Patterns in the Distribution and Abundance of Zebra Mussels (Dreissena polymorpha) in the St. Lawrence River in Relation to Substrate and Other Physico-Chemical Factors

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E. Mellina

Abstract

Using SCUBA and an in situ method of quantifying substrate characteristics, I 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 lack of zebra mussel along the north shore of the St. Lawrence River east of Montreal until Portneuf despite an abundance of suitable substrate. Calcium concentrations of 15 mg/L or less were found to limit the distribution of zebra mussel. The entire south shore from Cornwall, Ontario to Ile d'Orléans, Quebec was colonized by zebra mussel wherever suitable substrate was found. In the Hudson River, along the south shore of the St. Lawrence River and in Oneida Lake variability in density was primarily related to substrate type which explained between 38% and 91% of the variance. Other factors such as Secchi depth, calcium concentration of the water, the presence of crayfish, native unionid abundance and the maximum width of the river at the site increased the amount of explained variance across the different systems. The influence of substrate type on zebra mussel density and the predictions of the model were also tested using data from the literature, where substrate type explained 75% of the variability in density. The scatter of the literature data above the predictions of the empirical model suggests that North American zebra mussel populations may continue to grow before reaching equilibrium levels. While water chemistry parameters may be useful predictors of the

presence or absence of zebra mussel in a given water body, physical factors play a far greater role in determining local abundance.

Résumé

Cette étude décrit la distribution des moules zébrées (Dreissena polymorpha) du fleuve St. Laurent, de la rivière Hudson et du lac Oneida de l'état de New York ainsi que les charactéristiques des substrats sur lesquels elles adhèrent. Des modèles empiriques ont aussi été développés pour évaluer leur densité. La rive- nord du fleuve St-Laurent, de Montréal à Portneuf (Québec) ne contenait aucune moule à cause d'une faible teneur en calcium dissous de l'eau provenant des rivières drainant le Bouclier Canadien, ceci même avec une abondance de substrats convenables. Une concentration de calcium dissous de 15 mg/l ou moins semble limiter la distribution des moules zébrées. Par contre, la rive-sud du fleuve, de Cornwall (Ontario) à l'Ile d'Orléans (Québec) est colonisée par des moules zébrées, là ou il y a présence de substrat adéquat. Le long de la rive-sud du fleuve St- Laurent, dans la rivière Hudson et dans le lac Oneida, la variabilité de l'abondance des moules est reliée principalement au type de substrat. Entre 38% et 91% de la variance s'explique par la qualité de celui-ci. D'autres facteurs, comme la profondeur visible à l'aide d'un Secchi, la concentration de calcium dissous, la présence d'écrevisses, l'abondance de moules Unionides et la largeur maximale de la rivière à chaque site ont tous aidé à expliquer une portion de la variabilité de la densité des moules zébrées de ces trois systèmes. L'influence du substrat sur les densités des moules et les prédictions des modèles développés ont aussi été vérifiées par des données provenant de la littérature, où le type de substrat explique 75% de la variabilité de la densité de

moules. Une dispersion des données provenant de la littérature au-dessus du modèle empirique semble suggérer que les populations de moules zébrées de l'Amérique du Nord vont probablement augmenter avant de s'établir à des niveaux plus stables. Bien que certains paramètres de la chimie de l'eau peuvent être utiles afin de prédir la présence ou l'absence de moules zébrées dans un cours d'eau, les facteurs physiques tels que les substrats jouent un plus grand rôle dans la détermination de la densité locale.

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Preface

The Faculty of Graduate Studies and Research of McGill University requires the following to be cited in theses that include manuscripts as part of the thesis in order to inform the external reader of Faculty regulations:

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- The thesis must still conform to all other requirements of the "Guidelines Concerning Thesis Preparation" and should be in a literary form that is more than a mere collection of manuscripts published or to be published. **The thesis must include, as separate chapters or sections:** (1) a Table of Contents, (2) a general abstract in English and French, (3) an introduction which clearly states the rationale and objectives of the study, (4) a comprehensive general review of the background literature to the subject of the thesis, when this review is appropriate, and (5) a final overall conclusion and/or summary.
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candidate's interest to make perfectly clear the responsibilities of the different authors of co-authored papers."

This thesis has been prepared in the format of one manuscript which has been submitted to the Canadian Journal of Fisheries and Aquatic Sciences. The supervisor of my thesis, Dr. J.B. Rasmussen, appears as the sole co-author. With respect to the allocation of different responsibilities, **all the data collection (including all the SCUBA diving, water chemistry analyses and literature searches) was conducted by myself. I also analyzed all the data and wrote in full both the thesis and manuscript.** Dr. Rasmussen provided constructive discussions and editorial criticisms in addition to the normal supervision and advice given by the thesis supervisor.

The originality of this research is first believed to lie in the documentation of previously unknown distributional and abundance patterns of zebra mussels in the St. Lawrence River. In addition, this study describes a novel in situ method of quantifying different substrate types allowing for the development of empirical zebra mussel abundance models for both rivers and lakes, and allows for direct density comparisons to be made between different sites or across different water bodies. Finally, this study proposes a calcium threshold level that is believed to limit the distribution of zebra mussels based on data gathered across a naturally occurring calcium gradient along the St. Lawrence River.

Acknowledgements

First and foremost, I am indebted to my supervisor, Dr. Joseph Brasen Rasmussen, for his trust and confidence in my abilities and for the invaluable help and training I have received from him during my undergraduate and graduate years at McGill University. During this time he has not only become my mentor through our discussions and interactions, but also my friend and for this I extend to him my most sincere gratitude. His constant support and encouragement made the realization of this thesis possible.

I would also like to thank Bettina Sander and Stephan Kesting for their invaluable support which kept me sane throughout this project. In addition to their field assistance, they provided me with moral support and friendship when I needed it most. I would especially like to acknowledge Bettina's continuous encouragement and to thank Stephan for saving my life on the St. Lawrence River in the early stages of this project.

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Finally, I would like to express my heart-felt gratitude and appreciation to my mother, Ingrid Liesegang Mellina, for her unfaltering support in all my endeavors.

Introduction

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

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

Although the availability of suitable substrate is essential for the survival of post veliger zebra mussel (Stanczykowska 1977; Lewandowski 1982; Mackie et al. 1989), no published models have used substrate variables predictively. Physical factors are important determinants of zoobenthic biomass (Rasmussen 1988), and Harman (1972), Horne and McIntosh (1979) and Stern (1983) have shown qualitatively how different substrate types influence freshwater unionid abundance and distribution. A quantitative evaluation of 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-Bartels 1990). The purpose of this 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. I hypothesize that along the north shore in areas draining the Canadian Shield low calcium concentrations would make mussels rare or absent. By contrast, high calcium levels and a good supply of larvae from the Great Lakes along the south shore would probably result in the potential for a high degree of substrate related variability in zebra mussel density. An in situ method for quantitative substrate characterization was developed that enabled me to determine the influence of substrate type on zebra mussel density and to develop empirical models using linear regression analysis. The applicability of the method was also tested in the Hudson River and in Oneida Lake, New York. Finally, the robustness of the empirical models was tested with data from literature studies that reported both zebra mussel densities as well as general descriptions of associated substrates.

Materials and Methods

Study Areas

The St. Lawrence study area comprised 57 freshwater sites along the St. Lawrence River between Cornwall, Ontario and Ile d'Orléans, Quebec, including 4 sites in the Lake of Two Mountains, Quebec (Fig. 1). This portion of the river was chosen for the variability in the underlying geology of the drainage basins that gave me the opportunity to study the effect of water chemistry on zebra mussel distribution. Ile d'Orléans represents the limit of salt water coming from the Gulf of St. Lawrence, and tides are felt upstream until Lac St. Pierre (Couillard 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 sedimentary rock (Clark and Stearn 1968; Bobée et al. 1981). East of Montreal the existence of different hydrological corridors results in a 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) joined 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 obliterating the water chemistry gradient (Couillard 1982).

Sampling along the St. Lawrence River was conducted between mid-July and the end of August, 1992. Sites were chosen using navigational charts published by Fisheries and Oceans Canada which give approximate substrate compositions. Between Montreal and Lac St. Pierre the river bed is primarily sandy and was therefore sampled less intensively than the rest of the river. Sites were also chosen to maximize the variability in calcium, depth, and Secchi visibility. In addition to natural substrates, 2 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 freshwater tidal section of the Hudson River from Catskill to New Hamburg during the first week of July, and at 5 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 the method of substrate quantification in a second river system and in a lake. In addition, these 2 systems were also characterized by early stages of zebra mussel colonization making them ideal for comparisons with the St. Lawrence River.

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 m^2 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 the counts. While this sampling protocol was not strictly random, biases have further been reduced by averaging estimates over each site when performing the analyses.

The quadrat had a measuring tape attached to it to allow for measurements of mussel and rocks and was adjustable so that smaller areas could be counted when densities exceeded approximately 100/m^2. The number of replicate quadrats that were counted (and their areal coverage) were determined according to Downing and Downing (1992), who predicted that with a density of 100 mussels 2 replicate 1 m^2 quadrats were required to obtain a precision of 20%. Since I attempted to count approximately 100 mussels for each quadrat (this being the optimum number based on experience to preserve reliability, efficiency and safety), the quadrat size varied from 0.01 m^2 to 1 m^2 and the number of quadrats counted at each site varied accordingly (from 3 to 20). Replicate quadrats were counted at each site where zebra mussel were present with the exception of 5 sites in the St. Lawrence where only 1 quadrat was counted per site due to difficulties encountered with fast currents. An underwater light was used to aid in the detection of mussel in areas of low visibility. Size distributions and biomass of zebra mussel were not recorded due to fast currents which did not allow me 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 to the _in situ_ counts for the same quadrats. Differences between the 2 methods did not exceed 5%. Densities from test counts ranged from approximately 10 mussels to 150 mussels, 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, 50% boulders of 30 cm diameter). The different substrate types were converted to the phi scale by transforming them to the negative log base 2 of the particle size in millimeters (Hakanson and Jansson 1983). Each substrate's phi value was multiplied by its percent contribution to the total 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 an estimate of zebra mussel density (which included all zebra mussel counted within a quadrat) and an associated measure of substrate size was obtained. Artificial walls 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 1 000 mm particle). Sampling methods remained constant across the 3 systems (the St. Lawrence and Hudson Rivers and Oneida Lake) and all measurements were made by the same diver 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 m^2 at each site and was accounted for in the regression models with a dummy variable Native unionid abundance was estimated semi-quantitatively by grouping them into 3 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 model with a dummy variable. 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 the lowest normal tide. The maximum width of the river as well as the distance from site to shore at each site were 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 Clesceri et al. (1989) by Hach, Inc. for use on a Hach portable colorimeter: Calcium (titration using CalVer^R indicator), true and apparent color (platinum-cobalt colorimetric method) and total phosphorus (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 $\log_{10}$ (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. I 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 me to analyze the entire data set for the St. Lawrence using 2 approaches: 1) by grouping the variables a posteriori according to shore (to remove the affect 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 the 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 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 a similar protocol) from an additional 11 sites sampled during a preliminary study conducted in 1991 (Fig. 1). These density estimates were compared, using an ANCOVA, to 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 2 years.

