Patterns in the Distribution and Abundance of Zebra Mussel (Dreissena polymorpha) in Rivers and Lakes in Relation to Substrate and Other Physicochemical Factors

Eric Mellina and Joseph B. Rasmussen
Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montreal, QC H3A 1B1, Canada


Using SCUBA and an in situ method of quantifying substrate characteristics, we describe patterns of zebra mussel (Dreissena polymorpha) distribution along the St. Lawrence and Hudson rivers and in Oneida Lake, New York, and develop empirical models for their abundance. Calcium-poor waters originating from rivers draining the Canadian Shield resulted in a complete lack of zebra mussel colonization along the north shore of the St. Lawrence River east of Montreal despite an abundance of suitable substrate. Calcium concentrations of 15 mg/l or less limited the distribution of zebra mussel. The entire south shore from Cornwall, Ontario, to Île d'Orléans, Québec, was colonized by zebra mussel wherever suitable substrate was found. Among the three systems, substrate size explained between 38 and 91% of the variability in density. Other factors such as Secchi depth, calcium concentration in the water, the presence of crayfish, native unionid abun-
dance, and the maximum width of the river at the site increased the amount of explained variance across the different systems. A model based on substrate size also successfully explained patterns of zebra mussel abundance from published sources.

Au moyen de SCUBA et d'une méthode in situ de quantification des caractéristiques des substrats, nous décrivons les profils de distribution de la moule zébrée (Dreissena polymorpha) le long du Saint-Laurent et de la rivière Hudson, ainsi que dans le lac Oneida, État de New York, et nous développons des modèles empiriques de leur abondance. C'est par les eaux pauvres en calcium des cours d'eau qui drainent le bouclier canadien qu'on peut expliquer pourquoi la moule zébrée n'a pas colonisé la rive nord du Saint-Laurent à l'est de Montréal, malgré une abondance de substrats appropriés. Dans sa distribution, la moule zébrée est limitée par une concentration en calcium de 15 mg/l, ou moins. L'ensemble de la rive sud, à partir de Cornwall en Ontario jusqu'à l'Île d'Orléans au Québec, est colonisé par la moule zébrée sur tous les substrats qui s'y prêtent. Dans les trois réseaux étudiés, l'importance des substrats permet d'expliquer pour 38 à 91 % les variations de densité. D'autres facteurs comme la transparence au discrètement de Secchi, la concentration en calcium de l'eau, la présence d'écrevisses, l'abondance d'unionidés indigènes et la largeur maximale du cours d'eau à hauteur de la station, accordent la variance expliquée d'un réseau à l'autre. Un modèle qui s'appuie sur l'importance des substrats a aussi permis d'expliquer les profils d'abondance de la moule zébrée à partir de renseignements publiés.

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The zebra mussel (Dreissena polymorpha) has spread rapidly since its introduction and subsequent discover-
y in Lake St. Clair in 1988 (Hebert et al. 1989) and is now firmly established in all the Great Lakes and in water-
ways along much of northeastern North America (Neary and Leach 1992; New York Sea Grant Extension 1993). Considering the mussel's potential economic and ecologi-
cal impacts (Cookley 1991; Griffiths 1993), identifying factors affecting their abundance and distribution would be invalu-
able for the design and implementation of control programs.

To date, there are no powerful predictive models for zebra mussel abundance. Attempts at modelling have focused on water chemistry variables as the primary predictors of zebra mussel density. Stanczykowski (1964) found no direct cor-
relation between mussel densities and limnological variables such as pH, Secchi depth, and calcium concentrations of the wa-
ter. Strayer (1991) was only able to find a weak, although significant, correlation between density and mean annual air temperature and concluded that it was not possible to pre-
dict zebra mussel abundance from published sources based on available environmental data. More recently, Ramcharan et al. (1992b) had better success in predicting zebra mussel occurrence and density using calcium, phos-
phate, nitrate, and pH as predictors.

Although the availability of suitable substrate is essential for the survival of postveliger zebra mussel (Stanczykowski 1977; Lewandowski 1982; Mackie et al. 1989), no pub-
lished models have used substrate variables predictively. Physical factors are important determinants of zoothe-
benthic biomass (Rasmussen 1988), and Harman (1972), Horne and McIntosh (1979), and Stern (1983) have shown qualitatively how different substrate types influence freshwater unionid abun-
dance and distribution. A quantitative evaluation of

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substrate in combination with important water chemistry parameters may therefore improve the predictions of zebra mussel abundance models.

