located at the mouth of the discharge canal. Quagga mussel were 18% more abundant at PL than predicted using water depth. Zebra mussel were at 26% of their predicted level. We collected two substrate particles at the PL site, from which we removed 901 quagga mussels but only 3 zebra mussels. Bottom temperature at PL was 12°C higher than at any other site sampled.

Discussion

Species-specific density variation patterns with increasing depth were largely consistent with previous studies. Zebra mussel became more abundant with increasing depth in this study despite being widely considered a shallow-water species. In Europe, peak densities are generally reached at 2–12 m (for review see Stanczykowska 1977), although in Lake Constance they can be found at depths of up to 55 m (Walz

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Fig. 1. In each model, $n = 109$. The surfaces were generated using the full model regressions, i.e., regressions including nonsignificant terms, for quagga mussel (*a*) and zebra mussel (*b*). Points are individual observations. Open points lie above the surface and solid points, below.

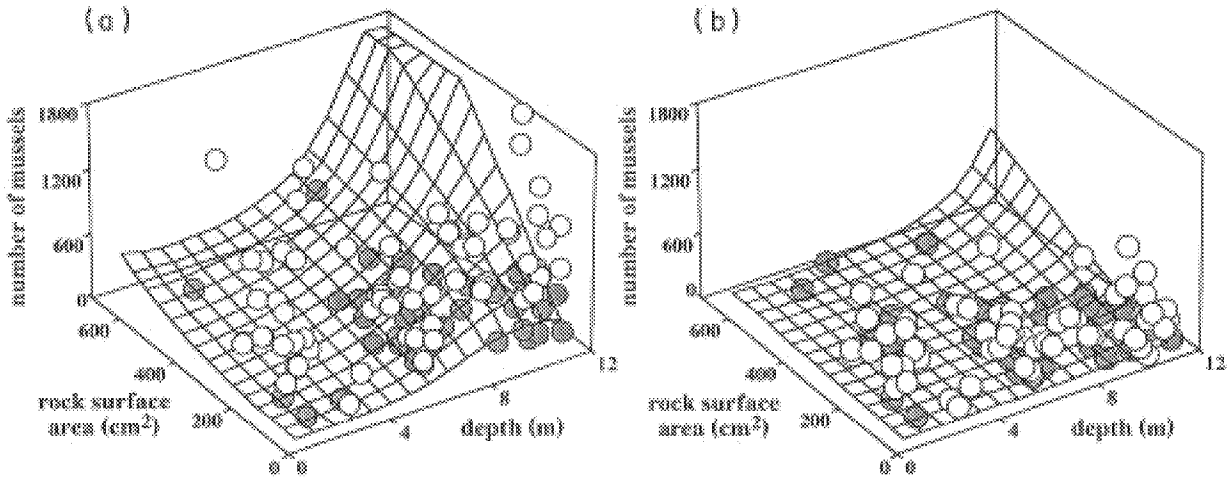

Table 2. Results of multiple regressions of ln(mussel count + 1) on depth and ln(rock surface area) for zebra and quagga mussels.

	ln(zebra mussel count + 1)		ln(quagga mussel count + 1)	
	Coefficient	*p*	Coefficient	*p*
Constant	−4.051	0.001	−7.429	0.005
Lrsa	1.096	<0.001	1.752	<0.001
Depth	0.260	<0.001	1.441	<0.001
Depth^2	—	—	−0.034	0.007
(Lrsa)(depth)	—	—	−0.122	0.047
(Lrsa)(depth^2)	—	—	—	—

Note: In each regression, $n = 109$. Initially, depth^2 was included in both models, as were interactions between ln(rock surface area) and each depth term. Nonsignificant interactions were sequentially removed and models rerun. For each species, the table gives the coefficients associated with the remaining (significant) terms and the associated probabilities. If no coefficient appears, then that term was not a significant predictor of mussel abundance for the species. Lrsa, ln(rock surface area).

1973). Mills et al. (1993) found settled zebra mussel at 110 m in Lake Ontario, albeit in low densities. In Lake Erie, zebra mussel densities peak below 10 m (Dermott and Munawar 1993). The range of depths used in our study was relatively narrow. The maximum depth sampled, 11.9 m (site ST5), is well within the range at which zebra mussels commonly occur. The pattern we observed probably reflects the narrow range of depths encountered. On the basis of previous studies, we doubt that zebra mussel densities would continue to increase at deeper sites near Nanticoke.

