

Planktonic invaders of the St. Lawrence estuarine transition zone: environmental factors controlling the distribution of zebra mussel veligers

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Abstract: The St. Lawrence estuarine transition zone (ETZ) is a productive ecosystem supporting a larval fish nursery. Since 1994, *Dreissena polymorpha* veligers have become the dominant zooplankton (up to 260 individuals·L⁻¹). The environmental factors controlling their distribution across the ETZ and their potential impact on the plankton were determined. Their horizontal distribution was limited by salinity, with maximum decreases in concentration at 2‰. A sharp decline in prey availability at >2‰ may be a secondary stressor for the veligers, in addition to the direct effects of salinity. Their vertical distribution was homogeneous throughout the water column, even in the presence of a pycnocline. Redundancy analysis showed that veliger concentrations were positively correlated with temperature and turbidity and negatively correlated with salinity and total phosphorus. Veligers were also positively correlated with chlorophyll *a* and picophytoplankton concentrations, suggesting little effect on their phytoplankton prey. Moreover, the veligers were positively correlated with the sestonic ratio of particulate to total phosphorus, indicating their positive association with good food quality. The veligers appear to have no severe negative impacts on the ETZ plankton community and are restricted to favourable conditions for their survival in the upstream, low salinity region of the ETZ.

Résumé : La zone de transition estuarienne (ZTE) du fleuve Saint-Laurent est reconnue pour sa grande productivité, tel que démontré par son rôle de pouponnière de larves de poissons. Depuis 1994, les larves véligères de *Dreissena polymorpha* ont envahi le plancton de cette zone (jusqu'à 260 individus·L⁻¹). Cette étude documente les facteurs environnementaux contrôlant leur distribution dans la ZTE et leurs impacts sur la communauté phytoplanctonique. Leur distribution horizontale était limitée par la salinité avec une diminution abrupte de leur abondance à 2 ‰. Un déclin simultané de la bio-disponibilité de leurs proies à >2 ‰ fut observé, impliquant que cette chute de bio-disponibilité pourrait constituer un stress additionnel à l'effet de la salinité. Leur distribution était homogène dans toute la colonne d'eau, même lors de la présence d'un gradient vertical de densité. Une analyse de redondance révèle que les véligères sont positivement corrélées à la température et à la turbidité, mais négativement corrélées à la salinité et au phosphore total. Les véligères sont positivement corrélées à leurs proies, i.e., à la biomasse de chlorophylle *a* et au picophytoplancton, impliquant qu'elles ne semblent pas avoir d'impacts sévères sur leurs proies phytoplanctoniques. Les véligères étaient positivement corrélées au seston de bonne qualité alimentaire et semblaient être associées aux conditions favorables pour leur croissance qui caractérisent les eaux de faibles salinités de la ZTE.

Introduction

Zebra mussels, *Dreissena polymorpha*, have spread throughout North American aquatic ecosystems since their introduction to the Great Lakes in the late 1980s (Hebert et al. 1989). This exotic species is remarkably versatile and adept at exploiting new niches. In some areas, *D. polymorpha* can reach densities of 175 000 m² within 2 or 3 years of colonisation (Mellina and Rasmussen 1994). As unsurpassed competitors for habitat and food, they continually outcompete native bivalves (Ricciardi et al. 1998) and cause great physi-

cal disturbance. Their invasion is linked to a significant decrease in phytoplankton (Caraco et al. 1997), flagellated protozoa (Findlay et al. 1998), and zooplankton (Pace et al. 1998). Contamination of the food web by their bioaccumulation of chemicals has also been documented (de Kock and Bowmer 1993). A vast literature exists on the distribution, biology, and ecological impacts of adult zebra mussels (Strayer and Smith (1993) and references therein). However, the environmental factors controlling the successful development of the veliger larval stage and its potential impacts on the microbial food web are poorly documented (Sprung

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1993), despite the fact that veligers can reach extremely high densities in the plankton of North American fresh waters (>400 individuals·L⁻¹; de Lafontaine et al. 1995).

Zebra mussels are well documented in North American rivers, and high proportions of veligers must be ultimately advected to the sea. However, little information is available on the physical factors limiting the horizontal and vertical distribution of veligers in estuaries. Although recognised as a freshwater species, the zebra mussel veligers are believed to tolerate salinities up to 4‰ for a short period of time, depending on water temperature and acclimation period (Strayer and Smith 1993; Kilgour et al. 1994; Wright et al. 1996). It remains unknown, however, how salinity may limit the downstream distribution of veligers in North American estuaries.

A few freshwater studies have found that veligers in lakes are situated within the upper few metres of the water column (Strayer and Smith 1993; Stoeckel et al. 1997). Fraleigh et al. (1993) found that their vertical distribution is controlled by water temperature, wind speed, and mixing rate. During the warmer month of July, the veligers were found at slightly lower temperatures in the deeper part of the epilimnion. Stratification was observed only when the wind speed was below 8 km·h⁻¹, and 64% of the individuals were found in the epilimnion between 4 and 6 m. In lakes, veligers are thus found slightly deeper in the water column when mixing rates are weak, probably owing to passive sedimentation (Garton and Haag 1993). Kern et al. (1994) observed that veligers are distributed evenly throughout the water column in the Rhine River, probably owing to higher mixing rates. *Dreissena* veligers have locomotive capacities, yet it is unknown if their vertical distribution is due to passive or active transport in estuaries where the water column may be stratified. A vertically stratified environment could prevent the veligers from crossing the density barrier (pycnocline) between the fresh and salt water, thereby resulting in a nonhomogeneous distribution.