Zebra mussel settlement and colonization along the St. Lawrence River was expected given the potential for rapid downstream dispersal of larvae from the Great Lakes and the influence of human activities (Griffiths et al. 1991). While there have been qualitative studies on the abundance of freshwater mussels in large rivers (e.g., Wolff 1969; Thiel 1981; Miller 1988), their habitat requirements remain largely unquantified due to sampling difficulties imposed by deep, fast-flowing waters (Stern 1983; Holland-Barctel 1990). The purpose of our study was to determine the physical and chemical factors that influence zebra mussel abundance and distribution along the St. Lawrence River across a naturally occurring gradient of calcium concentration between the north and south shores. We hypothesize that the northern shores, which drain the Canadian Shield, have lower calcium concentrations than the southern shores. The higher calcium levels and a good supply of larvae from the Great Lakes along the south shore probably result in the potential for a high degree of substrate-related variability in zebra mussel density. We developed an in situ method for quantitative substrate characterization that enabled us to determine the influence of substrate type on zebra mussel density and developed empirical models using linear regression analysis. We also tested the applicability of the method in the Hudson River and in Ossela Lake, New York. Finally, we tested the robustness of our models with data from literature studies that reported both zebra mussel densities as well as general descriptions of associated substrates.

Study Areas

The St. Lawrence study area comprised 57 freshwater sites along the St. Lawrence River between Cornwall, Ontario, and Île d'Orléans, Quebec, including four sites in the Lake of Two Mountains, Quebec (Fig. 1). Sampling was conducted between mid-July and the end of August 1992. An additional 11 sites were sampled in August 1991 during a preliminary study. This portion of the river was chosen for the
variability in the underlying geology of the drainage basins that gave us the opportunity to study the effect of water chemistry on zebra mussel distribution. Ille d’Orléans represents the limit of salt water coming from the Gulf of St. Lawrence, and tides are felt upstream until Lac St. Pierre (Coulliard 1982).

Almost the entire water mass along the St. Lawrence River between Cornwall and Montreal originates from the Great Lakes and is characterized by a greenish hue and relatively high calcium concentrations (Lamarche et al. 1982; Vincent et al. 1991). Along this section of the river, the drainage basin is composed primarily of calcareous sediments (Clark and Stein 1968; Bobée et al. 1981). East of Montreal the existence of different hydrological corridors results in distinct calcium gradient between the two shores of the river. Water along the south shore with its underlying calcareous geology is fed by the Great Lakes and continues to contain high calcium concentrations. Along the north shore, however, the main sources of water are the Ottawa and St. Maurice rivers, both of which drain parts of the erosion-resistant Canadian Shield (Frenette and Verrette 1976; Lamarche et al. 1982). The result is a thin band of brownish, calcium-poor water running along the north shore of the St. Lawrence River (east of the point of confluence with the Ottawa River) to a large band of green, calcium-rich water along the south shore originating from the Great Lakes (Lamarche et al. 1982; Vincent et al. 1991). This distinct calcium gradient remains stable until the vicinity of Portneuf (Fig. 1), where the tidal influence is sufficient to ensure complete mixing of the water mass, thereby obliterating the water chemistry gradient (Coulliard 1982).

Sites along the St. Lawrence River were chosen using a cartography published by the Department of Fisheries and Oceans which give approximate substrate compositions. Between Montreal and Lac St. Pierre the riverbed is primarily sandy and was therefore sampled less extensively than the rest of the river. Sites were also chosen to maximize the variability in calcium, depth, and velocity of flow. In addition to natural substrates, two sites were chosen along the river representing artificial structures: the walls (1) at the port of Becancour, Quebec, and (2) within Bassin Louise, Quebec, which is a completely enclosed basin with access to the main river limited by locks and protected from some of the physical factors affecting the rest of the river (i.e., wind, waves, and current).

Sampling was also conducted at 11 sites along a fresh-water tidal section of the Hudson River from Catskill to New Hamburg during the first week of July and at five sites in the hardwater, moderately eutrophic Oneida Lake in upper New York State during mid-June 1992 (Fig. 1). These two systems were investigated to assess whether zebra mussel distribution in relation to substrate was similar across different systems and to test the applicability of our method of quantifying substrates in a second river system and in a lake. In addition, these two systems were also characterized by early stages of zebra mussel colonization making them ideal for comparisons with the St. Lawrence River.