An increase in quagga mussel densities with depth is also consistent with previous studies. In Lake Erie, Dermott and Munawar (1993) found their highest quagga mussel densities in offshore sediments at depths of 40–63 m (Lake Erie's maximum depth). Mills et al. (1993) did not report densities, but reported quagga mussels in Lake Ontario at depths of 130 m. As with zebra mussel, the narrow range of depths examined leaves our estimate of a peak quagga mussel density at 15 m questionable, particularly since Dermott and Munawar's (1993) samples were also from Lake Erie's eastern basin. Factors governing mussel densities in deep water may be quite different from those influencing densities in this study.

Although the increase in quagga mussel densities with depth is consistent with previous studies, their numerical dominance in shallow water is not. Quagga mussel not only occurred at the shallowest sites we sampled, but they also clearly outnumbered their congener. Dermott and Munawar (1993) found that zebra mussel and quagga mussel coexisted in eastern Lake Erie but quagga mussel abundance only exceeded that of zebra mussel at depths greater than 10 m. Similarly, Mills et al. (1993) found that quagga mussel outnumbered zebra mussel below about 20 m in Lake Erie, and below approximately 60 m in Lake Ontario. Quagga mussel also occurred at greater depths than zebra mussel in Lake Ontario (130 versus 110 m). At Nanticoke, both species were abundant at greater depths. Quagga mussel's proportion of total abundance increased with depth, as in other studies, but they were more abundant than zebra mussel even at our shallowest sites.

Quagga mussel have successfully established along reaches of the Dneiper River, Ukraine, previously dominated by zebra mussel (Pligin 1984). Unlike zebra mussel, quagga mussel have not spread through Europe. However, the construction of dams and reservoirs along the Dneiper has allowed quagga mussel to move upstream along this river over the last 50 years, colonizing areas where previously only zebra mussel occurred and, in some reservoirs, replacing them. Pligin invoked reduced current velocity and greater bottom silting following

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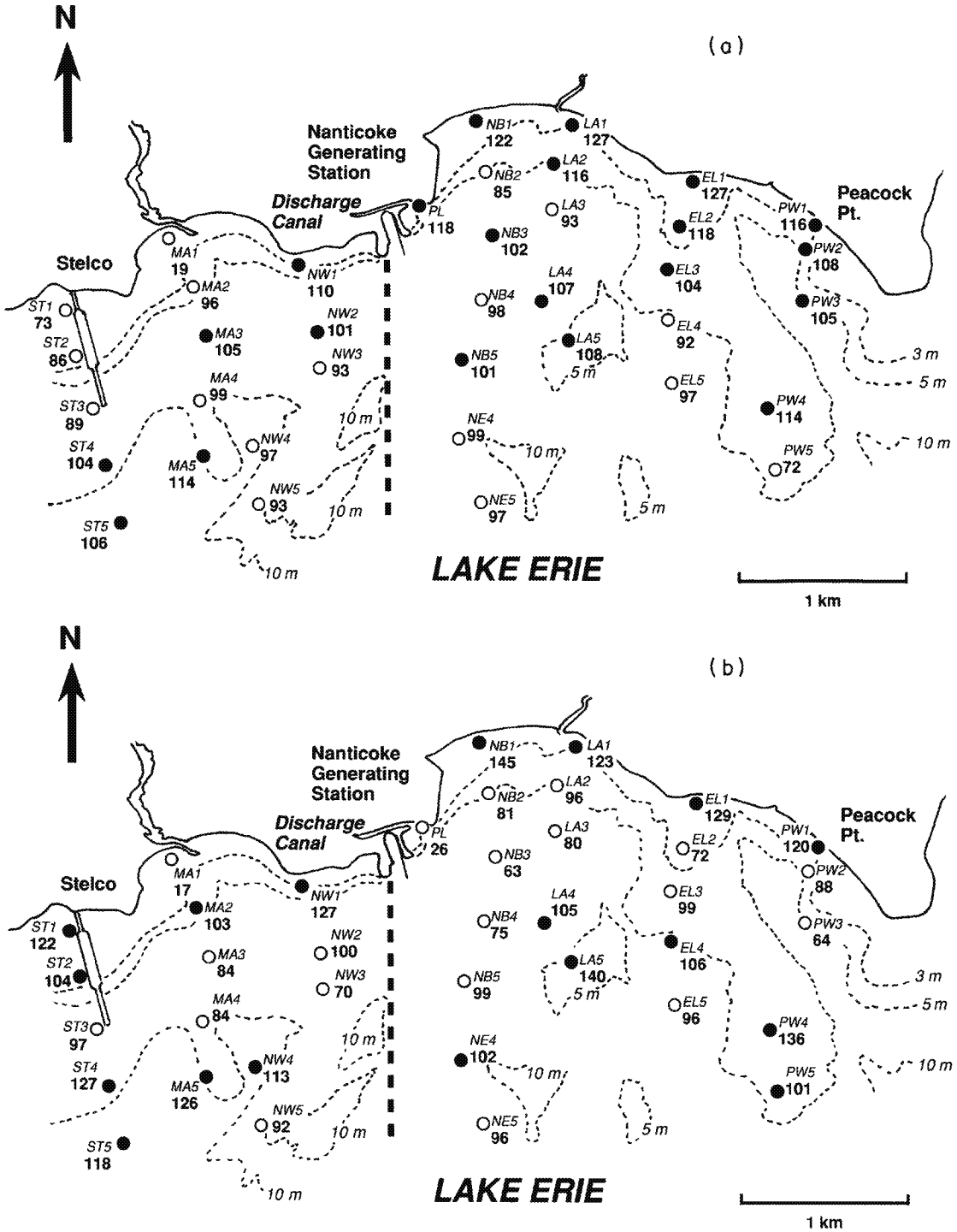
Fig. 2. Distribution across sample sites of residuals from regressions of abundance of quagga mussel (*a*) and zebra mussel (*b*) on depth and rock size. Numbers beside sites are means of residuals from samples collected at those sites. The vertical broken line separates the area considered to be influenced by the Nanticoke warmwater discharge (from the Nanticoke Generating Station east to Peacock Point) from that considered to be unaffected (from the generating station west to Stelco Pier). At sites marked with solid points, mussel density was greater than predicted; at those marked with open points, density was lower than predicted.