Zebra mussel veligers are primarily herbivores with a preference for algae rich in polyunsaturated fatty acids (PUFA) (Vanderploeg et al. 1996), but they also consume photosynthetic picoplankton, bacteria, flagellates, and detritus (Sprung 1993; Wright et al. 1996). According to these authors, the size spectrum of their prey varies between 1 and 9 µm. In addition, Wright et al. (1996) observed that in laboratory experiments, the veligers also fed on the estuarine algae *Isochrysis galbana* and *Pavlova lutheri*. Veligers tend to have a significantly higher survival rate when they consume plankton containing long-chained PUFAs, in particular algae containing the long-chained (*n*-3) PUFA, docosahexaenoic acid (Wacker et al. 2002). Under favourable conditions, a veliger can increase roughly 10 times its weight during its 1- to 3-week planktonic period (Sprung 1993). The impact of adult zebra mussels on the plankton through their filter feeding is well documented; however, little is known about how feeding by the veliger stage of this organism may affect phytoplankton abundance.

The St. Lawrence estuarine transition zone (ETZ) is situated between Ile d'Orléans and Ile-aux-Coudres and contains high concentrations of microplankton and macroplankton that support a productive fish nursery (Vincent and Dodson 1999; Winkler et al. 2003). The recent arrival of *Dreissena polymorpha* in this region has raised concerns about their poten-

tial competition with herbivorous zooplankton that provide the food supply to the larval fish community. Zebra mussel veligers were absent from the ETZ plankton samples obtained during cruises in 1991 to 1993. However, in 1994, 1995, and 2000, this situation changed dramatically as they were among the dominant zooplankton, contributing to more than 80% of the total number of animals and achieving densities >200 individuals·L⁻¹ (Vincent and Dodson 1999; G. Winkler, Université Laval, Département de biologie, Ste-Foy, QC G1K 7P4, unpublished data). The veligers are assumed to originate mainly from upstream and from the shores of the St. Lawrence, as adults are sparsely distributed on the fluvial bed of the ETZ (A. Casper, Département de biologie, Université Laval, Ste-Foy, QC G1K 7P4, unpublished data). Any impacts on the food web would therefore not be due to adult populations, but rather to the omnipresence of the veligers in the plankton. Hydrodynamic processes play a major role in controlling the distribution of organisms in this tidal estuary. For example, Frenette et al. (1995) documented the prolonged residence time for phytoplankton and protozoa in the ETZ and a combination of immigration and emigration pathways favouring larger particles and high taxon diversity. Hydrodynamic processes in combination with an abundant food supply from upstream similarly result in high populations of macrozooplankton in this region (Winkler et al. 2003). Zebra mussel veligers, in their most abundant stage, measure between 70 and 160 µm and also have the potential of being retained within the ETZ.

The overall aim of this study was to determine the role of several environmental variables in influencing the distribution of veligers in an estuarine transition zone. More specifically, the objectives were to determine the horizontal and vertical distribution of the veligers across the St. Lawrence ETZ and to assess the effects of salinity, depth, temperature, water column stratification, and temporal and tidal variation. In addition, we evaluated the potential impact of veligers on communities at the base of the food web by examining their relationship with total phytoplankton biomass (chlorophyll *a*), picophytoplankton cell concentrations, and the nutritional quality of the seston. The present study provides insights into the factors controlling the distribution and abundance of this invasive species in the upper estuary of a large river ecosystem.

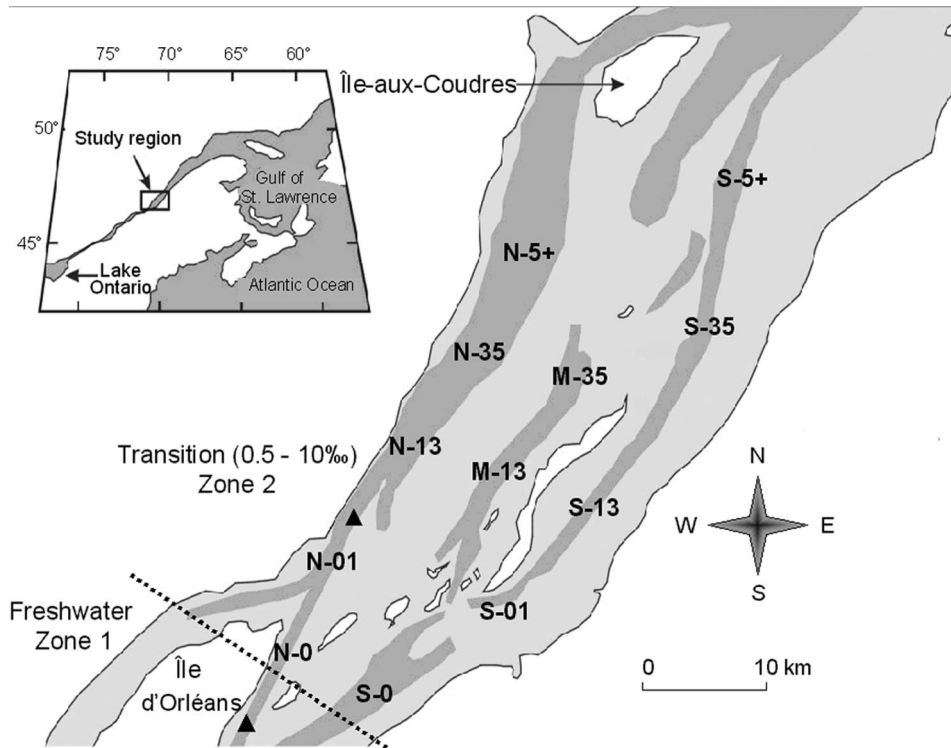
Materials and methods

Sampling site

The ETZ of the St. Lawrence River is situated ca. 50 km downstream from Québec City (Canada) between the islands of Ile d'Orléans and Ile-aux-Coudres (Fig. 1). These waters are characterized by salinities ranging from 0.1‰ to 10‰. The freshwater discharge averages 10 000 m³·s⁻¹ and current speeds may reach >2.5 m·s⁻¹ (d'Anglejan and Smith 1973).