Methods

Sampling Techniques

SCUBA diving was employed at all sites to determine zebra mussel densities. Under certain conditions, SCUBA gives more accurate estimates of density than bottom samplers (Wisniewski 1974; Stanczykowska 1977) and also allows for substrate observations (Stern 1983). In addition, the close proximity of the diver to the substrate meant that zebra mussel as small as 2–3 mm in length were clearly discernible.

A 1-m² aluminum quadrat was randomly placed on the river/lake bottom and all visible zebra mussel within it were counted in situ. Due to safety problems encountered with fast currents along the St. Lawrence River, subsequent quadrats within a site could only be placed by blindly throwing the quadrat away from the diver (thus minimizing bias) and repeating counts. While this sampling protocol was not strictly random, biases have further been reduced by averaging estimates over each site when performing the analyses. Because the diver attempted to count approximately 100 mussels for each quadrat (this being the optimum number based on experience to preserve reliability, efficiency, and safety), quadrat sizes varied from 0.03 to 1 m² and the number of quadrats counted at each site varied accordingly (from 3 to 20). The quadrat was adjustable so that smaller areas could be counted when mussel densities exceeded approximately 100 mussels/m². The size and number of replicate quadrats counted within a site were determined according to Downing and Downing (1992), who predicted that with a density of 100 mussels/m², two replicate 1-m² quadrats were required to obtain a precision of 20%. Replicate quadrats were counted at each site where zebra mussels were present with the exception of five sites in the St. Lawrence where only one quadrant per site was counted due to difficulties encountered with fast currents. An underwater light was used to aid in the detection of mussels in areas of low visibility. Size distributions and biomass of zebra mussel were not recorded due to fast currents which did not allow us time to remove all the mussels from the substrate. However, biomass of zebra mussel is usually related to density within a given water body (Stanczykowska 1976).

In situ counting proved the most efficient method for estimating zebra mussel density, enabling the diver to descend to the river/lake bottom unencumbered with collecting bags and allowing for a greater number of quadrats to be counted. The accuracy of the in situ density estimates was tested by removing zebra mussel from within 10 quadrats and bringing them to the surface for counting. These counts were then compared with the in-situ counts for the same quadrats. Differences between the two methods did not exceed 5%. Densities from test counts ranged from approximately 10 to 150 mussels/quadrat, which was within the range of mussels counted in each quadrat during sampling.

Substrate composition was also determined in situ by measuring the lengths of the different rocks within a quadrat and then visually estimating the percent areal coverage of each type of substrate of a given size (e.g., a quadrat could be covered by 25% sand, 25% gravel of 3-cm diameter, and 50% boulders of 30-cm diameter). The different substrate types were converted to the phi scale (4) by transforming them to the negative log base 2 of the particle size in millimeters (Hakanson and Jonsson 1983). Each substrate’s phi value was multiplied by its percent contribution to the total areal coverage and then summed to give a mean weighted particle size (henceforth referred to as substrate size) for each quadrat. The more negative the substrate size, the larger the particle. Thus, for each quadrat, we obtained an estimate

of zebra mussel density (which included all zebra mussel counted within a quadrat) and an associated measure of substrate size. Artificial quadrats were dealt with by assuming they represented a particle with a length of 1 m and were assigned a phi value of ~9.967 (100% cover with a 1000-mm particle). Sampling methods remained constant across the three systems (the St. Lawrence and Hudson rivers and Owasco Lake) and all measurements were made by the same aver so as to minimize bias when assessing mussel density and substrate size.

The presence or absence of crayfish was determined by uncovering rocks around an area of approximately 100 m² at each site and was accounted for in the regression models with a dummy variable. Native unionid abundance was estimated semiquantitatively by grouping them into three categories based on their areal coverage within a quadrat: low (0–25%), medium (26–50%), and high (>50%), and was accounted for in the multiple regression models with a dummy variable. Only their abundances (and not their contributions as a substrate) were considered in the models. Because sites along the St. Lawrence River downstream from Lac St. Pierre, Quebec, as well as sites along the Hudson River experience daily fluctuations in water levels due to tides, all depth estimates were taken from navigational charts on which depths were reduced to Lower Low Water (Canadian Tidal Datum). The maximum width of the river as well as the distance from site to shore at each site was also measured from these charts. Sites within Bassin Louise were included in the multiple regressions for the St. Lawrence River and were accounted for with a separate lentic/lotic dummy variable due to their isolation from the main river channel.