Literature studies

To test the robustness of the 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. The model included a categorical variable to distinguish between lakes and rivers and also included Bassin Louise (which was classified 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 5 recent studies of zebra mussel in the Great Lakes and a preliminary study carried out in the Great Lakes in 1991 by myself which yielded 6 additional sites. These 6 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 10 cm and a phi value of -6.644. Where densities were reported for hydrotechnical installations it was assumed these were taken from walls and were therefore assigned a phi value of -9.967 as the corresponding substrate size. Some studies (e.g. Lundbeck 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 composed 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 3 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 based on this calcium threshold level of 15 mg/L. Calcium levels in the water were significantly different between shores (t-test, $p<0.001$) and ranged from 8-14 mg/L for the north shore of the St. Lawrence and 16-38 mg/L for the south shore (Table 1). North shore sites were localized along the section of the river between Montreal and Portneuf while south shore sites were located along the entire section of the river between Cornwall and Ile d'Orléans.

The north shore was devoid of zebra mussel despite an abundance of large rocks while the entire south shore was colonized where ever suitable substrate (defined as having a substrate size value less than 2 which corresponds to 100% sand) was found (Table 1). I 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 Becancourt and off the island of Montreal. 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 6-fold 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 (r^2=0.83) had zebra mussel density negatively correlated to substrate size, Secchi depth and the presence of crayfish and positively correlated to the categorical classification of unionid abundance, to the lotic/lentic dummy variable and to calcium concentrations in the water (Table 2). The addition of north shore sites 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) were violated.

Hudson River and Oneida Lake

When the density and substrate size data were combined across all 3 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 (r^2=0.89) had zebra mussel density negatively correlated to substrate size and positively correlated to 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 3 systems (ANOVA, $p<0.001$).

The slopes of the regressions of density against substrate size were similar in all 3 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, $p>0.30$), the intercept for the Oneida Lake regression was higher than those of the 2 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 3 systems (Table 3).

Literature Studies

The composite model explained 67% of the variability in zebra mussel density from the 3 systems I 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 set 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

Chemical factors

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 10-12 mg/L to be unsuitable for normal zebra mussel calcium metabolism. The minimum calcium requirement for survival and growth of adult zebra mussel was also 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, pers. comm.). 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 28.3 mg/L reported by Ramcharan et al. (1992a) may be an overestimation 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, my calcium estimates are derived from single samples, while the data from Ramcharan et al. (1992a) were averaged over longer periods of time. To test whether or not my estimates are representative of mean values, I 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 situated near Becancour, Quebec. Similarly, Couillard (1982) found mean calcium concentrations of 12 mg/L for north shore sites and 47 mg/L for south shore sites covering a period of 5 months, and Vincent (1981) reported a mean calcium concentration of 29 mg/L averaged over a period of a year for a south shore site situated 40 km east of Lac St. Pierre, an area in which I found adult zebra mussel. Further support for the validity of my threshold level of 15 mg/L can be found if one considers that marked seasonal fluctuations in calcium levels usually occur in hard-water systems, while calcium levels in soft water 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), I can only apply my 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 Shiled are successfully colonized by zebra mussel.

While calcium may limit zebra mussel distribution, it is in itself a poor predictor of abundance. In the density models for the St.

Lawrence and Oneida Lake, calcium was a significant predictor but only explained a small portion of the variability in mussel density (Table 2). In addition, Ramcharan et al. (1992a) 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 mine were averaged over different sites.

Physical factors

Within sites with suitable water chemistry, the survival of zebra mussel is dependent on their finding suitable substrates (Stanczykowska 1977; Lewandowski 1982). In the present study, 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 (Figs. 3, 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 densities in each system were affected by different factors, substrate size remained the dominant factor across the 3 systems (Table 4). 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 usually lower in rivers than in lakes (Stanczykowska 1977) and in comparing the 3 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 substrate 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 lowered adult densities in rivers when compared to lakes

Other physical variables in the data set that potentially affect sediment particle size such as slope and exposure (Rowan et al. 1992) were not of significant value in the models, possibly due to the narrow range of these values and the overriding importance of substrate size. Exposure however was highly correlated ($r=0.74$) to 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 the sites, can provide important substrates for larval settlement (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 the method of quantifying substrate.

Mussel densities were only determined within a projected metre square boundary and hence did not take into account real surface area available for colonization. The precision of the models may therefore be improved by including 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 areal cover by different substrates, an underwater photograph can be taken of the quadrat on the river or lake bottom (Bohnsack 1979; Foster et al. 1991). The photo 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 models and reducing between diver bias.

The negative correlation between zebra mussel abundance and Secchi depth (Table 2) may reflect a preference for dark areas in the St. Lawrence River. Post veliger zebra mussel exhibit negative phototaxis in that they preferentially colonize the undersides and crevices of different substrates (Morton 1969a), although this preference may also be linked to the avoidance of predators, water turbulence, and current and ice scour (Yankovich and Haffner 1993). Secchi was found to be collinear with total phosphorus (TP), and if TP can be considered a measure of productivity in rivers then the correlation between Secchi and abundance may reveal a positive association between abundance and productivity. Ramcharan et al. (1992a) found phosphorus concentrations to be negatively correlated to zebra mussel density although over a wider range of nutrient levels. Stanczykowska (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 their model and mine.

Unionid abundance was also an important factor in determining zebra mussel abundance in the St. Lawrence River (Table 2). When presented with a choice of different substrates on which to settle, Lewandowski (1976) found native unionids to be preferred by zebra mussel. In addition, on soft substrates (e.g. mud, sand) unionids often provide the only hard substrate for initial mussel colonization (Lewandowski 1976; Hebert et al. 1991; Hunter and Bailey 1992) Unionids were heavily 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 mussels begin colonizing soft substrates by forming mats extending from an initial point of colonization such as on native unionids or on dead zebra mussel shells (Morton 1969b; Lewandowski 1982; Ramcharan et al 1992a).

Although crayfish are unlikely to control whole zebra mussel populations, they may limit local densities and size distributions (H.J. MacIssac, University of Windsor, pers. comm.). 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 Size selective predation of zebra mussel by crayfish has also been shown by Piesek (1974). Blue crabs (*Callinectes sapidus*) may have a similar effect on local densities of zebra mussels 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 positively correlated to mussel density (Table 2). However, as Strayer (1991) pointed out, no ecological mechanisms are known to explain this pattern.

Comparison with literature studies

In certain European lakes zebra mussel populations have fluctuated dramatically (Stanczykowska and Lewandowski 1993), and the temporal variability in densities must be addressed before any predictive model can be successfully used. While the present study sheds little light on this aspect, if one assumes European estimates to be representative of more equilibriated populations than those seen in North America, the literature model suggests that densities in Oneida Lake are likely to continue to increase whereas the river populations may be closer to equilibrium levels (Fig. 5). Alternatively, some authors have suggested that populations may overshoot 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; MacIsaac 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. 1992b).

There is evidence for increases in zebra mussel populations between 1991 and 1992 within the 3 systems I investigated. During this period the population along the Hudson River increased bv 100-1000 times (Strayer et al. 1993), while in Oneida Lake densities have increased approximately 30-fold from June to October of 1992 (E. Mills, Cornell University, unpublished data). Along the St. Lawrence River the increase has been less dramatic, with densities increasing 6-fold on average. Further monitoring may help to establish the extent of future population increases in these 3 systems, and may also help determine whether or not the river populations are approaching equilibrium compared to Oneida Lake.

Conclusions

In summary, this study linked zebra mussel abundance to a variety 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, physical factors (in particular substrate size) tend to limit their local abundance. My sediment evaluation method allows for a quick visual assessment of the substrate and a simple mathematical conversion. This method also allows for density comparisons to be made between different sites or across diferent systems by simply comparing comparable substrate values. In addition, this study reinforces the need for site specific data given the local nature of zebra mussel settlement and colonization. Predictive models such as these in conjunction with maps forecasting the potential spread of zebra mussels will be highly effective in aiding control and monitoring programs by pinpointing areas most likely to be invaded and allowing for an assessment of the degree of infestation.

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Table 1. Averaged physical and chemical characteristics of sites along the St. Lawrence and Hudson Rivers and Oneida Lake. SE is standard error; n is the number of sites.