The bottom morphology of the ETZ consists of three channels, one following the north shore, one short channel in the middle, and one following the south shore. The north channel is used for maritime transport and is characterized by deeper waters and stronger currents. The middle channel consists of an archipelago of small islands with Ile d'Orléans and Ile-aux-Coudres being the largest islands and marking its eastern and western boundaries. Finally, the south channel has

Fig. 1. Estuarine transition zone (ETZ) of the St. Lawrence River, Québec, Canada. Summer 2000: stations are indicated by a letter representing the channel (N, north; S, south; M, middle) followed by numbers indicating the salinity (0, 0‰; 01, 0–1‰; 13, 1–3‰; 35, 3–5‰; 5+, 5+‰). Summer 2001: triangles (▲) mark the fixed stations.



slower currents and shallower waters than the north channel. Large mudflats are found on the south shore near Montmagny, whereas vast intertidal marshes ($3 \times 10^6 \text{ m}^2$) are located on the shores of the north channel at Cap Tourmente (Lucotte and d'Anglejan 1986).

Sampling was conducted during the summers of 2000 and 2001. The research goals of the summer of 2000 were to determine the factors controlling the veligers' horizontal distribution across the ETZ and to assess the physical, chemical, and biological variables associated with veliger abundance. During the summer of 2001, the veligers' vertical distribution was assessed in the strictly freshwater zone of the ETZ (zone 1), as well as directly in the ETZ (zone 2) during different tidal regimes. Veliger abundance was evaluated as a function of depth and water column stratification.

Summer 2000 sampling

Five cruises were undertaken during the summer of 2000: 4 and 14 June, 15 and 28 July, and 8 August. During these cruises, 12 stations were sampled consisting of five in the north channel (N), two in the middle channel (M), and five in the south channel (S) (Fig. 1). Each station was chosen according to salinity, and therefore the geographical position of the station differed with every sampling period, depending on the tidal state. Five salinities were selected for the stations in the north and south channels: 0‰ (0), 0–1‰ (01), 1–3‰ (13), 3–5‰ (35), and finally 5‰ or more (5+). The salinity of the stations in the middle channel varied between 1–3 and 3–5‰. Because of unfavourable meteorological conditions, certain stations had to be eliminated during

the first and last cruise, specifically S-13, N-0, N-01, N-13, and N-35 during the first cruise and M-13 and M-35 during the last cruise.

Physical variables

The site of each station was chosen according to surface salinity, which was determined with a salinometer (Yellow Springs Instrument Co., Yellow Springs, OH 45387). Water column salinity and temperature as a function of depth were recorded using a CTD (conductivity–temperature–depth meter; sea logger SBE-19; Sea Bird Electronics, Inc., Bellevue, WA 98005), which was lowered from the surface to 2 m from the bottom. At each station, water was collected at the surface (0–2 m) and near the bottom (2 m from the bottom) with a 5-L Go-Flo bottle (General Oceanics Inc, Miami, FL 33169). These water samples were stored cool and in the dark. Upon arrival at the laboratory, turbidity for each sample was recorded using a nephelometer (model DRT15-CE; HF Scientific, Inc., Fort Myers, FL 33916).

Veligers

To collect *D. polymorpha* veligers, a bottom-to-surface haul was made using a plankton net (63- μm mesh with a 50-cm diameter), and an additional haul was made from 2 m to the surface. The contents were filtered through a 63- μm screen to eliminate smaller particles and were then preserved in denatured ethanol (95%) at a final concentration of approximately 80%. Because of clogging of the net with sediments and subsequent loss of material during the haul, the veliger densities from the full water column hauls were equal to or lower than the veliger densities from surface hauls; hence, only surface data were used in the statistical analyses for

this year. To improve the method for the summer 2001 sampling, Go-Flo bottles were used to collect veligers.

Veliger counts were conducted in the laboratory using cross-polarisation according to Johnson (1995). This method renders the veligers visible and easily distinguishable from other zooplankton and detritus. The volume of the counts had to correspond to a minimum of 10% of the total sample volume. If 300 individuals were counted before reaching this 10%, another subsample was counted to use the average of the two counts.

Chlorophyll *a*

Upon arrival at the laboratory, the water collected with the Go-Flo bottles was passed through GF/F (Whatman plc, Kent, U.K.) 25-mm filters in duplicate. These filters were then frozen ($-20\text{ }^{\circ}\text{C}$) and kept in the dark until extraction. They were subsequently ground in 90% acetone and extracted over 24 h. The extracts were then cleared by centrifugation and assayed by spectrofluorometry (Varian Cary-Eclipse; Varian, Inc., Palo Alto, CA 94304-1030) before and after acidification ($0.001\text{ mol}\cdot\text{m}^{-3}\text{ HCl}$). Chlorophyll *a* (Chl *a*) from *Anacystis nidulans* (Sigma-Aldrich Corp., St. Louis, MO 63103) was used for calibration.

Photosynthetic picoplankton

In a darkened room, immediately upon arrival in the laboratory, approximately 15–20 mL of water sample were filtered onto Anodisc (Whatman) filters, which were mounted on slides using Aquapolymount (Polysciences, Inc., Warrington, PA 18976). These slides were immediately stored in the dark at $4\text{ }^{\circ}\text{C}$ for 24 h and then stored frozen ($-20\text{ }^{\circ}\text{C}$). Within days of the slide preparation, counting was undertaken with an Olympus epi-fluorescence microscope (Olympus America Inc., Melville, NY 11747) with exchangeable blue and green excitation filters and 1000 \times oil immersion. When excited with a green light source, photosynthetic picoplankton with phycocyanin and (or) Chl *a* fluoresce bright red (PC), whereas phycoerythrin-rich photosynthetic picoplankton (PE) fluoresces bright orange (Lovejoy et al. 1993). Three hundred individuals were counted with a minimum of 15 fields. A minimum of 50 fields was counted when counts were low.