A water sample was taken at each site in clean, plastic bottles and refrigerated for future analysis. In the laboratory, samples were analyzed for water chemistry according to the following methods modified from Cleves et al. (1989) by Hach, Inc. for use on a Hach portable colorimeter: calcium (titration using CalVer® indicator), true and apparent color (platinum–cobalt colorimetric method), and total phosphorus (TP) (ascorbic acid method according to Griesbach and Peters 1991).

**Linear Regression Analysis**

All statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1989). Any variable spanning more than 1 order of magnitude was log base 10 transformed, while zebra mussel densities were log10(X+1) transformed to reduce undue influences of large values and to stabilize the variance of the dependent variable (Kleinbaum et al. 1988). In addition, estimates of all the variables were averaged over each site before performing the analyses. We searched for statistical relationships between zebra mussel density and the physical and chemical variables gathered at each site. Significant differences in calcium levels between shores along the St. Lawrence River led us to analyze the entire data set for the St. Lawrence using two approaches: (1) by grouping the variables a posteriori according to shore (to remove the effect of substrate size on density along the calcium–poor north shore) and (2) by analyzing the entire data set irrespective of shore.

Linear regression analysis was first attempted between mussel density and our quantitative characterization of substrate for each system separately to determine the amount of variability in density that could be explained using substrate size alone. Multiple regressions were run using the entire data set for each system to generate the most powerful predictive models. Regression diagnostics analysis (including residual analysis, normal probability plots, and tests for multicollinearity between predictors) were run for all the regression models to ensure the appropriateness of a linear regression.
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<th>Substrate</th>
<th>Temperature (°C)</th>
<th>Depth (m)</th>
<th>Secchi (m)</th>
<th>Max. width of river at site (m)</th>
<th>Distance from site to shore (km)</th>
<th>pH</th>
<th>Conductivity (µS/cm)</th>
<th>Calcium (mg/L)</th>
<th>TP (µg/L)</th>
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model, that the assumptions underlying the models were not violated, and that spurious correlations were not generated (Kleinbaum et al. 1988).

The extent (if any) of the increase in zebra mussel abundance along the St. Lawrence River between 1991 and 1992 was also determined using density and substrate size estimates (gathered using similar protocols) from the 11 additional sites sampled in 1991 (Fig. 1). These density estimates were compared, using an ANCOVA, with estimates from 11 sites in the present study that had comparable substrate size values. The regression coefficient for the year factor was used as an estimate of the average increase in density along the river between the two years.

Literature Studies

To test the robustness of our method of quantifying substrate and to support the importance of substrate size in determining zebra mussel density, a composite model was formed relating density to substrate size using the data gathered in Oneida Lake and along the Hudson River and the south shore of the St. Lawrence River. This model included a categorical variable to distinguish between lakes and rivers and also included Bassin Louise (which was classed as a lake given the protected nature of the enclosure). The predictions of this composite model were then tested with a literature data set compiled from mostly European studies of lakes and rivers that jointly reported a general description of substrate type and zebra mussel abundance. The literature studies were chosen regardless of the methods used to gather density estimates. A total of 38 studies were found, including five recent studies of zebra mussel in the Great Lakes and a preliminary study carried out in the Great Lakes in 1951 by ourselves that yielded six additional sites. These six sites were not combined with the sampling data set, since quantitative density estimates were coupled to qualitative substrate descriptions.

Substrate descriptions were converted to the phi scale according to Hakanson and Jansson (1983) and to the Wentworth classification as follows: mud/clay = 9, silt = 6.5, sand = 2, gravel = 3.5, and boulders = −8. Stones were arbitrarily assigned a length of 19 cm and a phi value of −6.644. Where densities were reported for hydrotechnical installations, it was assumed that these were taken from walls and were therefore assigned a phi value of −9.967 as the corresponding substrate size. Some studies (e.g., Landbeck 1926; Stankovic 1951) reported mussel densities on a bed of empty shells (a "shell zone"). In these cases the substrate was assumed to be completely covered with shells averaging 2 cm in length and was assigned a phi value of −4.322 (100% cover with 2-cm shells).