	Density (no.m $^{-2}$)	Substrate	Temperature (^{0}C)	Depth (m)	Secchi (m)	Max. Width of River at Site (km)	Distance from site to shore (km)	pH	Conductivity (uS/cm)	Calcium (mg/L)	Total Phosphorus (ug/L)	Apparent Color (Pt-cobalt units)
St. Lawrence North Shore (East of Montreal and the Lake of Two Mountains)												
Max.	0.00	1.58	21.40	4.60	2.00	5.50	2.00	9.70	223.00	14.00	83.33	541.00
Min.	0.00	-9.97	8.10	0.50	0.20	2.00	0.10	6.29	50.00	8.00	12.84	48.00
Mean	0.00	-4.89	15.56	2.18	1.04	3.45	0.64	7.38	114.30	10.89	29.47	109
SE	0.00	1.15	1.62	0.35	0.15	0.30	0.19	0.31	15.35	0.61	6.27	43.77
n	11	11	11	11	11	11	11	11	11	11	11	11
St. Lawrence South Shore												
Max.	26883	3.72	21.20	11.00	5.25	14.50	3.00	8.60	666.00	37.60	46.40	88.00
Min.	0	-9.97	16.30	1.80	0.50	0.50	0.10	7.25	140.00	16.20	4.57	6.00
Mean	2444	-3.64	19.27	4.01	2.07	4.14	1.00	7.90	267 95	31.82	20 38	25 05
SE	925	0 51	0.22	0.31	0.16	0.36	0.11	0.05	10.74	0.77	1 25	2.62
n	46	46	46	46	46	46	46	30	46	46	46	46
Hudson River												
Max.	37500	6.14	24.30	8.84	1.20	1 40	0.56	7.19	214.00	26.40	140 36	101 50
Min.	0	-9 97	23.00	1.82	0.40	0.68	0.04	6.83	183.00	22.00	28.50	29.00
Mean	5091	-2.97	23.38	2.96	0 96	1.10	0 28	7.10	199 38	23.96	67 68	48.27
SE	3440	1 95	0 14	0.60	0 06	0.07	0 06	0.03	3.76	0.41	10 46	6.14
n	11	11	11	11	11	11	11	11	8	11	11	11
Lake Oneida												
Max.	3161	5.86	21.80	6.71	3.50	n/a	2 96	8.20	336.00	45.00	44.71	70.00
Min.	42	-4 83	19.40	3 05	2 50		0.28	7.99	298 00	22 20	3.50	17 33
Mean	1155	-0 55	20 54	4 05	2 90		1 33	8.14	311.80	37 76	14 51	30 57
SE	624	1 96	0 41	0 71	0 19		0.45	0.04	6.38	3.99	7 28	9.91
n	5	5	5	5	5		5	5	5	5	5	5

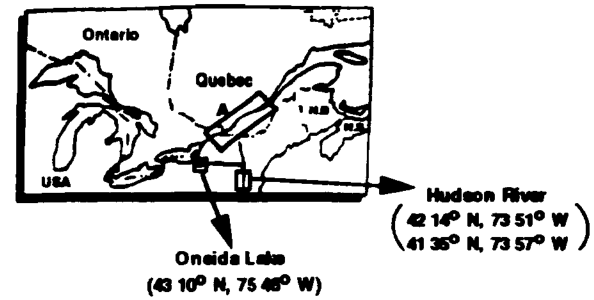
Table 2. Multiple regression models obtained for zebra mussel density for the St. Lawrence and Hudson Rivers, Oneida Lake and the literature studies. Numbers in brackets following predictors are standard errors of the coefficients. Significance: * $p<0.05$, ** $p<0.005$, *** $p<0.001$.

Equation	r^2	SE of est.	n
St. Lawrence River (South Shore)			
(1) Log Density = 0.05 - 0.13 Substrate (0.03)*** - 1.86 Log Secchi (0.39)***	0.83	0.45	46
+ 0.05 Calcium (0.05)** + 0.69 Clams (0.13)*** - 0.41 Crayfish (0.16)*			
+ 2.21 Lentic Site (0.32)***			
St. Lawrence (North and South Shores)			
(2) Log Density = -1.67 - 0.09 Substrate (0.02)*** - 1.79 Log Secchi (0.38)***	0.82	0.56	57
+ 0.11 Calcium (0.01)*** + 0.52 Clams (0.13)*** + 2.78 Lentic Site (0.33)***			
Hudson River			
(3) Log Density = - 3.35 - 0.30 Substrate (0.03)***	0.89	0.51	11
+ 4.20 Max. Width of River (0.96)**			
Lake Oneida			
(4) Log Density = 1.70 - 0.17 Substrate (0.003)*** + 0.02 Calcium (0.001)**	0.99	0.02	5
Composite Model (St. Lawrence south shore, Hudson, Oneida)	0.67	0.66	62
(5) Log Density = 1.38 - 0.19 Substrate (0.02) *** + 1.14 Lake (0.23) ***			
Literature Studies (Lakes)			
(6) Log Density = 2.34 - 0.23 Substrate (0.02)***	0.75	0.82	72
Literature Studies (Rivers)			
(7) Log Density = 1.43 - 0.14 Substrate (0.05)***	0.29	1.05	18

Table 3. Comparison of predictors and their influence on zebra mussel density in the models for the St. Lawrence and Hudson Rivers and Oneida Lake.

St. Lawrence River (all sites)	p value	Hudson River	p value	Oneida Lake	p value
Substrate (Phi) (-)	<0.001	Substrate (Phi) (-)	<0.001	Substrate (Phi) (-)	<0.001
Log Secchi (-)	<0.001	Max. Width of River (+)	0.002	Calcium (+)	0.003
Calcium (+)	<0.001				
Clams (+)	<0.001				
Crayfish (-) (south shore only)	0.01				
Lentic Site (+)	<0.001				

Figure 1. Study areas along the St. Lawrence River. Stippled areas indicate calcium poor waters. Approximate coordinates for the section of the Hudson River that was sampled and for Oneida Lake are shown.


Ontario
Quebec
USA
Hudson River
(42 14° N, 73 51° W
41 35° N, 73 57° W)
Oneida Lake
(43 10° N, 75 46° W)

A

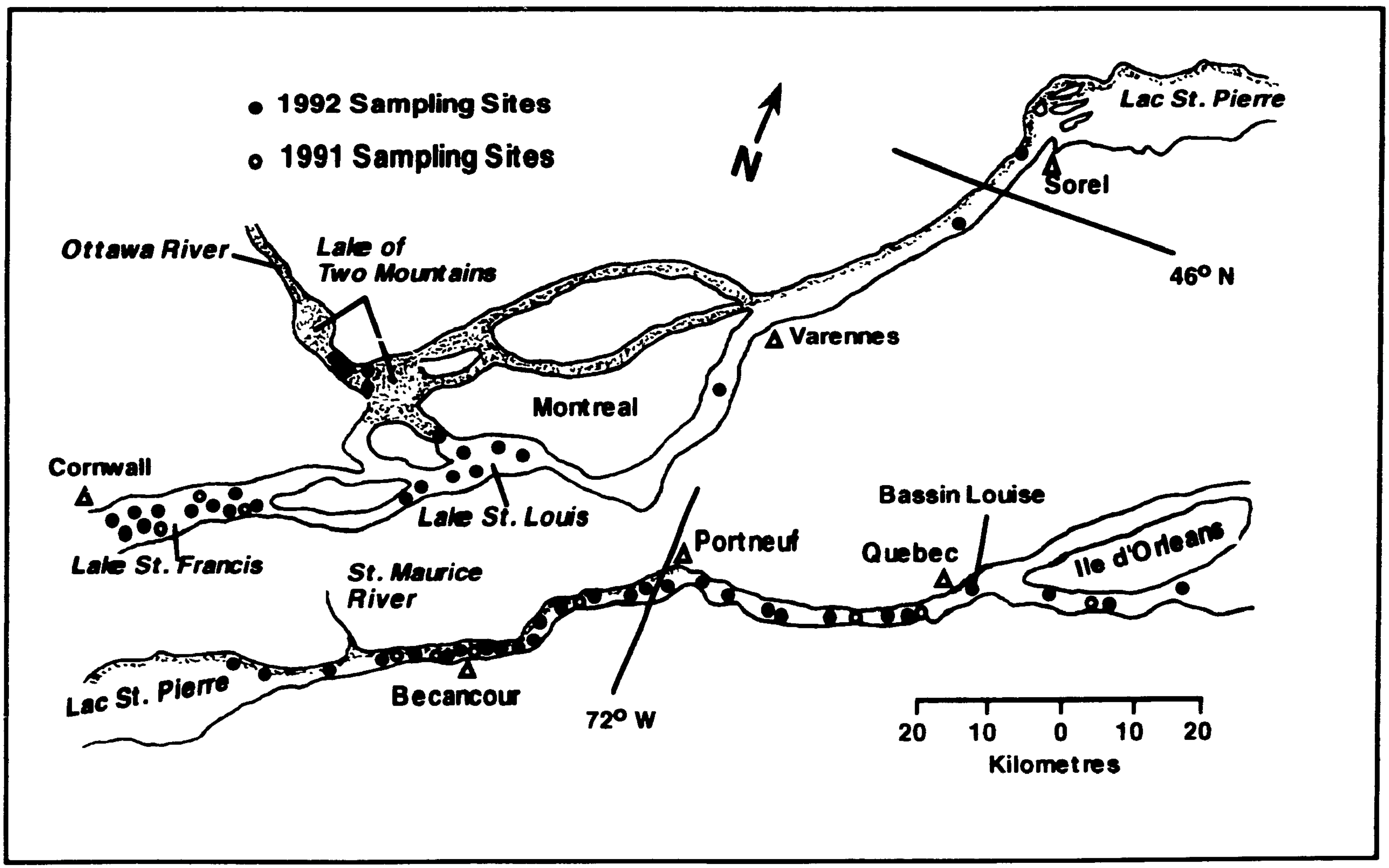

1992 Sampling Sites
1991 Sampling Sites
N
Lac St. Pierre
Sorel
46° N
Ottawa River
Lake of Two Mountains
Varennes
Montreal
Cornwall
Lake St. Louis
Lake St. Francis
Bassin Louise
Portneuf
Quebec
Ile d'Orleans
St. Maurice River
Lac St. Pierre
Becancour
72° W
20 10 0 10 20
Kilometres

Figure 2. Plot of zebra mussel density versus calcium concentration of the water (averaged over each site) for the combined data set including all 3 systems. Only those density estimates associated with suitable substrate sizes (with phi values less than 2) were chosen to remove the effects of unsuitable substrate on mussel density. The threshold concentrations suggested by this study and by Ramcharan et al. (1992) are shown.