Protist communities

Samples for protists (phytoplankton and protozoa) were examined and prepared using the procedures outlined by Lovejoy et al. (1993). These samples were fixed immediately with 1% glutaraldehyde and 0.1% paraformaldehyde (final concentrations), stored in the dark at $4\text{ }^{\circ}\text{C}$, and later settled in Utermöhl chambers. The auto- and fluorochrome (DAPI) fluorescence allowed us to differentiate organisms from abiotic particles and to locate and characterize cells. The organisms were grouped into two broad categories: autotrophs (including mixotrophs) and heterotrophs.

Chemical variables

Particulate organic carbon (POC), nitrogen (PON), and phosphorus (PP) were obtained by filtering 20–100 mL (depending on turbidity) of water through precombusted and acid-washed GF/F filters. These were then stored frozen in the dark ($-20\text{ }^{\circ}\text{C}$). For the dissolved components (NO_3^- , total nitrogen (TN), and soluble reactive phosphorus (SRP)),

the water was filtered through precombusted GF/F filters and stored cool in the dark until analysis. For total phosphorus (TP), unfiltered water was immediately acidified (1 mL 30% H_2SO_4 per 100 mL sample) upon arrival at the laboratory. All analyses were conducted at the National Laboratory for Environmental Testing (NLET) in Burlington, Ontario, according to the standard methods (NLET 1994).

Summer 2001 sampling

Two cruises were undertaken to assess the short-term dynamics of veliger vertical abundance at fixed stations during different tidal states. Both cruises occurred during the spring tides of June and July 2001. One fixed station was located in the strictly freshwater zone ($46^{\circ}52'86''\text{N}$, $70^{\circ}55'60''\text{W}$) and the other directly in the transition zone ($47^{\circ}06'71''\text{N}$, $70^{\circ}42'44''\text{W}$) (Fig. 1). Each site was sampled at three high, three low, and four intermediate tides, thus a total of six high, six low, and eight intermediate tides for each station for both cruises.

The veligers were collected with two 5-L Go-Flo bottles. These bottles collected water at the surface (0–2 m), in the middle of the column (depending on the column depth), and near the bottom (1–2 m from the bottom). The water was then filtered through a 63- μm sieve and preserved and counted as described above.

Data analysis

Spatial autocorrelation was tested in the summer 2000 veliger data by constructing a correlogram obtained using Moran's *I* (Legendre and Fortin 1989). This correlogram was globally significant at the $\alpha = 5\%$ level because several individual values were significant at the Bonferroni corrected level (unpublished data) (Legendre and Fortin 1989). To account for the spatial structure in the data, spatial components were incorporated into the statistical analyses (Legendre 1993). For the summer 2001 data, the statistical model constructed took into account spatial and temporal autocorrelation (see below).

Water column stratification

A measure of water column stratification (Δs) was calculated as the difference between salinity at the surface and at the bottom of the water column for the stations in zone 2 (summer 2001). If veliger larvae are passively transported, the vertical stratification of their distribution (abundance at the bottom – abundance at the surface = Δ_{vel}) should be correlated with Δs . Because these values (Δ_{vel} and Δs) did not have normal distributions, Spearman's nonparametric test was used to evaluate the correlation.

Spatial and temporal distribution of the veligers

Temporal variation in veliger abundance between the four cruises undertaken in summer 2000 data was tested using a repeated measure ANOVA (analysis of variance, mixed-effect model) with SAS (version 8.2; SAS Institute Inc., Cary, NC 27513-2414). The date was a fixed effect and the station was a random effect. Temporal dependency was adjusted with heterogeneous compound symmetry based on the Akaike information criteria. Multivariate normality was verified using the Mardia Skewness and Kurtosis statistic. Multiple com-

parisons were made using the protected least significant difference (LSD) method.

For the vertical distribution assessed during the summer of 2001, a split-split plot ANOVA (mixed-effects model) was used to fit the veliger abundance data. The effects of zone (1 and 2), depth (surface, mid-column, and bottom), and tidal cycle (high, low, and intermediate) on veliger abundance were verified. In the main plot, the date (cruise) was a random effect and zone was a fixed effect. The effect of depth was in the subplot, whereas the effect of the tidal states was in the sub-subplot. This model took into account the possible correlations between observations in the same zone.

Relationships between environmental, spatial, and biological variables (RDA)

Redundancy analysis (RDA; CANOCO program 4.0, ter Braak 1998) was used to determine whether variation in species abundance was coordinated in response to environmental and spatial gradients. The variation in species abundance was partitioned into independent components: pure environmental, pure spatial, spatial component of environmental variation, and unexplained (Borcard et al. 1992). This method was used to partial out the intrinsic spatial component of community structure and to establish the relative contribution of environmental factors in controlling the species distribution.

To choose between a linear and nonlinear model, a detrended canonical correspondence analysis (DCCA) was employed, and RDA was chosen over canonical correspondence analysis (CCA) because the range of the ordination sample scores in a detrended correspondence analysis (with detrending by segments and nonlinear rescaling) was less than 1.5 standard deviation units (ter Braak 1998). This indicated that the application of a linear method was appropriate. This multivariate technique for direct gradient analysis graphically summarises the relationships between the species and the abiotic environmental and spatial variables.