When a combination of different substrates was reported, their respective contributions to the weighted phi value were equally divided. For example, if sand and gravel were reported as the substrate for a particular site, then 50% of the final phi value was comprised of sand and 50% was composed of gravel. Whenever a study reported different mussel densities for a particular substrate type, the densities were averaged for that substrate within the study. Sites with macrophytes were avoided, since macrophytes were rare in the present study and were not accounted for in the models.

Results

St. Lawrence River

When the calcium and density data were pooled for all three systems, there appeared to be a calcium threshold level of 15 mg/L below which no zebra mussel were found (Fig. 2). For the St. Lawrence River, with its natural calcium gradient between the north and south shores, sites were classified according to shore zone on this calcium threshold level of 15 mg/L. Calcium levels in the water were different between shores (t-test, p < 0.001) and ranged
Table 2. Multiple regression models obtained for zebra mussel density for the St. Lawrence and Hudson rivers, Oneida Lake, and the literature studies. Numbers in parentheses following predictors are SE of the coefficients. Significance: *p < 0.05, **p < 0.005, ***p < 0.001.

<table>
<thead>
<tr>
<th>Equation</th>
<th>r²</th>
<th>SE</th>
<th>n</th>
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<tbody>
<tr>
<td>St. Lawrence River (south shore)</td>
<td></td>
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<tr>
<td>(1) log density = 0.05 - 0.13 substrate (0.03)*** + 1.86 log Secchi (0.39)*** + 0.05 calcium (0.05)** + 0.69 clams (0.13)*** - 0.41 crayfish (0.16)* + 2.21 lentic site (0.33)***</td>
<td>0.83</td>
<td>0.45</td>
<td>46</td>
</tr>
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<td>St. Lawrence (north and south shore)</td>
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</tr>
<tr>
<td>(2) log density = -1.67 - 0.09 substrate (0.02)*** - 1.79 log Secchi (0.38)*** + 0.11 calcium (0.01)** + 0.52 clams (0.13)*** + 2.78 lentic site (0.33)***</td>
<td>0.82</td>
<td>0.56</td>
<td>57</td>
</tr>
<tr>
<td>Hudson River</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(3) log density = -3.35 - 0.30 substrate (0.03)*** + 4.20 max. width of river (0.36)**</td>
<td>0.89</td>
<td>0.51</td>
<td>11</td>
</tr>
<tr>
<td>Oneida Lake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(4) log density = 1.70 - 0.17 substrate (0.003)*** + 0.02 calcium (0.001)**</td>
<td>0.99</td>
<td>0.02</td>
<td>5</td>
</tr>
<tr>
<td>Composite model (St. Lawrence south shore, Hudson, Oneida)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(5) log density = 1.38 - 0.19 substrate (0.02)*** + 1.14 lake (0.23)***</td>
<td>0.67</td>
<td>0.66</td>
<td>62</td>
</tr>
<tr>
<td>Literature studies (lakes)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(6) log density = 2.34 - 0.23 substrate (0.02)***</td>
<td>0.75</td>
<td>0.82</td>
<td>72</td>
</tr>
<tr>
<td>Literature studies (rivers)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(7) log density = 1.43 - 0.14 substrate (0.05)***</td>
<td>0.29</td>
<td>1.05</td>
<td>18</td>
</tr>
</tbody>
</table>

from 8 to 14 mg/L for the north shore of the St. Lawrence and from 16 to 38 mg/L for the south shore (Table 1). The north shore (Montreal to Port aux Basques) was devoid of zebra mussel despite an abundance of large rocks, while the entire south shore (Cornwall to Île d'Orléans) was colonized wherever suitable substrate (defined as having a phi value less than 2, which corresponds to 100% sand) was found (Table 1). We did not find settled zebra mussel directly on sand or on smaller grain sizes. At sites where the substrate was composed of sand or silt, native unionids often provided the only available hard substrate. The highest zebra mussel densities were found in Bassin Louise, at the port of Beauce, and off the island of Montréal. In general, densities were higher on artificial substrates than on natural substrates. No settled zebra mussel were found in the Lake of Two Mountains. In addition, the comparison between densities at the 11 sites from 1991 with comparable sites from this study revealed an average sixfold increase in zebra mussel abundance along the St. Lawrence River between 1991 and 1992.