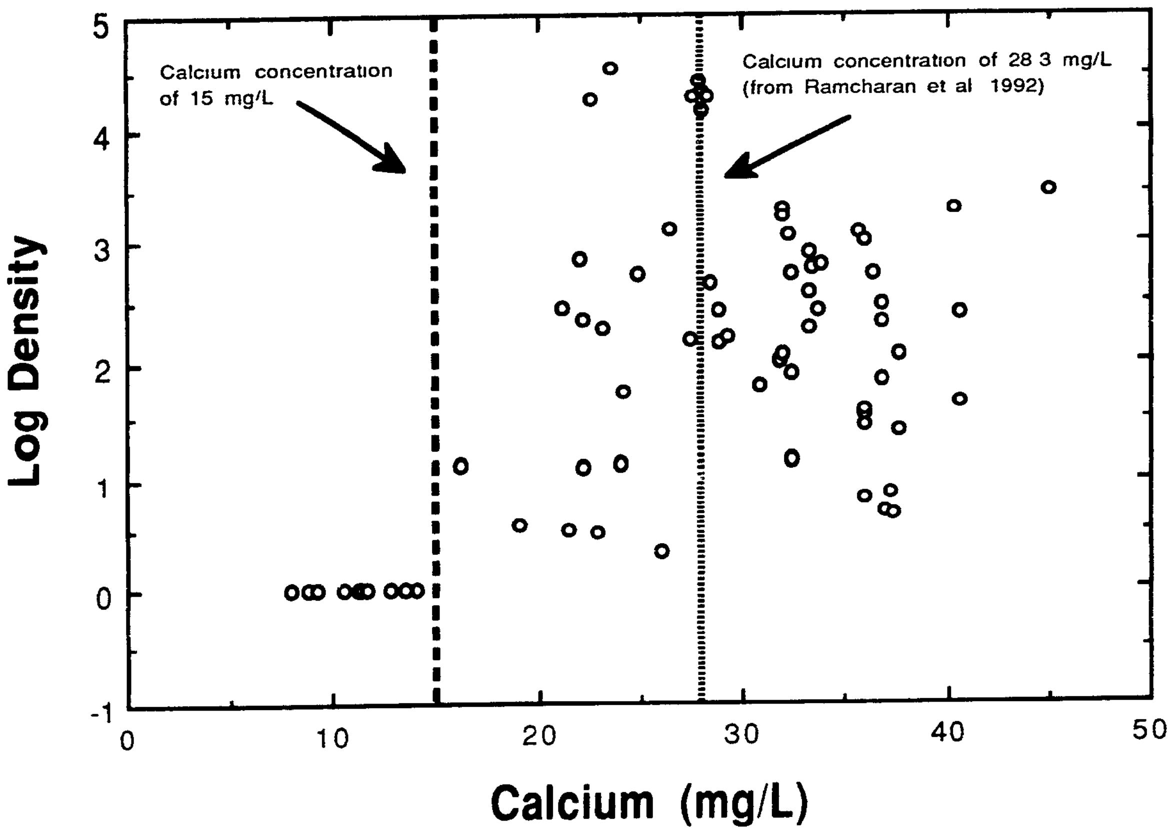
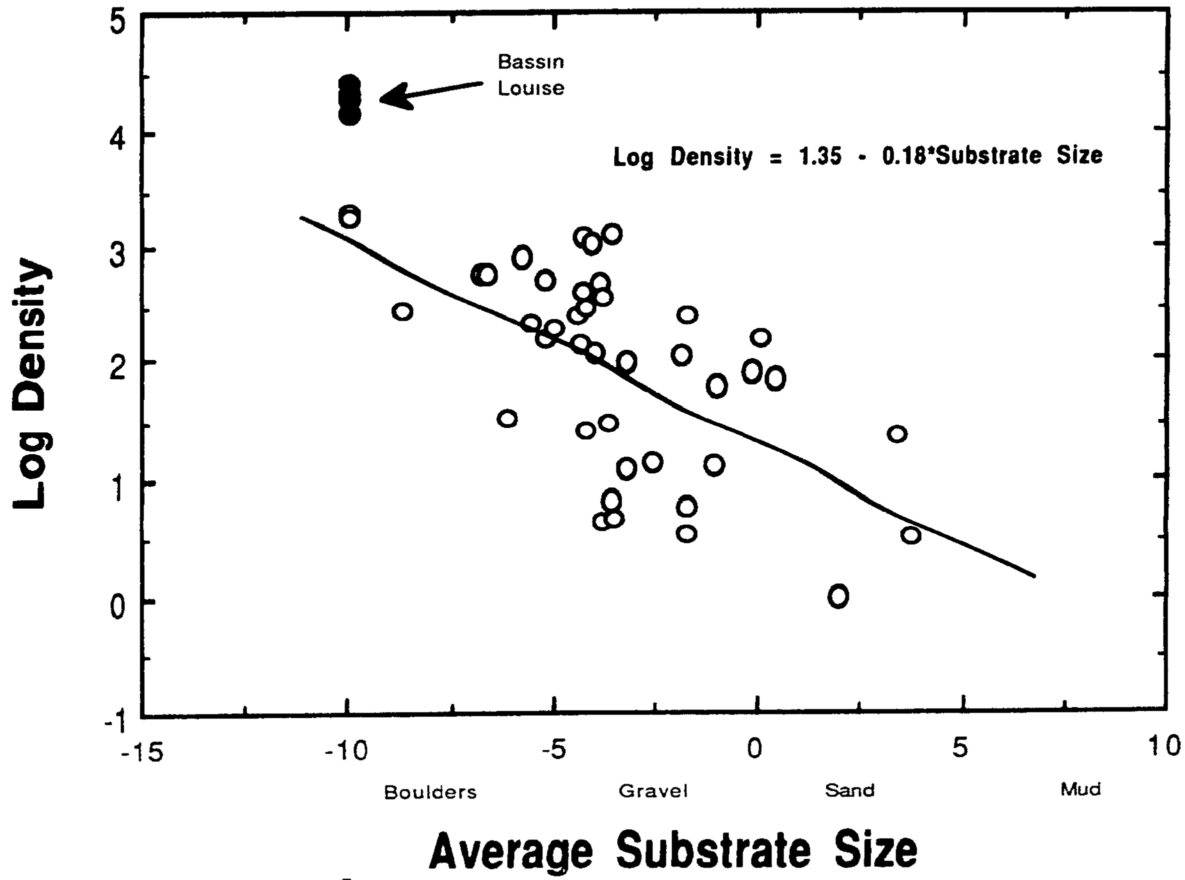

Calcium concentration
of 15 mg/L
Calcium concentration of 28 3 mg/L
(from Ramcharan et al 1992)
Log Density
Calcium (mg/L)
5
4
3
2
1
0
-1
0
10
20
30
40
50

Figure 3. Relationship between zebra mussel density and substrate size (the mean weighted phi value for each quadrat averaged over each site) for the St. Lawrence River (R^2 =0.38, $p<0.001$, n=41). Densities from Bassin Louise are not included in the regression.



Bassin Louise
Log Density = 1.35 - 0.18*Substrate Size
Log Density
5
4
3
2
1
0
-1
-15
-10
-5
0
5
10
Boulders
Gravel
Sand
Mud
Average Substrate Size

Figure 4. Relationship between zebra mussel density and substrate size averaged over each site for the 3 systems combined. The regression equations for the Hudson River and Oneida Lake, respectively, are:

(1) Log density = 1.53 - 0.20 * Substrate Size (R^2=0.67, $p<0.001$, n=11)

(2) Log density = 2.55 - 0.17 * Substrate Size (R^2=0.91, $p<0.001$, n = 5)