Data from summer 2000 sampling were used whereby the species variables consisted of veliger and picophytoplankton (PE and PC categories) numerical densities and Chl *a* biomass. The environmental variables were salinity, temperature, turbidity, TP, Cl^- , SO_4^{2-} , SRP, NO_3^- , TN, and date (cruises 3, 4, and 5) to test for temporal variation in species abundance. Logarithmic and square root transformations were used to normalise the distribution of the data. To account for differences in units, the species data were centred and standardised (ter Braak 1998). The spatial component was a matrix of two-dimensional geographic coordinates including all of the terms of a cubic trend surface polynomial, as suggested by Legendre (1990, cited from Borcard et al. 1992). This surface regression was of the form $Z = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2 + b_8X^3 + b_9Y^3$, where X was the longitude and Y was the latitude in universal transverse mercator co-ordinates. This matrix represented the geographic surface over which the species were sampled, and the model tested its relative influence on the variation in species abundance.

Forward selection of environmental variables and polynomial terms was applied to select the set of variables that significantly explained the variation in abundance of the species

($p < 0.05$). To account for collinearity, environmental variables with variance inflation factors greater than 15 were eliminated. Once the significant environmental and spatial variables were identified, four analyses were conducted to partition the variance in the species data following Borcard et al. (1992): (1) RDA of the species matrix constrained by the environmental variables; (2) RDA of the species matrix constrained by the spatial variables; (3) like analysis 1 after removing the effect of the spatial variables; and (4) like analysis 2 after removing the effect of the environmental variables. In RDAs calculated using CANOCO, the sum of all canonical eigenvalues can be interpreted as the fraction of explained variation (r^2). Monte Carlo permutation tests (999 unrestricted permutations) were used to assess the statistical significance of the relationship between the species and independent variables. The total explained variation (r^2) was the sum of the explained variation in analyses 1 and 4 or in analyses 2 and 3. The “pure” environmental variation was defined by analysis 3, and the “pure” spatial variation was defined by analysis 4. The variation “shared” by the spatial and the environmental components was calculated by subtracting analysis 3 from analysis 1 or analysis 2 from analysis 4. The unexplained portion of the variation was obtained by subtracting the total variation explained from one.

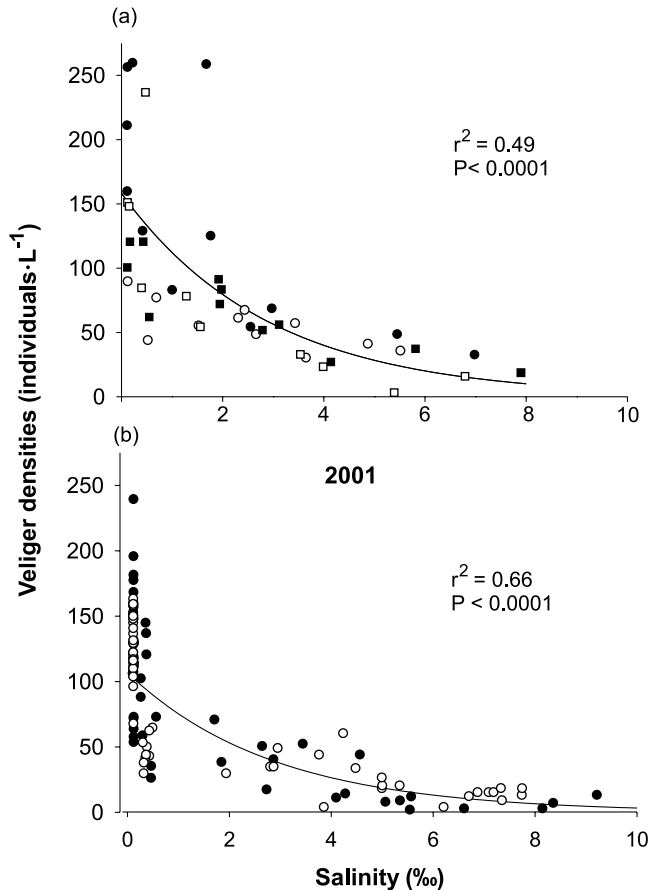
Results

Horizontal and temporal distribution

Concentrations of veliger larvae dropped precipitously across the freshwater-saltwater gradient of the ETZ, and there was a negative exponential relationship with salinity (Fig. 2). For summers 2000 and 2001, the maximum decrease in veliger abundance occurred at approximately 2‰, which may correspond to a physiological threshold. For summer 2000, the highest densities were obtained during the second and fourth cruises, with densities reaching up to 260 individuals·L⁻¹ at stations in the north channel and salinities between 0 and 1‰. For summer 2001, the highest densities were observed in the freshwater zone (240 individuals·L⁻¹). The greatest relative decrease in mean abundance occurred between salinity intervals 0–2 and 2–4‰, with decreases from 75.9 to 18.0 and from 75.2 to 13.2 individuals·L⁻¹ for summers 2000 and 2001, respectively. The sampling undertaken during summer 2001 (spring tides of June and July) showed a sharp decline in veliger abundance with an increase in salinity from the freshwater zone 1 to the transition zone 2 (Fig. 3). Densities were lowest during high and ebbing tides. The strong influence of salinity on veliger abundance, rather than geographical position, was evident when sampling was conducted from the fixed stations.

The presence of veligers in early summer appears to be determined by the water temperature, as spawning occurs around 18 °C (Sprung 1993). During the first cruise (4 June 2000), their abundance was sparse, consistent with the low water temperatures between 12.5 and 15 °C. For the second cruise (26 June 2000) onwards, water temperatures were >18 °C and the veligers were abundant at low salinities (<2‰). Date had a significant effect on the variation in veliger concentrations (df = 3,31, $F = 5.58$, $p = 0.0035$). Veliger densities from cruise 2 were significantly higher than those

Fig. 2. Veliger larvae densities in the St. Lawrence estuarine transition zone (ETZ) as a function of salinity for (a) summer 2000 cruises (●, 14 June; ○, 15 July; ■, 28 July; □, 8 August) and (b) summer 2001 fixed stations in zones 1 and 2 (●, 25–29 June; ○, 23–27 July). The statistics are for an exponential fit (solid line) to the data.



from cruises 3, 4, and 5. Densities from cruises 3, 4, and 5 were not significantly different. This was also evident in the RDA results with the near absence of correlation between veligers and cruises 3 and 5 (Fig. 4).