Using linear regression, average substrate size by itself was able to explain 38% of the variability in zebra mussel density for south shore sites (Fig. 3). In the protected site of Bassin Louise, densities were over an order of magnitude higher than in the main river channel (Fig. 3). The best overall abundance model for the south shore (r² = 0.83) had zebra mussel density negatively correlated with substrate size, Secchi depth, and the presence of crayfish and positively correlated with the categorical classification of unidonal abundance, with the lotic/lentic dummy variable, and with calcium concentrations in the water (Table 2). The addition of north shore sites (those below the calcium threshold) resulted in a slight decrease in the predictive power of the multiple regression model, and the presence of crayfish no longer became a significant predictor at the 0.05 level (Table 2). Sampling was not biased by the date on which it took place, as calendar day was an insignificant predictor in the model. There was no multicollinearity between predictors and none of the assumptions underlying linear regression models (Kleinbaum et al., 1988) was violated.

Hudson River and Oneida Lake

When the density and substrate size data were combined across all three systems, mussel densities in the Hudson were comparable to those found in the St. Lawrence, while densities in Oneida Lake were generally an order of magnitude higher given the same substrate size values (Fig. 4). In the Hudson River, substrate size as a predictor was able to account for 67% of the variability in zebra mussel density (Fig. 4). The best multiple regression model for the Hudson (r² = 0.89) had zebra mussel density negatively correlated with substrate size and positively correlated with the maximum width of the river at the site (Table 2). In Oneida Lake, substrate size accounted for 91% of the variability in zebra mussel density (Fig. 4). Adding calcium concentrations of the water as a predictor in a multiple

regression explained a further 8% of the variability (Table 2). Oneida Lake also had the highest calcium concentrations of all three systems (ANOVA, p < 0.001).

The slopes of the regressions of density against substrate size were similar in all three systems (t-tests, p > 0.15; Fig. 4). However, while the intercepts of the St. Lawrence and Hudson River regressions were also similar to each other (t-test, p > 0.36), the intercept for the Oneida Lake regression was higher than those of the two river systems (t-test, p < 0.001). The St. Lawrence sites that were judged to be lentic (Bassin Louise) fell along the Oneida Lake regression line. Substrate size accounted for the greatest proportion of variability in zebra mussel density in the models and was the common thread across the three systems (Table 3).

### Literature Studies

The composite model explained 67% of the variability in zebra mussel density from the three systems we investigated (Table 2). In testing this model, the literature lake densities tended to fall above those predicted by the lake regression (Fig. 5). This is particularly evident for the North American lakes. The river densities, on the other hand, tended to be scattered on either side of the predicted river regression (Fig. 5). In a model generated from the literature data, substrate size explained 75% of the variability in zebra mussel density for the 72 lake sites and 29% of the variability in density for the 18 river sites (Table 2).

### Discussion

Suitable water chemistry seems primarily to set the threshold for the presence of zebra mussels rather than determine their abundance, and calcium levels along the north shore of the St. Lawrence River may be the limiting factor affecting their distribution within the river. Sprung (1987) observed limited survival of zebra mussel larvae at calcium concentrations of 12 mg/L, while Vinogradov et al. (1993) found waters with calcium concentrations below 5.0-12 mg/L to be unsuitable for normal zebra mussel calcium metabolism. The minimum calcium requirement for survival and growth of adult zebra mussel was found to be between 3 and 8 mg/L.

but in the order of 13 mg/L, for veligers (S. Hincks and G.L. Mackie, University of Guelph, Guelph, Ont., personal communication). These results support the findings of the present study of a calcium threshold of 15 mg/L limiting zebra mussel distribution along the St. Lawrence River.