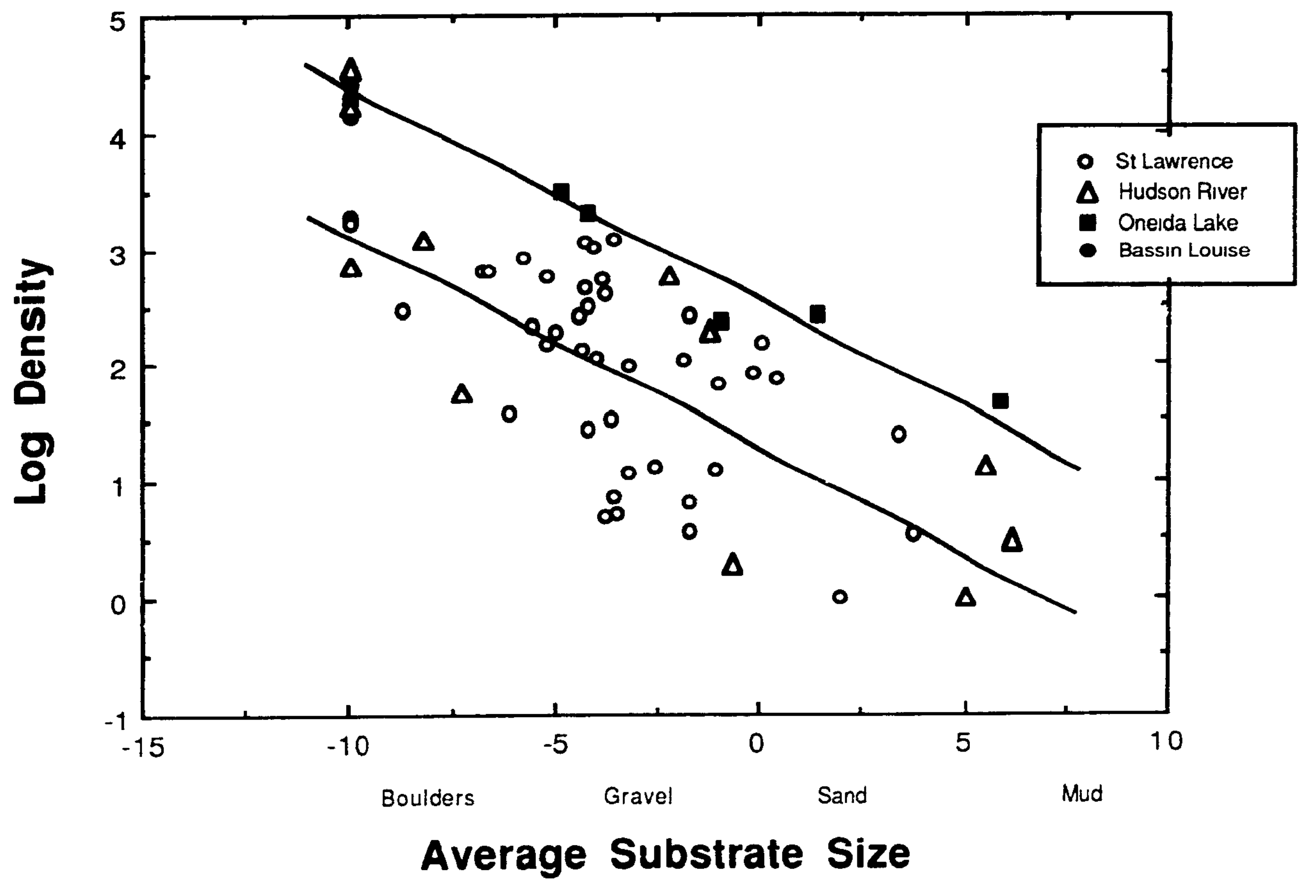
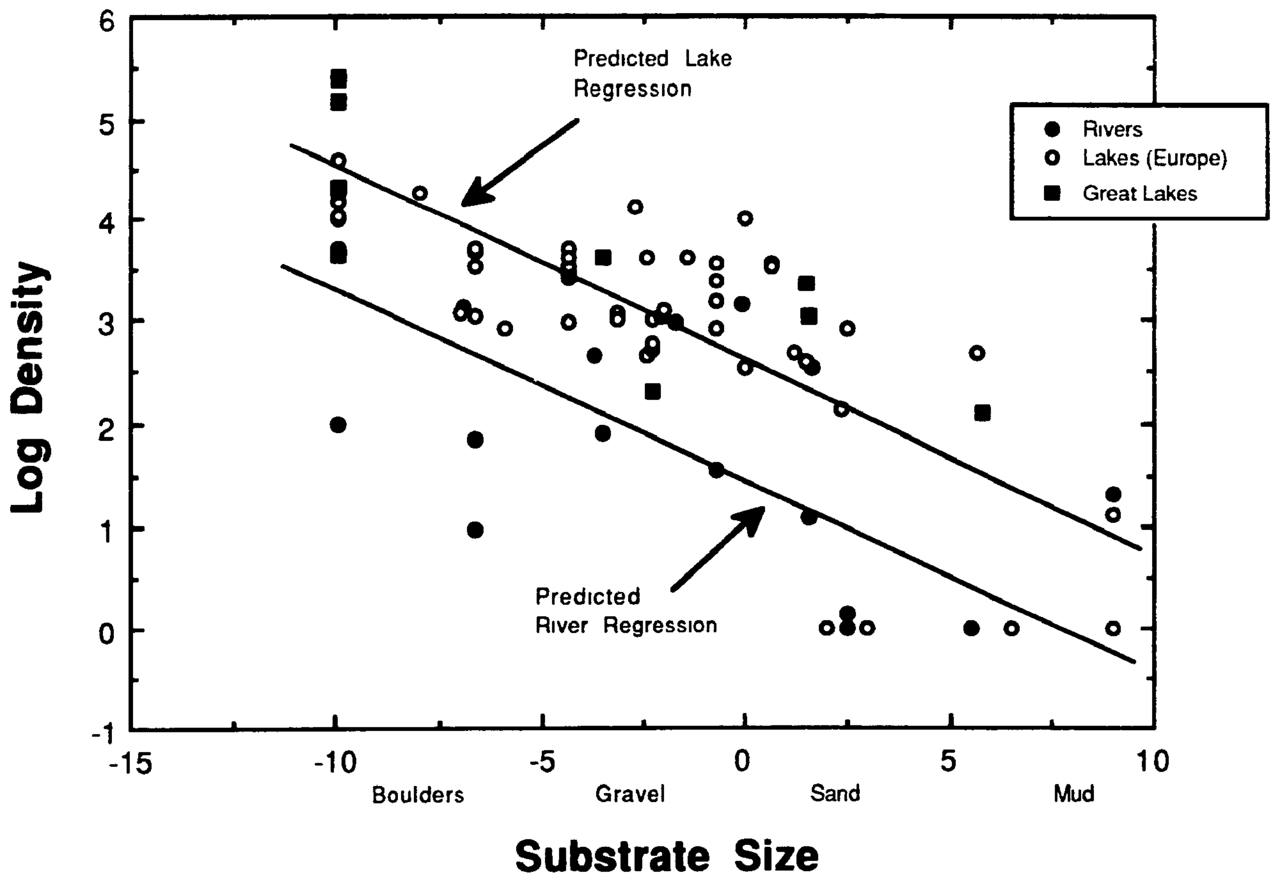

St Lawrence
Hudson River
Oneida Lake
Bassin Louise
Log Density
5
4
3
2
1
0
-1
-15
-10
-5
0
5
10
Boulders
Gravel
Sand
Mud
Average Substrate Size

Figure 5. Test of the predictions of the composite model (formed by pooling the sampling data from all 3 systems) using literature data. The solid lines represent the predicted regressions for rivers and lakes according to model 5 in Table 3. Literature references comprise. **1) Rivers:** Behning 1928 (River Volga); Berg 1948 (River Susaa); Kachalova and Sloka 1964 (Daugava River); Kovalak et al. 1993 (Detroit River); Smit et al. 1993 (River Ijssel); Wielgosz 1979 (River Lyna), Wielgosz 1981 (River Wel); Zhadin and Gerd 1968 (River Volga) **2) European Lakes**: Berg 1938 (Lake Esrom); Bianchi et al. 1974 (Lake Garda); Biryukoi et al. 1964 (Babiinski backwater); Dall et al. 1984 (Lake Esrom); Dusoge 1966 (Lake Mikolajskie); Ehrenberg 1957 (Grosser Ploner See, Kleiner Ploner See, Trammer See); Gizinski and Toczek-Boruchowa 1972 (Goplo Lake); Gizinski and Kadulski 1972 (Goplo Lake); Jonasson 1978 (Lake Esrom); Kachanova 1962 (Uchinsk Reservoir - cited in Morton 1969b); Kajak and Dusoge 1976 (Lake Sniardwy); Kornobis 19¯7 (unspecified-one of the Konin lakes); Lewandowski 1991 (Lake Kolowin); Lewandowski and Stanczykowska 1986 (Lake Zarnowieckie); Lundbeck 1926 (Suhrer See, Trammer See, Ploner See, Becken See, Schaal See); Michalkiewicz 1991 (Rosnowskie Duze Lake); Mikulski and Gizinski 1961 (Wdzydze Lake); Pieczynska 1972 (Lake Mikolajskie); Sapkarev 1975 (Lake Doiran); Shevtsova and Kharchenko 1981 (N. Crimean canal); Stanczykowska 1977 (Lake Konin); Stankovic 1951 (Lake Doiran); Walz 1973 (Lake Constance); Wisniewski 1990 (Lake Druzno, Wloclawek Dam); Wisniewski 1974 (Goplo Lake); Wundsch 1924 (Muggel See); Zhadin and Gerd 1968 (Sartlan Lake) **3) Great Lakes**: Dermott et al 1993 (Lake Erie); Hebert et al. 1989, 1991 (Lake St.

Clair); Kovalak et al. 1993 (Lake Erie); Leach 1993 (Lake Erie); our 1991 study (Lake Erie, Lake St. Clair).


Predicted Lake
Regression
Predicted
River Regression
Rivers
Lakes (Europe)
Great Lakes
Log Density
6
5
4
3
2
1
0
-1
-15
-10
-5
0
5
10
Boulders
Gravel
Sand
Mud
Substrate Size

Appendix 1. Zebra mussel densities and chemical and physical variables measured along the St. Lawrence River in 1992. Mussel densities and substrate values of the 11 sites used to estimate the increase in densities between 1991 and 1992 are also included.

Appendix 1: St. Lawrence River 1992

Site No.	Shore S=South N=North	Quadrat No.	Density (No /m²)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (^0C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
1	S	1	0	-4.92	8	81	21.1	1.5	6.77	52	31.33
2	S	1	0	-8 966	8.8	80	21.1	1.5	6.85	60	28
3	S	1	0	-5.75	8.8	80	20.8	1.25	6.85	60	28
4	S	1	0	-3.83	11.2	94	21.4	2	7.95	48	30
5	S	1	0	-8.31	9.2	50	20.5	1	.	68.5	38
6	S	1	0	-1.1	10.5	102	8.1	0.9	9.7	59.3	35.5
7	S	1	0	0.45	12.8	223	9.9	0.2	7.35	541	20
8	S	1	0	-9.967	11.6	107	12.6	0.75	6.76	62.25	36.7
9	S	1	0	- 6	11.4	114	13.1	0.75	6.29	62	31.3
10	S	1	0	- 7	13.5	139	12.1	0.5	7.27	133.75	39.3
11	S	1	0	1.58	14	187	10.5	1.1	7.96	52.3	31.7
12	N	1	3	-2.39	37.4	302	16.3	3	7.69	53	7
	N	2	1	-2.82	37.4	302	16.3	3	7.69	53	7
	N	3	7	-6.08	37.4	302	16.3	3	7.69	53	7
13	N	1	4	-3.48	37	304	16.6	3	7.95	15	6
14	N	1	625	-3.83	36.4	299	16.3	3.5	7.25	19	7
	N	2	420	-3.89	36.4	299	16.3	3.5	7.25	19	7
15	N	1	8	-2.49	37.2	302	16.8	3	7.85	16	7
	N	2	7	-2.76	37.2	302	16.8	3	7.85	16	7
	N	3	8	-4.32	37.2	302	16.8	3	7.85	16	7
	N	4	2	-4.72	37.2	302	16.8	3	7.85	16	7
16	N	1	124	-2.16	37.6	300	16.7	3	8.11	8	8
	N	2	168	-2.99	37.6	300	16.7	3	8.11	8	8
	N	3	44	-0.5	37.6	300	16.7	3	8.11	8	8
17	N	1	140	-5.39	36.8	301	16.8	3	7.83	11.5	8
	N	2	476	-2.99	36.8	301	16.8	3	7.83	11.5	8
18	N	1	3	-4.71	36	285	18	4	7.6	12.5	9