Vertical distribution (summer 2001)

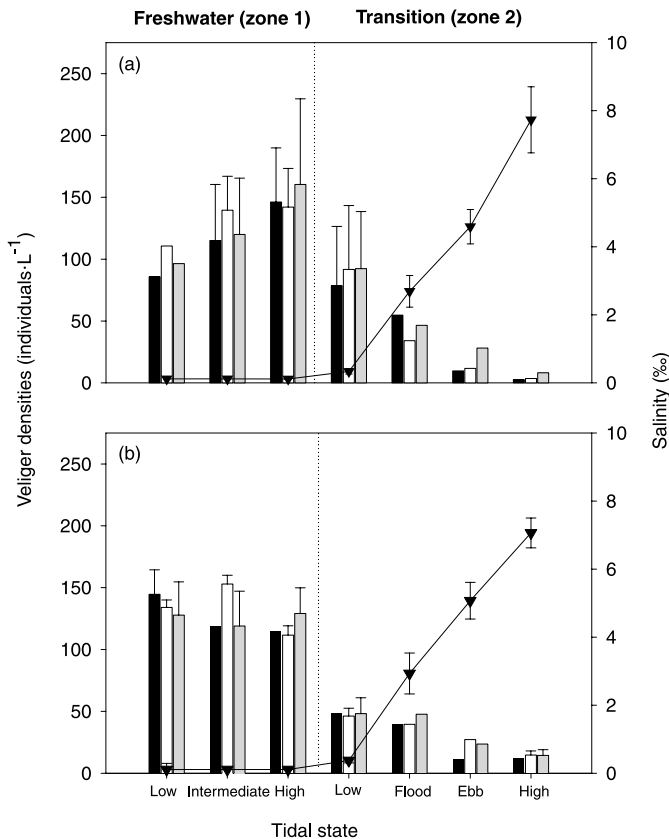
Veligers in zones 1 and 2 were homogeneously distributed throughout the water column. No vertical stratification in distribution was observed (Table 1; Fig. 3), even in stratified water columns. However, the zone and tidal state affected veliger abundance. There was a sharp decline in veliger densities when going from zone 1 to zone 2, and tidal state played a significant role in influencing veliger densities in the transition zone only. Consistent with these results, there was no statistical relationship between Δ_{vel} and Δs when all transition zone stations were considered (Spearman's rho = 0.02, $p > 0.05$, $n = 19$) or when only stratified stations were considered (Spearman's rho = -0.02, $p > 0.05$, $n = 9$). These results underscore the homogeneous distribution of the veligers in the water column, regardless of stratification and mixing conditions.

Relationships between environmental, spatial, and biological variables (RDA)

Six of the nine environmental variables were selected using forward selection ($p < 0.05$): temperature, salinity, turbidity, TP, cruise 3, and cruise 5. After environmental variable selection, the Monte Carlo tests of significance for the first canonical axis of analysis 1 yielded an eigenvalue of 0.399 (F ratio = 17.926, $p = 0.001$) and of 0.630 for all canonical axes (Table 2). The first two axes explained 53.9% (39.9 + 14.0) of the total variance in the species data. The fraction of the species–environment variation that was jointly explained by the first two axes was high (0.855), thus little information on species–environment relationships was lost by discarding the additional axes. Because the eigenvalue of the third axis was small compared with the first two ($\lambda_1 = 0.399$, $\lambda_2 = 0.140$, $\lambda_3 = 0.074$), it can be ignored, as can the higher numbered ordination axes. Veliger densities, Chl *a* biomass, and PC picoplankton were positively cross-correlated, with temperature and turbidity strongly related to them (Fig. 4). For interpretations of the biplot diagram, arrows pointing in the same direction indicate positively correlated variables, perpendicular arrows indicate lack of correlation and arrows pointing in opposite directions indicate negatively correlated variables. The angles between environmental and species arrows and the length of the arrows can be used jointly to infer the direction and intensity of species responses to environmental variables (ter Braak 1998). However, RDAs only reveal the shared variation among species variables explained by the environmental variables. Thus the relationship between veliger abundance and the species variables was verified separately from this analysis and revealed that veligers were indeed positively correlated with Chl *a* (Pearson $r = 0.48$, $p = 0.004$) and PC picoplankton (Pearson $r = 0.45$, $p = 0.008$). Salinity and TP were negatively related to the veliger densities and Chl *a* biomass, but positively correlated to PE picoplankton. Turbidity and temperature were negatively correlated with salinity and TP.