Neary and Leach (1992) stressed the need to account for the natural temporal variability in calcium concentrations when trying to determine threshold levels. The calcium threshold value of 23.3 mg/L reported by Ramcharan et al. (1992b) may be as over-estimation given the presence of zebra mussel along the south shore of the St. Lawrence River at sites with calcium concentrations of 16 mg/L (Table 1). However, our calcium estimates are derived from single samples, while the data from Ramcharan et al. (1992b) were averaged over longer periods. To test whether or not our estimates are representative of mean values, we turned to published studies that report calcium data for the St. Lawrence River averaged over longer time periods. Vincent et al. (1991) found mean calcium concentrations (averaged over a period between May and August 1982) of 17 mg/L for a north shore site and 48 mg/L for a south shore site in the home range of zebra mussels. Superficial support for the validity of our threshold level of 15 mg/L can be found if one considers that marked seasonal variations in calcium levels usually occur in hardwater systems, while calcium levels in softwater systems (typically below saturation levels) exhibit only minor seasonal variations (Wetzel 1983). Given that the amount of dissolved calcium in a water body depends on many other factors (such as temperature and pH), we can only apply our threshold level of 15 mg/L, with confidence to the St. Lawrence River. Future studies may investigate the generality of this threshold by seeing whether softwater lakes draining the Canadian Shield are successfully colonized by zebra mussels. This study was supported by the Natural Sciences and Engineering Research Council of Canada.
While calcium may limit zebra mussel distribution, it is in itself a poor predictor of abundance. In the density models for the St. Lawrence River and Oneida Lake (Table 2), calcium was a significant predictor but only explained a small portion of the variability in mussel density. In addition, Ramcharan et al. (1992b) had greater success in predicting zebra mussel occurrence (presence/absence) than density using pH and calcium as predictors, although in their study the data were averaged for different water bodies, while ours were averaged over different sites.

Within sites with suitable water chemistry, the survival of zebra mussel is dependent on their finding suitable substra- tes (Stancyzkowska 1977; Lewandowski 1982). The majority of variability in zebra mussel density along the St. Lawrence and Hudson rivers and in Oneida Lake was accounted for by substrate size (Fig. 3 and 4), supporting the idea that physical factors play a more important role in determining local abundance than water chemistry variables (Neary and Leach 1992). In addition, although mussel den- sities in each system were affected by different factors (Table 3), substrate size remained the dominant factor across the three systems. Even in the absence of these detailed data, a conversion of gross substrate descriptions to the phi scale showed substrate size to be an important determinant of mussel density in the literature data set (Table 2; Fig. 5).

The contribution of substrate size to explaining variability in density varied between systems, explaining a greater portion in lake models than in river models (Table 2; Fig. 4). While this may simply be an artifact of disparate sample sizes, it may also reflect some fundamental differences between rivers and lakes. Zebra mussel densities are usu- ally lower in rivers than in lakes (Stancyzkowska 1977), and in comparing our three systems, densities in Oneida Lake were generally 1 order of magnitude higher than in either river system given the same substrate size values (Fig. 4). If densities in lakes are governed primarily by sub- strate size (as shown by the Oneida Lake model), then mussel populations in rivers may be affected by other factors such as the effects of current on larval settlement and the possible dilution of larval densities due to rapid flushing in rivers. These effects may be manifested indirectly in lower adult densities in rivers when compared with lakes.

Other physical variables that potentially affect sediment particle size such as slope and exposure (Kwam et al. 1992) were not of significant value in our models, possibly due to the narrow range of these variables and the overriding impor- tance of substrate size. Exposure, however, was highly cor- related (r = 0.74) with substrate size in the Oneida Lake data set and may prove useful as a surrogate variable for substrate in future studies. Macrophytes, although absent at our sites, can provide important substrates for larval settle- ment (Lewandowski 1982) and will need to be included in future general models of zebra mussel abundance.

The scatter around the density—substrate size models may be further reduced by refining our method of quantifying substrate. Mussel densities were only determined within a projected net square boundary which did not take into account the entire surface area available for colonization. The precision of the models may therefore be improved by includ- ing a measure of surface area in addition to the conversion to phi. To further reduce bias and improve the accuracy of the assessment of percent cover by different substrates, a photograph can be taken of the quadrat on the river or lake bottom (Bohnsoek 1979; Foster et al. 1991). The pho- tograph can then be scanned with the aid of a computer and the percent cover of each substrate type determined more accurately, possibly increasing the predictive power of mod- els and reducing between-donor bias.

The negative correlation between zebra mussel abundance and Secchi depth in our model (Table 2) may reflect a pref- erence for dark areas in the St. Lawrence River. Postveliger zebra mussel exhibit negative phototaxis in that they prefer- enceoly colonize the undersides and crevices of different substrates (Morton 1969a), although this preference may also be linked to the avoidance of predators, water turbu- lence, and current and ice scour (Yankovich and Hassner 1993). Secchi depth was colinear with TP, and if TP can be considered a measure of productivity in rivers, then the correlation between Secchi and abundance may indicate a positive association between abundance and productivity. Ramcharan et al. (1992b) found phosphorus concentra- tions to be negatively correlated with zebra mussel density, although the increased range in their TP values relative to ours may account for this difference. Stancyzkowska (1984) suggested that nutrient levels may only adversely affect abundance at high concentrations, and the difference in the range of values may account for the difference in trends observed between our model and ours.