river impoundment to explain this. Ludyanskiy et al. (1994) also examined relative densities of the two dreissenids in the Dneiper and found that quagga mussel tended to dominate benthic areas while zebra mussel were more abundant in the littoral zone. Quagga mussel did occasionally reach 50% of total dreissenid abundance in shallow water. Like Pligin (1984), Ludyanskiy et al. (1994) suggested that quagga mussel may be more tolerant of silt. They also suggested that quagga mussel may be more tolerant of low dissolved oxygen levels. The success of quagga mussel in the Dneiper, albeit in that

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river's deeper stretches, confirms our observation that quagga mussel may not be restricted to the deep, offshore sediments of lakes.

Like Pligin (1984) and Ludyanskiy et al. (1994), Dermott and Munawar (1993) implicated substrate differences as an explanation for changes in dreissenid species composition with depth. Quagga mussels may be better suited for survival and growth on the soft substrates common in deep water. Dermott and Munawar distinguished a third dreissenid morphospecies, the profunda mussel. They characterized zebra mussel as preferring hard substrates, quagga mussel as preferring sandy substrates, and profunda as preferring silt substrates. Spidle et al. (1994) have since shown using allozyme variation that profunda are a form of *D. bugensis*. This does not alter the characterization of zebra mussel as a hard-substrate species and quagga mussel as a soft-substrate species. However, zebra mussel also occur on silt in shallow water (Hunter and Bailey 1992) and deep water (Mills et al. 1993). Also, in this study, quagga mussel outnumbered zebra mussel on hard substrates (cobble overlying bedrock, Table 1) in shallow water. Substrate type may affect the density of either or both species, but it is an unlikely candidate as the underlying factor determining the relative abundance of dreissenid species.

Shallow nearshore areas are also turbulent, possibly making such areas less suitable for quagga mussel. Unlike zebra mussel, quagga mussel are not ventrally flattened (May and Marsden 1992; Pathy and Mackie 1993), so they may not be able to fasten themselves as securely to the substrate. Mills et al. (1993) therefore suggested that quagga mussel may be restricted to deep water because they are washed or scoured off the substrate in shallow water to a greater extent than are zebra mussel. However, Ackerman et al. (1995) used a calibrated force scale to compare the strength of attachment of zebra and quagga mussels and found quagga mussel to be marginally more difficult to remove. This test would not take into account the morphological differences that led to the suggestion of Mills et al. (1993), since Ackerman et al. (1995) used a vertically directed force, whereas wave action would be better modelled as a shear force.

Nearshore turbulence can also lead to scouring by ice or by wave-borne rocks. In the latter case, mussels on the underlying substrate will be scraped off or crushed. The same will be true of mussels attached to the tumbling rock itself. Scouring could well explain the paucity of mussels at MA1, the shallowest site we sampled. On rocks collected at this site we observed many byssal scars where mussels had once been attached. The interaction between rock size and water depth in our model for quagga mussel abundance (Table 1; Fig. 2) can also be explained as a result of small rocks being rolled across the lake bottom nearshore, crushing or detaching mussels. In deep water, currents would not be a strong, nor, on a silt–clay substrate, would rocks roll as easily. Mussel densities on small rocks could then increase. No interaction between rock size and water depth was apparent in our model of variation in numbers of zebra mussel. Possibly, zebra mussel densities at Nanticoke are too low for such an effect to be detectable. Alternatively, as Mills et al. (1993) suggested, zebra mussel may better resist detachment.