Site No.	Shore S=South N=North	Quadrat No.	Density (No /m²)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (°C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
18	N	2	44	-2.49	36	285	18	4	7.6	12.5	9
	N	3	31	-5.44	36	285	18	4	7.6	12.5	9
19	N	1	2	-3.65	36	289	18.5	4.8	7.9	10	8
	N	2	4	-4.8	36	289	18.5	4.8	7.9	10	8
	N	3	100	-9.967	36	289	18.5	4.8	7.9	10	8
20	N	1	162	-3.9	36.8	302	17.8	4	7.62	6	5
	N	2	294	-7.45	36.8	302	17.8	4	7.62	6	5
	N	3	183	-5.28	36.8	302	17.8	4	7.62	6	5
21	N	1	10	-1.2	32.4	272	18.7	3	7.68	16.67	6
	N	2	14	-3.29	32.4	272	18.7	3	7.68	16.67	6
	N	3	14	-3.22	32.4	272	18.7	3	7.68	16.67	6
22	N	1	24	-1.56	36	292	18	2.8	8	11	4
	N	2	39	-3.98	36	292	18	2.8	8	11	4
	N	3	32	-5.32	36	292	18	2.8	8	11	4
23	N	1	424	-5.03	28.8	242	19.5	2	7.94	17	14
	N	2	256	-3.73	28.8	242	19.5	2	7.94	17	14
	N	3	100	-4.42	28.8	242	19.5	2	7.94	17	14
24	N	1	1044	-4.05	36	302	18.4	2.4	8.01	13	6
25	N	1	9	-1.57	36	290	19.4	2.8	8.28	7	6
	N	2	4	-0 961	36	290	19.4	2.8	8 28	7	6
	N	3	7	-3.49	36	290	19 4	2.8	8.28	7	6
	N	4	2	-0.88	36	290	19.4	2 8	8.28	7	6
26	N	1	1156	-4 25	32 2	273	19.6	1 5	7.81	20	10
27	N	1	824	-5 77	33.2	272	19 6	1 3	7.89	20	10
28	N	1	592	-4.2	32.4	250	19.8	1 3	7 94	27	9.5
	N	2	468	-6 18	32 4	250	19.8	1.3	7 94	27	9.5
29	N	1	204	-4.47	33.2	274	19.3	1.5	7.62	27	11
	N	2	174	-5 45	33 2	274	19.3	1.5	7 62	27	11

Site No.	Shore S=South N=North	Quadrat No.	Density (No /m2)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (^0C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
30	N	1	680	-8.966	33.8	270	19.6	1.4	7.76	25	11.5
	N	2	580	-4.57	33.8	270	19.6	1.4	7.76	25	11.5
31	N	1	0	2	28.4	243	19.7	1.1	7.72	49.33	15
32	N	1	288	-3.27	33.2	250	20	1.5	.	16	8
	N	2	292	-3.94	33.2	250	20	1.5	.	16	8
	N	3	552	-4 09	33.2	250	20	1.5	.	16	8
33	N	1	96	-4.56	32	253	20	1.75	.	10.67	4.33
	N	2	160	-3.25	32	253	20	1.75	.	10.67	4.33
	N	3	89	-4.12	32	253	20	1.75	.	10.67	4.33
34	N	1	648	-6.65	33.4	250	19	1.3	.	12.5	7
	N	2	576	-7.15	33.4	250	19	1.3	.	12.5	7
	N	3	620	-6.09	33.4	250	19	1.3	.	12.5	7
35	N	1	262	-1.75	33.6	250	19	1.25	.	36.67	6
36	N	1	73	-3.12	31.8	245	19.5	0.9	.	19	7
	N	2	104	-5.02	31.8	245	19.5	0.9	.	19	7
	N	3	112	-1.46	31.8	245	19.5	0.9	.	19	7
37	N	1	204	-6.31	21.2	160	20	0.75	.	43.5	32
	N	2	316	-8.42	21.2	160	20	0.75	.	43.5	32
	N	3	368	-9.966	21.2	160	20	0.75	.	43.5	32
	N	4	255	-9.966	21.2	160	20	0.75	.	43.5	32
38	N	1	121	-2.19	30.8	240	20	1	.	35	20
	N	2	5	0.23	30.8	240	20	1	.	35	20
39	N	1	1192	-4.9	35.6	303	20.7	5.25	.	7	7
	N	2	1268	-3.23	35.6	303	20.7	5.25	.	7	7
	N	3	1128	-2.65	35.6	303	20.7	5.25	.	7	7
40	N	1	8	-2.92	22.2	178	21.2	0.9	.	77.5	31
	N	2	14	-3.44	22.2	178	21.2	0.9	.	77.5	31
41	N	1	153	-5.92	27.4	235	21.1	1.2	.	43.5	17

Site No.	Shore S=South N=North	Quadrat No.	Density (No /m2)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (0C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
41	N	2	58	-4.5	27.4	235	21.1	1.2	.	43.5	17
	N	3	240	-5.2	27.4	235	21.1	1.2	.	43.5	17
42	N	1	166	0.19	29.2	255	20.4	1.4	.	46.67	17
	N	2	144	-0.045	29.2	255	20.4	1.4	.	46.67	17
43	N	1	1979	-9.966	32	666	20.2	0.5	.	88	16
44	N	1	23	-1.49	28.8	250	21	1	.	26	12
	N	2	162	-5.07	28.8	250	21	1	.	26	12
	N	3	204	-8.3	28.8	250	2 i	1	.	26	12
	N	4	136	-1.75	28.8	250	21	1	.	26	12
	N	5	166	-5.04	28.8	250	21	1	.	26	12
45	N	1	42	0.72	32.4	278	20.9	1.6	.	21	16.33
	N	2	76	1.19	32.4	278	20.9	1.6	.	21	16.33
	N	3	112	-0.37	32.4	278	20.9	1.6	.	21	16.33
	N	4	82	-2.07	32.4	278	20.9	1.6	.	21	16.33
46	N	1	0	5.86	21.4	194	20.6	2.2	.	20	19
	N	2	0	6.5	21.4	194	20.6	2.2	.	20	19
	N	3	11	1.32	21.4	194	20.6	2.2	.	20	19
	N	4	1	0 81	21.4	194	20.6	2 2	.	20	19
	N	5	1	1.98	21 4	194	20.6	2.2	.	20	19
	N	6	1	5.84	21 4	194	20.6	2.2		20	19
47	N	1	5	-5 08	19	140	18	2	.	29	22
	N	2	1	-2.3	19	140	18	2	.	29	22
	N	3	2	2.28	19	140	18	2	.	29	22
48	N	1	1	5.86	37 6	280	18.5	1 75	8.24	9	5
	N	2	1	6 37	37 6	280	18 5	1 75	8.24	9	5
	N	3	0	6.37	37 6	280	18 5	1.75	8 24	9	5
	N	4	1	6 37	37 6	280	18.5	1 75	8 24	9	5
	N	5	1	6 37	37.6	280	18.5	1 75	8 24	9	5

Site No.	Shore S=South N=North	Quadrat No	Density (No /m^2)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (^{0}C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
48	N	6	48	-4.05	37.6	280	18.5	1.75	8.24	9	5
	N	7	102	-4.32	37.6	280	18.5	1.75	8.24	9	5
	N	8	23	3.94	37.6	280	18.5	1.75	8.24	9	5
	N	9	31	3.94	37.6	280	18.5	1.75	8.24	9	5
49	N	1	5	1.58	36.8	270	20	3.12	8.6	8	5
	N	2	3	1.83	36.8	270	20	3.12	8.6	8	5
	N	3	188	0.34	36.8	270	20	3.12	8.6	8	5
	N	4	128	-0.5	36.8	270	20	3.12	8.6	8	5
	N	5	184	-0.5	36.8	270	20	3.12	8.6	8	5
	N	6	57	-0.08	36.8	270	20	3.12	8.6	8	5
	N	7	48	-0.08	36.8	270	20	3.12	8.6	8	5
	N	8	37	-0.08	36.8	270	20	3.12	8.6	8	5
	N	9	33	0.34	36.8	270	20	3.12	8.6	8	5
	N	10	30	1.17	36.8	270	20	3.12	8.6	8	5
50	N	1	1696	-9.966	32	270	21	0.88	8.37	21	9
	N	2	1488	-9.966	32	270	21	0.88	8.37	21	9
	N	3	1100	-9.966	32	270	21	0.88	8.37	21	9
	N	4	1425	-9.966	32	270	21	0.88	8.37	21	9
	N	5	1250	-9.966	32	270	21	0.88	8.37	21	9
	N	6	1376	-9.966	32	270	21	0.88	8.37	21	9
	N	7	1520	-9.966	32	270	21	0.88	8.37	21	9
	N	8	1725	-9.966	32	270	21	0.88	8.37	21	9
	N	9	1650	-9.966	32	270	21	0.88	8.37	21	9
	N	10	1750	-9.966	32	270	21	0.88	8.37	21	9
	N	11	2368	-9.966	32	270	21	0.88	8.37	21	9
	N	12	1904	-9.966	32	270	21	0.88	8.37	21	9
	N	13	2350	-9.966	32	270	21	0.88	8.37	21	9
	N	14	1225	-9.966	32	270	21	0.88	8.37	21	9