Among the nine terms in the surface polynomial, the following ones were retained in the forwards selection: $Z = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2$. After variable selection, the Monte Carlo tests of significance for analysis 2 for all canonical axes yielded an eigenvalue of 0.239, which was not significant (Table 2). Variation partitioning indicated that the total variation explained by environmental and spatial variables together accounted for 74.4% of the total variation, whereas 25.6% was left unexplained. The environmental variables accounted for 63% of the total variation explained in the species matrix. Approximately 23% of this variation can also be predicted by the spatial matrix. Only 15% of the variation is attributable to spatial effects and cannot be related to the measured environmental variables (Table 2). This portion of variation acts partly as a descriptor of unmeasured underlying processes such as external causes or underlying biotic processes such as growth, reproduction, predation, input from various source populations, and stress-dependent mortality. The purely spatial effect was weak or insignificant. This statistical result is to be expected given that water masses are advected up and down the estuary by as much as several tens of kilometres over each semidiurnal tidal cycle, and rapid changes take place at any fixed x - y lo-

Fig. 3. Veliger larvae densities as a function of tidal state and salinity in the estuarine transition zone (ETZ) for (a) cruise 1 (25–29 June 2001) and (b) cruise 2 (23–27 July 2001). For the transition zone, tidal cycles were further divided into flood and ebb tides, as veliger densities varied significantly between the two tidal regimes. Values are the means \pm standard deviation (when available). Solid bars, surface densities; open bars, mid-column densities; shaded bars, bottom densities; \blacktriangledown , salinity.



cus. Biological and chemical properties are therefore more closely related to the shifting salinity field rather than geographic position. As for the environmental variable component, 66% of the total variation is accounted for by the purely environmental effects, indicative of the selected variables being effective descriptors of the species data in the ETZ. This underscores the influence of the position of the salinity front in the transition zone and its subsequent effects on community composition.

Food quality

According to the approximate limits set by Healey and Hendzel (1980) and Hecky et al. (1993), the stoichiometric ratios obtained of the ETZ seston showed no apparent nutrient deficiencies (Fig. 5). The values for C:P, N:P and C:N ($\mu\text{mol}:\mu\text{mol}$) were consistently below the thresholds for limitation, with the exception of the C:N ratio, where N seemed moderately deficient. The C:Chl *a* ratios were exceptionally high, which may indicate general nutrient deficiency or high concentrations of heterotrophic organisms as well as detritus. Turbidity was highly positively correlated with particulate C, N, and P (Fig. 6). The C:N:P ratios (Table 3) lay well

below the Redfield ratio of 106:16:1, which reveals the absence of nutrient limitation in the ETZ seston. In addition, SRP and nitrate were always at detectable levels (means = $0.011 \pm 0.004 \text{ mg}\cdot\text{L}^{-1}$ and $0.28 \pm 0.076 \text{ mg}\cdot\text{L}^{-1}$, respectively), implying adequate nutrient supply for the phytoplankton. Finally, veliger densities were weakly but positively correlated with the PP/TP ratio ($r^2 = 0.18$, $p = 0.0001$, $n = 46$) as well as with PP ($r^2 = 0.14$, $p < 0.05$, $n = 46$), indicative of their association with good quality seston.

Particle aggregation

Particle size appears to be one aspect that affects the food availability for zebra mussel veligers (Sprung 1993; S. Bernier, Département de biologie, Université Laval, Ste-Foy, QC G1K 7P4, unpublished data). We therefore examined the extent of cell aggregation across the ETZ given the known flocculation characteristics of salinity gradients (Kranck 1979). We found a strong decrease in the bioavailability of the veligers' prey (Fig. 7). This effect was greatest for the autotrophs with a 2.9-fold increase of organisms within aggregates $>10 \mu\text{m}$ from salinity interval 1–2‰ to 2–3‰. At this latter interval, up to 80% of the potential autotrophic prey were within aggregates and thus too large to be consumed by veligers.

Discussion

Spatial distribution of the veligers

The pattern of change in the veliger distribution across the ETZ showed several characteristics consistent with the joint effects of abiotic and biotic controlling factors. The changes in veliger density during the summer 2000 cruises can be explained by (1) salinity, (2) stress due to advective transport, (3) retention and turbidity, (4) bioavailability of the veligers' prey, and (5) predation.

Salinity

The longitudinal distribution of zebra mussel veligers in the St. Lawrence ETZ was a strong function of salinity and tidal state. The highest densities were found at salinities below 2‰, but individuals were found up to 10‰. The maximum decrease in veliger abundance occurred around 2‰, which corresponds to a lower tolerance threshold than that reported in the literature. These results are consistent with the recent findings of S. Bernier (Département de biologie, Université Laval, Ste-Foy, QC G1K 7P4, unpublished data), who noted a sharp decrease in filtration rates of veligers at salinities greater or equal to 2‰. Past studies have indicated that their lethal incipient tolerance to salinity is at ~ 4.5 ‰, and maximum growth rates have been observed up to 2‰ (Strayer and Smith 1993; Kilgour et al. 1994; Wright et al. 1996). Their tolerance to salinities between 4‰ and 5‰ is for a short period of time, depending on the water temperature and acclimation period. Veliger abundance was positively correlated to temperature, but this is likely to reflect the close negative correlation between temperature and salinity. Temperature is not likely to have had a strong negative impact on the veligers as it never dropped below 11.5 °C in the ETZ and veligers can tolerate temperatures between 0 and 29 °C (Sprung (1993) and references cited

Fig. 4. (a) Redundancy analysis biplot of the species matrix constrained by the environmental variables. Percent variance in species data for each axis is specified in parentheses. Species are indicated by solid arrows. Significance of axis 1 is $P = 0.001$, significance of overall test is $P = 0.001$. Environmental variables are indicated by dotted arrows (TP, total phosphorus; PC, photosynthetic picoplankton (phycocyanin-rich and (or) Chl *a*); PE, photosynthetic picoplankton (phycoerythrin-rich). (b) Chl *a* biomass and picoplankton (PC and PE) densities are stacked as a function of the station for each cruise. Note that picoplankton densities were available solely for cruises 3, 4, and 5. Cruises: cross-hatched bars, 14 June (cruise 2); solid bars, 15 July (cruise 3); open bars, 28 July (cruise 4); shaded bars, 8 August 2000 (cruise 5).