While turbulence and (or) scouring may influence mussel densities, their effects are not responsible for the different depth distributions of the two dreissenids. Both quagga mussel morphology and our observation of an interaction between rock size and depth in predicting densities of this species indicate that if either species is negatively influenced by nearshore turbulence, it is quagga mussel. At Nanticoke, quagga mussel outnumbered zebra mussel in shallow water despite these effects.

Finally, depth zonation of the two dreissenids may be due to temperature differences. Deep water is normally colder, especially during the ice-free season. Initially, our results indicated that quagga mussel occur in deep water even though they prefer warm water. In water affected by the plume, quagga mussel were more abundant than expected (Fig. 2*a*). This result is in contrast to those of Domm et al. (1993) and Spidle and Mills (1994), who found in laboratory trials that zebra mussel were more resistant to high temperatures than were quagga mussel.

One possible explanation of this difference stems from recognition that the discharge from the Nanticoke generating station also alters winter low temperatures. During winter, when the ambient nearshore temperatures in the lake drop below 4°C, water discharged from the generating station is warmer and denser as it cools to 4°C, and therefore it spreads across the bottom, not the surface. Mussels living in the area influenced by the plume will not experience as cold a winter. Possibly, one factor limiting quagga mussel success in shallow waters is not the high temperature experienced in the summer, but the cold experienced over winter. Winter temperatures in deep water will not drop as low as at shallow, nearshore sites. MacIsaac (1994) transplanted quagga mussel from eastern Lake Erie to the warmer, western basin and obtained survival rates of 100% (5-mm mussels) and 98% (15-mm mussels). He concluded that high summer temperatures are unlikely to restrict quagga mussel distributions in the southern Great Lakes.

Graney et al. (1980) used a thermal discharge to examine temperature preferences of another exotic mollusc, the Asiatic clam, *Corbicula fluminea*. The clams reached higher densities in the thermally enriched waters. Graney et al. (1980) suggested that plumes from such discharges may allow Asiatic clams to extend their northern range by providing the mussel with a refuge from winter temperatures that might otherwise be too low. If low winter temperatures rather than high summer temperatures constrain dreissenid distributions, then the same risk will apply.

It is also possible that zebra mussel require a greater drop in winter temperature than quagga mussel. Although the population density of zebra mussel appeared to be unaffected by the presence of the plume, the species was almost entirely absent from samples taken at the mouth of the discharge canal. Here, the low temperatures experienced elsewhere would never occur. Results of Polish studies of zebra mussel populations in heated lakes, however, do not support this conjecture. In the Konin lakes, spawning begins earlier in the year and veligers are present in the water column longer than in unheated lakes (Kornobis 1977; Lewandowski and Ejsmont-Karabin 1983; Stanczykowska et al. 1988). Kornobis (1977) found that adult mussels in heated lakes occurred at higher densities and in shallower water, grew faster, but did not live as long as in unheated lakes. In contrast, Stanczykowska et al. (1988) failed to detect any differences in adult densities in the same lake

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complex. Neither result can explain the low densities of zebra mussel found at Nanticoke.

The plume's effect on quagga mussel density suggests revisions to current explanations of habitat partitioning by dreissenids. However, it does not fully explain the pattern observed at Nanticoke. Quagga mussels at Nanticoke reach their highest densities in deep, thermally enriched waters. They are at their lowest densities in shallow water unaffected by the Nanticoke discharge. Thus, the warmwater plume allows a distinction to be made between deep water and cold water or, we argue, warmer water over winter. However, in shallow water unaffected by the discharge, densities of quagga mussel still exceed those of zebra mussel. Therefore, the warmwater discharge is not a sufficient explanation for differences in the relative densities of the two species.

One final possibility has been suggested by MacIsaac (1994). Quagga mussel were introduced in the Great Lakes later than were zebra mussel. Also, they may not have the same potential for rapid dispersal. This possibility is supported by their much slower spread through the Bug and Dneiper rivers in Europe, as compared with the spread of zebra mussel (Ludyanskiy et al. 1994). The current distribution of quagga mussel, predominantly in deep offshore waters, may reflect its point of introduction and pattern of dispersal, not its potential to colonize nearshore areas. The spread of quagga mussel through the Dneiper has not been restricted to deep water, and quagga mussel have replaced zebra mussel in some areas. If quagga mussel settled at Nanticoke in 1987 or 1988 (Domm et al. 1993), then Nanticoke must have been one of the first sites colonized by the species in North America. The high quagga mussel densities we found at Nanticoke, even at shallow sites, may be a preview of things to come elsewhere in the Great Lakes.

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