Site No.	Shore S=South N=North	Quadrat No.	Density (No./m^2)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (^{0}C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
50	N	15	2300	-9.966	32	270	21	0.88	8.37	21	9
	N	16	1968	-9.966	32	270	21	0.88	8.37	21	9
	N	17	1696	-9.966	32	270	21	0.88	8.37	21	9
	N	18	2976	-9.966	32	270	21	0.88	8.37	21	9
	N	19	1750	-9.966	32	270	21	0.88	8.37	21	9
	N	20	1600	-9.966	32	270	21	0.88	8.37	21	9
51	N	1	18700	-9.966	28	225	21	2.25	7.82	20	14
	N	2	22300	-9.966	28	225	21	2 25	7.82	20	14
	N	3	16864	-9.966	28	225	21	2.25	7.82	20	14
	N	4	24096	-9.966	28	225	21	2.25	7.82	20	14
52	N	1	17408	-9.966	27.6	225	21	2.25	7.82	20	14
	N	2	19056	-9.966	27.6	225	21	2.25	7.82	20	14
	N	3	19500	-9.966	27.6	225	21	2.25	7.82	20	14
53	N	1	40200	-9.966	27.8	225	21	2.25	7.82	20	14
	N	2	29500	-9 966	27.8	225	21	2.25	7 82	20	14
	N	3	10950	-9.966	27.8	225	21	2 25	7.82	20	14
54	N	1	23600	-9.966	28.2	225	21	2.25	7.82	20	14
	N	2	18160	-9 966	28.2	225	21	2.25	7.82	20	14
	N	3	19968	-9 966	28 2	225	21	2 25	7.82	20	14
	N	4	12784	-9.966	28.2	225	21	2 25	7.82	20	14
55	N	1	12720	-9.966	28	225	21	2 25	7 82	20	14
	N	2	14160	-9 966	28	225	21	2 25	7 82	20	14
	N	3	15200	-9.966	28	225	21	2 25	7.82	20	14
56	N	1	65	-3.22	28 4	235	21	1	8.1	23	12
	N	2	262	-5.53	28 4	235	21	1	8.1	23	12
	N	3	824	-3 89	28 4	235	21	1	8 1	23	12
	N	4	137	-0 6	28.4	235	21	1	8.1	23	12
	N	5	824	-5.08	28 4	235	21	1	8.1	23	12

Site No.	Shore S=South N=North	Quadrat No	Density (No /m2)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (^0C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
56	N	6	336	-2.61	28.4	235	21	1	8.1	23	12
	N	7	704	-8.966	28.4	235	21	1	8.1	23	12
57	N	1	0	2	16.2	163	20.7	1.1	.	55	33
	N	2	11	-1.34	16.2	163	20.7	1.1	.	55	33
	N	3	22	-2.97	16.2	163	20.7	1.1	.	55	33
	N	4	16	-1.92	16.2	163	20.7	1.1	.	55	33

Appendix 1 (continued): St. Lawrence River 1992

Site No.	Total Phosphorus (ug/L)	Max. Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)	Crayfish (Pres./ Abs.)	Lotic/ Lentic Site 0=Lotic 1=Lentic
1	24.36	2.6	0.2	3.3	2	0	0
2	16.57	4.2	2	3	0	0	0
3	16.57	5.5	1.7	2.4	2	0	0
4	17.07	2	0.5	4.6	2	0	0
5	83.33	3.2	0.6	1.2	0	0	0
6	19.29	3.57	0.3	2	0	0	0
7	28.51	3	0.4	1	0	0	0
8	12.84	4.5	0.2	0.5	0	0	0
9	18.37	3.75	0.2	2.5	0	0	0
10	42.48	3.1	0.1	1.5	0	0	0
11	44.82	2.5	0.8	2	0	0	0
12	28.93	0.5	0.1	7.01	0	1	0
	28 93	0.5	0.1	7.01	0	1	0
	28 93	0.5	0.1	7.01	0	1	0
13	14 57	1.5	0.35	6.1	0	0	0
14	15.29	1	0.5	11	2	0	0
	15.29	1	0.5	11	2	0	0
15	16.43	3	0.1	8.5	0	1	0
	16.43	3	0.1	8.5	0	1	0
	16.43	3	0.1	8.5	0	1	0
	16.43	3	0.1	8.5	0	1	0
16	11.21	6.5	2.5	1.8	2	0	0
	11 21	6.5	2 5	1.8	2	0	0

Site No.	Total Phosphorus (ug/L)	Max. Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)	Crayfish (Pres / Abs)	Lotic/ Lentic Site 0=Lotic 1=Lentic
16	11.21	6.5	2.5	1.8	1	0	0
17	12	6.5	3	6.1	2	0	0
	12	6.5	3	6.1	2	0	0
18	7.57	4.5	0.3	2.7	1	0	0
	7.57	4.5	0.3	2.7	1	0	0
	7.57	4.5	0.3	2.7	1	0	0
19	5.04	6.25	2	3.4	0	0	0
	5.04	6.25	2	3.4	0	0	0
	5.04	6.25	2	3.4	0	0	0
20	4.57	5.75	2.75	4.6	1	0	0
	4.57	5.75	2.75	4.6	1	0	0
	4.57	5.75	2.75	4.6	1	0	0
21	13.21	5.5	1	3.7	1	0	0
	13.21	5.5	1	3.7	1	0	0
	13.21	5.5	1	3.7	1	0	0
22	18.86	6.75	2.5	3.4	1	1	0
	18.86	6.75	2.5	3.4	1	1	0
	18.86	6.75	2.5	3.4	0	1	0
23	17.57	3.5	0.25	3.35	1	0	0
	17.57	3.5	0.25	3.35	1	0	0
	17.57	3.5	0.25	3.35	1	0	0
24	14.93	4.25	0.75	6.5	1	0	0
25	11.07	10	0.75	2.75	0	0	0
	11.07	10	0.75	2.75	0	0	0
	11.07	10	0.75	2.75	0	0	0
	11.07	10	0.75	2.75	0	0	0
26	16.29	1.72	0.8	9.1	2	0	0

Site No.	Total Phosphorus (ug/L)	Max. Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)	Crayfish (Pres./Abs.)	Lotic/ Lentic Site 0=Lotic 1=Lentic
27	21.07	1.76	0.92	2.2	1	0	0
28	25.71	2.72	0.6	4.2	1	0	0
	25.71	2.72	0.6	4.2	1	0	0
29	25.36	3	1.4	2.5	1	1	0
	25.36	3	1.4	2.5	1	1	0
30	17.86	2.68	0.6	3.7	0	0	0
	17.86	2.68	0.6	3.7	1	0	0
31	32.5	3.64	1.4	4	0	0	0
32	20.57	4	0.68	3.3	i	1	0
	20.57	4	0.68	3.3	1	1	0
	20.57	4	0.68	3.3	1	1	0
33	17.64	3.92	1.08	3.9	1	0	0
	17.64	3.92	1.08	3.9	1	0	0
	17.64	3.92	1.08	3.9	1	0	0
34	46.4	3.04	0.4	5	1	1	0
	46.4	3.04	0.4	5	1	1	0
	46.4	3 04	0.4	5	1	1	0
35	24 14	3.2	0.84	2.1	1	1	0
36	14.29	4.4	1 7	6.1	1	1	0
	14.29	4.4	1.7	6.1	1	1	0
	14.29	4.4	1.7	6.1	1	1	0
37	34.21	4.4	1.6	3.4	1	0	0
	34.21	4.4	1.6	3.4	0	0	0
	34 21	4.4	1 6	3.4	0	0	0
	34 21	4.4	1.6	3.4	0	0	0
38	21 14	2.4	0.25	3	1	0	0
	21.14	2 4	0.25	3	0	0	0

Site No	Total Phosphorus (ug/L)	Max Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance Categorical)	Crayfish (Pres / Abs)	Lotic/ Lentic Site 0=Lotic 1=Lentic
39	21.5	3.3	0.36	3.4	1	0	0
	21.5	3.3	0.36	3.4	1	0	0
	21.5	3.3	0.36	3.4	1	0	0
40	35.86	3.1	0.24	2	0	1	0
	35.86	3.1	0.24	2	1	1	0
41	19.43	3.7	1	2.5	1	1	0
	19.43	3.7	1	2.5	1	1	0
	19.43	3.7	1	2.5	1	1	0
42	31.71	6	0.75	4	1	0	0
	31.71	6	0.75	4	1	0	0
43	14.71	14.5	0.25	2	0	0	0
44	20.43	4.6	2	5	0	0	0
	20.43	4.6	2	5	0	0	0
	20.43	4.6	2	5	0	0	0
	20.43	4.6	2	5	0	0	0
	20.43	4.6	2	5	0	0	0
45	16.71	4	1.2	3	0	0	0
	16.71	4	1.2	3	0	0	0
	16.71	4	1.2	3	0	0	0
	16.71	4	1.2	3	0	0	0
46	19.07	5.75	1.25	2.7	0	0	0
	19.07	5.75	1.25	2.7	0	0	0
	19.07	5.75	1.25	2.7	0	0	0
	19.07	5.75	1.25	2.7	0	0	0
	19.07	5.75	1.25	2.7	0	0	0
	19.07	5.75	1.25	2.7	0	0	0
47	39.93	2.8	0.44	2.2	1	1	0

Site No.	Total Phosphorus (ug/L)	Max. Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)	Crayfish (Pres / Abs.)	Lotic/ Lentic Site 0=Lotic 1=Lentic
47	39.93	2 8	0.44	2.2	1	1	0
	39.93	2 8	0.44	2.2	1	1	0
48	23 57	3.5	0.5	6.5	0	0	0
	23.57	3.5	0.5	6.5	0	0	0
	23.57	3.5	0 5	6.5	0	0	0
	23.57	3.5	0.5	6.5	0	0	0
	23.57	3.5	0.5	6.5	0	0	0
	23.57	3.5	0.2	2.5	1	0	0
	23.57	3.5	0.2	2.5	1	0	0
	23.57	3.5	0.3	3.5	1	0	0
	23.57	3.5	0.3	3.5	1	0	0
49	15.34	6.5	2.5	2	0	0	0
	15 34	6.5	2.5	2	0	0	0
	15.34	6.5	2.5	4.25	1	0	0
	15.34	6.5	2.5	4.5	1	0	0
	15.34	6.5	2.5	4.5	1	0	0
	15 34	6.5	2.5	6	1	0	0
	15.34	6.5	2.5	6.5	1	0	0
	15 34	6.5	2 5	8	1	0	0
	15.34	6.5	2.5	8	1	0	0
	15.34	6.5	2 5	8	1	0	0
50	14.47	1.89	0.68	2	0	0	0
	14 47	1 89	0 68	2	0	0	0
	14.47	1.89	0 68	2	0	0	0
	14 47	1 89	0 68	2	0	0	0
	14.47	1.89	0.68	2	0	0	0
	14.47	1 89	0 68	4	0	0	0