Unidirectional abundance was also an important factor in determin- ing zebra mussel abundance in the St. Lawrence River. When presented with a choice of different substrates on which to settle, Lewandowski (1976) found native unionoids to be preferred by zebra mussel. On soft substrates (e.g., mud, sand), unionoids often provide the only hard substrate for initial mussel colonization (Lewandowski 1976; Hebert et al. 1991; Hunter and Bailey 1992). Unionoids were heav- ily colonized in the Hudson River and in Oneida Lake, but were not significant predictors in the models representing these systems. The importance of hard substrate availability may also decrease over time as zebra mussel begin coloniz- ing soft substrates by forming mats extending from an initial point of colonization such as on native unionoids or on dead zebra mussel shells (Morton 1969b; Lewandowski 1982; Ramcharan et al. 1992b).

Although crayfish are unlikely to control whole zebra mussel populations, they may limit local densities and size distributions (H.J. MacIsaac, University of Windsor, Windsor, Ont., personal communication). The negative correlation between mussel density and the presence of crayfish in the St. Lawrence River (Table 2) may be an indication of the potential impact crayfish can exert on mussel densities. Predation of zebra mussel by crayfish has also been shown by Piesek (1974) and Love and Savino (1993). Blue crab (Callinectes sapidus) may have a similar effect on local populations of zebra mussel in the Hudson River where the two ranges overlap (Strayer et al. 1993), and although crabs were noticed during sampling in the Hudson, they were not sampled rigorously and therefore not included in the analyses.

Based on 16 European studies, Strayer (1991) found zebra mussel abundance to be related to stream size in running waters, with mussels rarely occurring in streams less than 30 m wide. A similar pattern appeared in the Hudson River, where the maximum width of the river at the site was posi- tively correlated with mussel density (Table 2). However, as Strayer (1991) pointed out, no ecological mechanisms are known to explain this pattern.
In certain European lakes, zebra mussel populations have fluctuated dramatically (Stanizewskaya and Lewandowski 1995), and the temporal variability in densities must be addressed before any predictive model can be successfully used. While the present study sheds little direct light on this aspect, we might expect North American zebra mussel populations to continue increasing relative to European pop-
ulations; examination of the literature model with respect to this question suggests that densities in Oneida Lake are likely to continue to increase, while the river populations may be closer to an equilibrium level (Fig. 5). Alternatively, some authors have suggested that populations may over-
shoot equilibrium levels only to crash to more stable levels as a result of food or of some other resource-limitation (Cooley 1991; O’Neill and MacNeill 1991; Macnae et al. 1992), but the evidence for this is tenuous. Population fluctuations would also be more difficult to model, although attempts in this direction have been made (Ramcharan et al. 1992a).

There is evidence for increases in zebra mussel populations between 1991 and 1992 within the three systems we investi-
gated. During this period, the population along the Hudson River increased by 100-1000 times (Strayer et al. 1993), while in Oneida Lake, densities have increased approxi-
ately 30-fold from June to October 1992 (E. Mills, Canesell University, New Yor., Y.N., personal communication). Along the St. Lawrence River the increase has been less dramatic, with densities increasing sixfold on average. Further moni-
toring may help to establish the extent of future population increases in these three systems and may also help deter-
mine whether or not the river populations are approaching equilibrium compared with Oneida Lake.

In summary, we linked zebra mussel abundance to a vari-
cy of physical and chemical variables in rivers and lakes. Water chemistry appears to set a threshold level for the presence of zebra mussels, and once waters are chemically suited to support zebra mussel physiological processes, phys-
ical factors (in particular, substrate size) tend to limit their local abundance. Our sediment evaluation method allows for a quick visual assessment of the substrate and a simple mathematical conversion. This method also allows for den-
sity comparisons to be made between different sites or across different systems by factoring in effects of substrate. In addi-
tion, this study reinforces the need for site-specific data given the local nature of zebra mussel settlement and colo-
nization. Predictive models such as these in conjunction with maps forecasting the potential spread of zebra mus-
sels will be highly effective in aiding control and monitor-
ing programs by pinpointing areas most likely to be invaded and allowing for an assessment of the degree of infestation.

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