Site No	Total Phosphorus (ug/L)	Max Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)	Crayfish (Pres./Abs)	Lotic/Lentic Site 0=Lotic 1=Lentic
50	14 47	1.89	0.68	4	0	0	0
	14.47	1 89	0.68	4	0	0	0
	14.47	1.89	0.68	4	0	0	0
	14.47	1.89	0.68	4	0	0	0
	14.47	1.89	0.68	6	0	0	0
	14.47	1.89	0 68	6	0	0	0
	14.47	1.89	0.68	6	0	0	0
	14.47	1.89	0.68	6	0	0	0
	14.47	1.89	0.68	6	0	0	0
	14 47	1.89	0.68	7	0	0	0
	14.47	1.89	0.68	7	0	0	0
	14.47	1.89	0.68	7	0	0	0
	14.47	1.89	0.68	7	0	0	0
	14.47	1.89	0.68	7	0	0	0
51	22.65	2.04	0.6	2	0	0	1
	22.65	2.04	0.6	2	0	0	1
	22.65	2.04	0.6	2	0	0	1
	22.65	2.04	0.6	2	0	0	1
52	23	2.04	0.6	4	0	0	1
	23	2.04	0.6	4	0	0	1
	23	2.04	0.6	4	0	0	1
53	22.11	2.04	0.6	4	0	0	1
	22.11	2.04	0.6	6	0	0	1
	22.11	2.04	0.6	6	0	0	1
54	23.27	2.04	0.6	6	0	0	1
	23.27	2.04	0.6	6	0	0	1
	23.27	2.04	0.6	6	0	0	1

Site No.	Total Phosphorus (ug/L)	Max. Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)	Crayfish (Pres./ Abs.)	Lotic/ Lentic Site 0=Lotic 1=Lentic
54	23.27	2.04	0.6	8	0	0	1
55	22.51	2.04	0.6	8	0	0	1
	22.51	2.04	0.6	8	0	0	1
	22.51	2.04	0.6	7.5	0	0	1
56	26.5	2	0.4	2.1	0	1	0
	26.5	2	0.4	2.1	0	1	0
	26.5	2	0.4	3.1	1	1	0
	26.5	2	0.4	3.1	0	1	0
	26.5	2	0.4	3.1	1	1	0
	26.5	2	0.5	6.1	1	1	0
	26.5	2	0.5	8.1	0	1	0
57	25.57	4	0.72	3.7	0	0	0
	25.57	4	0.72	3.7	0	0	0
	25.57	4	0.72	3.7	0	0	0
	25.57	4	0.72	3 7	0	0	0

Appendix 1 (continued):
St. Lawrence River 1991

Site No.	Density (No./m²)	Substrate (Phi)
1	104	-7.9
2	720	-8.1
3	1150	-7
4	477.5	-6.45
5	8.75	-5.8
6	64	-5.75
7	137	-4.3
8	3.5	-3
9	1.8	-2.8
10	4.3	-2.75
11	0.1	-0.875

Appendix 2. Zebra mussel densities and chemical and physical variables measured along the Hudson River in 1992.

Appendix 2: Hudson River 1992

Site No.	Quadrat No.	Density (No /m2)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (°C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
1	1	15	5.14	24	195	23	0.95	6.83	54.5	16
	2	10	5.86	24	195	23	0.95	6.83	54.5	16
2	1	178	-9.966	22	192	23.1	0.9	6.98	55.5	15
	2	1250	-9.966	22	192	23.1	0 9	6.98	55.5	15
3	1	10000	-9.966	22.6	193	23.2	0.95	7.03	50.5	16
	2	25000	-9.966	22.6	193	23.2	0.95	7.03	50.5	16
4	1	41	-0 622	23.2	200	23	1	7.15	56	14
	2	338	-1.77	23.2	200	23	1	7.15	56	14
5	1	720	-1.08	24.8	183	23.1	1 1	7.12	29	16
	2	472	-3.12	24.8	183	23.1	1.1	7.12	29	16
	3	540	-2.6	24.8	183	23.1	1.1	7.12	29	16
	4	396	-1.97	24.8	183	23.1	1.1	7.12	29	16
6	1	1620	-9.966	26.4	207	23.2	1.2	7.17	32.5	17
	2	832	-9.966	26.4	207	23.2	1.2	7.17	32.5	17
	3	73	-2.69	26.4	207	23.2	1.2	7.17	32.5	17
	4	2489	-9 966	26.4	207	23.2	1.2	7.17	32.5	17
7	1	0	1.1	26	211	23.2	1.1	7.14	43	19
	2	2	-0.193	26	211	23.2	1.1	7.14	43	19
	3	1	-1.66	26	211	23.2	1.1	7.14	43	19
	4	1	-1.76	26	211	23.2	1.1	7.14	43	19
8	1	64	-9.966	24.2	214	23.3	1	7.14	33.5	16
	2	35	-1.82	24.2	214	23.3	1	7.14	33.5	16
	3	62	-9.966	24.2	214	23.3	1	7.14	33.5	16
9	1	0	6 5	22.8	.	24.3	1.1	7.19	43	20
	2	4	5.78	22.8	.	24.3	1.1	7.19	43	20
10	1	0	5.03	24	.	24.2	0.4	7.18	101.5	16
11	1	37500	-9.966	23.6	.	23.6	0.9	7.17	32	16
	2	34000	-9.966	23.6	.	23.6	0.9	7.17	32	16

Site No.	Total Phosphorus (ug/L)	Max. Width of River (Km)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)
1	74.36	1.28	0.48	1.82	0
	74.36	1.28	0.48	1.82	0
2	75.64	0.84	0.04	1.5	0
	75.64	0.84	0.04	2.5	0
3	140.36	1.12	0.56	1.82	0
	140.36	1.12	0.56	18.2	0
4	64.29	1.4	0.44	2.75	0
	64.29	1.4	0.44	2.75	0
5	46.86	1.16	0.48	2.14	0
	46.86	1.16	0.48	2.14	0
	46.86	1.16	0.48	2.14	0
	46.86	1.16	0 48	2.14	0
6	42.21	0.96	0.4	3 75	0
	42.21	0.96	0 4	2 5	0
	42.21	0.96	0 4	4.5	1
	42.21	0.96	0 4	2.75	0
7	69.29	1	0.08	2.4	0
	69.29	1	0 08	2.4	0
	69.29	1	0.08	2.14	0
	69.29	1	0.08	2.4	0
8	51 93	0.68	0.2	2.25	0
	51 93	0.68	0.2	2 75	0
	51 93	0 68	0 2	2	0
9	28.5	1.4	0.08	2 43	1
	28 5	1 4	0 08	2.43	1
10	118 21	1 16	0 16	2 75	0
11	32.79	1 08	0 12	8.84	0
	32 79	1 08	0 12	8 84	0

Appendix 3. Zebra mussel densities and chemical and physical variables measured in Lake Oneida in 1992.

Appendix 3: Lake Oneida 1992

Site No.	Quadrat No.	Density (No /m^2)	Substrate (Phi)	Calcium (mg/L)	Conductivity (uS/cm)	Temperature (^{0}C)	Secchi (m)	pH	Apparent Color (Pt-Co units)	True Color (Pt-Co units)
1	1	405	0.66	45	336	21.8	2.5	7.99	17.33	14
	2	6555	-6.41	45	336	21.8	2.5	7.99	17.33	14
	3	3760	-6.76	45	336	21.8	2 5	7.99	17.33	14
	4	2122	-4.31	45	336	21.8	2.5	7.99	17.33	14
	5	3522	-7.2	45	336	21.8	2.5	7.99	17.33	14
	6	2600	-4.93	45	336	21.8	2.5	7.99	17.33	14
2	1	60	5 86	40.6	309	21.1	2.5	8.2	22	12
	2	55	5.86	40.6	309	21.1	2.5	8.2	22	12
	3	24	5.86	40.6	309	21.1	2.5	8.2	22	12
	4	30	5 86	40.6	309	21.1	2.5	8.2	22	12
3	1	185	-1.33	22.2	298	19.4	3 5	8 15	70	18
	2	267	-0.59	22.2	298	19.4	3.5	8.15	70	18
4	1	408	1.17	40.6	308	20.2	3	8.16	20	15
	2	187	1.41	40.6	308	20.2	3	8.16	20	15
	3	179	1.58	40 6	308	20.2	3	8.16	20	15
5	1	208¯	-4.23	40.4	308	20.2	3	8.18	23.5	14

Site No	Total Phosphorus (ug/L)	Exposure (Km^2)	Distance from site-shore (Km)	Depth (m)	Unionid Abundance (Categorical)
1	4.36	177.28	0.8	5.5	2
	4.36	177.28	0.8	5.5	1
	4.36	177.28	0.8	4.6	1
	4.36	177.28	0.8	4.6	1
	4.36	177.28	0.8	3.05	0
	4.36	177.28	0.8	3.05	0
2	12.93	202.08	0.28	3.05	1
	12.93	202.08	0.28	3.05	1
	12.93	202.08	0.28	3.05	1
	12.93	202.08	0.28	3.05	1
3	3.5	202.08	2.96	6.71	0
	3.5	202.08	2.96	6.71	0
4	7.07	183.77	1.4	3.05	2
	7.07	183.77	1.4	3.05	2
	7.07	183.77	1.4	3.05	2
5	44.71	187.6	1.2	3.05	1