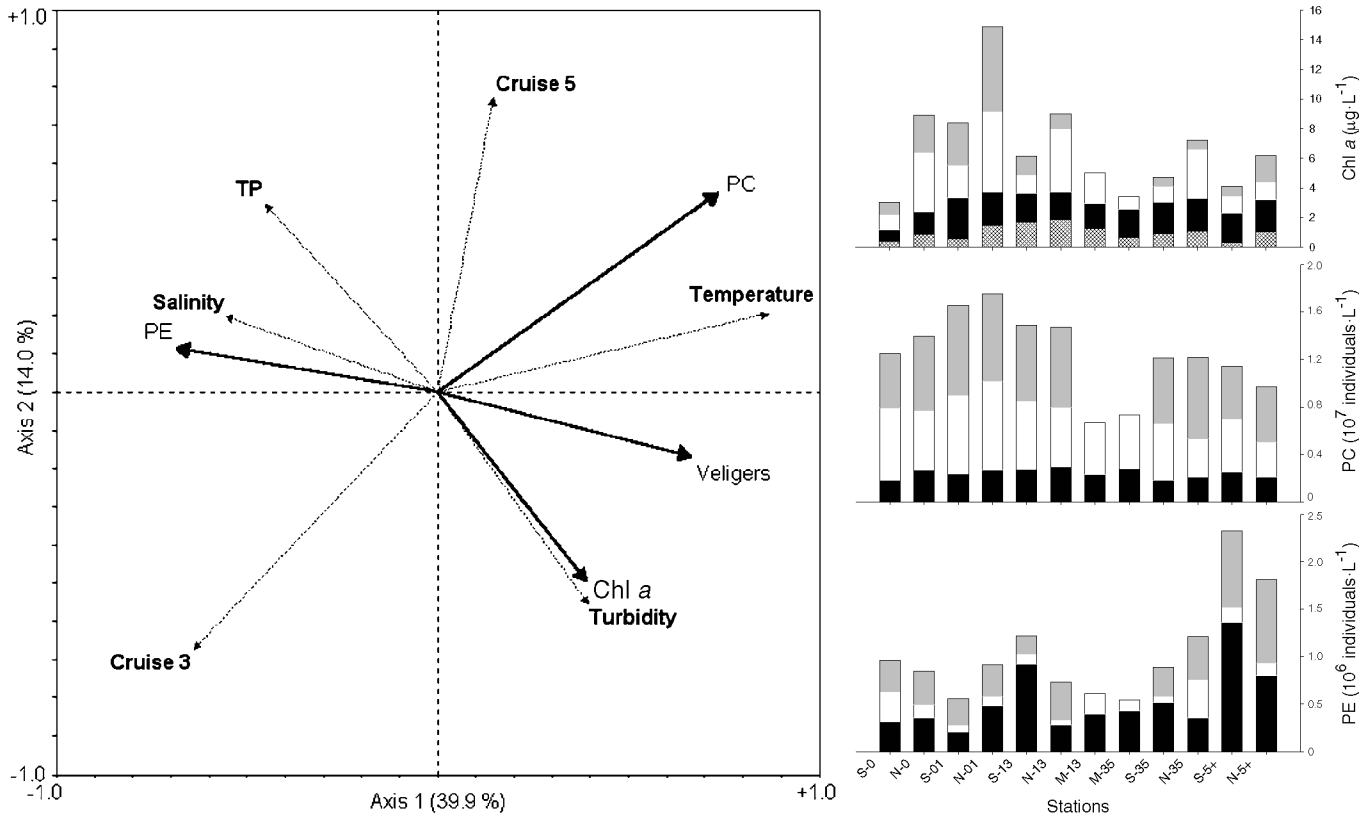


Table 1. The results from a split-split plot analysis of variance for the effects of depth (surface, mid-column, bottom), tidal state (high, intermediate, low), and zone (freshwater and transition) on veliger abundance for summer 2001 sampling from the two fixed stations in the St. Lawrence estuarine transition zone.

Source of variance	df	MS	F value	P
(a) Main plot				
Cruise	1	620.71	0.72	0.5524
Zone	1	224 609.99	259.88	0.0394
Error 1	1	864.27		
(b) Subplot				
Depth	2	321.40	5.87	0.0645
Zone × depth	2	202.14	3.69	0.1234
Error 2	4	54.72		
(c) Sub-subplot				
Tide	2	3 924.25	4.07	0.0204
Zone × tide	2	10 271.29	10.64	<0.0001
Depth × tide	4	309.96	0.32	0.8631
Zone × depth × tide	4	547.31	0.57	0.6871
Error 3	90	965.00		
Total	113			

Note: $n = 114$; results in bold are significant; df, degrees of freedom; MS, mean square; error 1 = cruise × zone; error 2 = (cruise × depth) + (cruise × zone × depth); error 3 = (cruise × tide) + (cruise × zone × tide) + (cruise × depth × tide) + (cruise × zone × depth × tide) + tidal replicates (cruise × zone × tide × depth).

Table 2. The results of variation partitioning in redundancy analysis.

	r^2	P
Analysis 1	0.630	0.001
Analysis 2	0.239	0.057
Analysis 3	0.488	0.001
Analysis 4	0.114	0.233
Total explained	0.744	
Pure environmental	0.488	
Pure spatial	0.114	
Shared	0.142	
Unexplained	0.256	

Note: The relative and shared contribution of the environmental and spatial components to the variation in the species data are indicated.

therein). At salinities exceeding 4‰, this freshwater species' physiological state deteriorates quickly and growth is inhibited (Sprung 1993). Zebra mussel veligers are extremely sensitive to sudden changes in salinity, but their tolerance to such changes increases significantly if these changes are gradual (Strayer and Smith 1993; Kilgour et al. 1994). In the ETZ, the prevailing high mixing rates may not allow for an appropriate acclimation period. The veligers may thus be exposed to abrupt changes in salinity associated with this mixing and the different tidal regimes, which may explain the sharp decrease in abundance at 2‰.

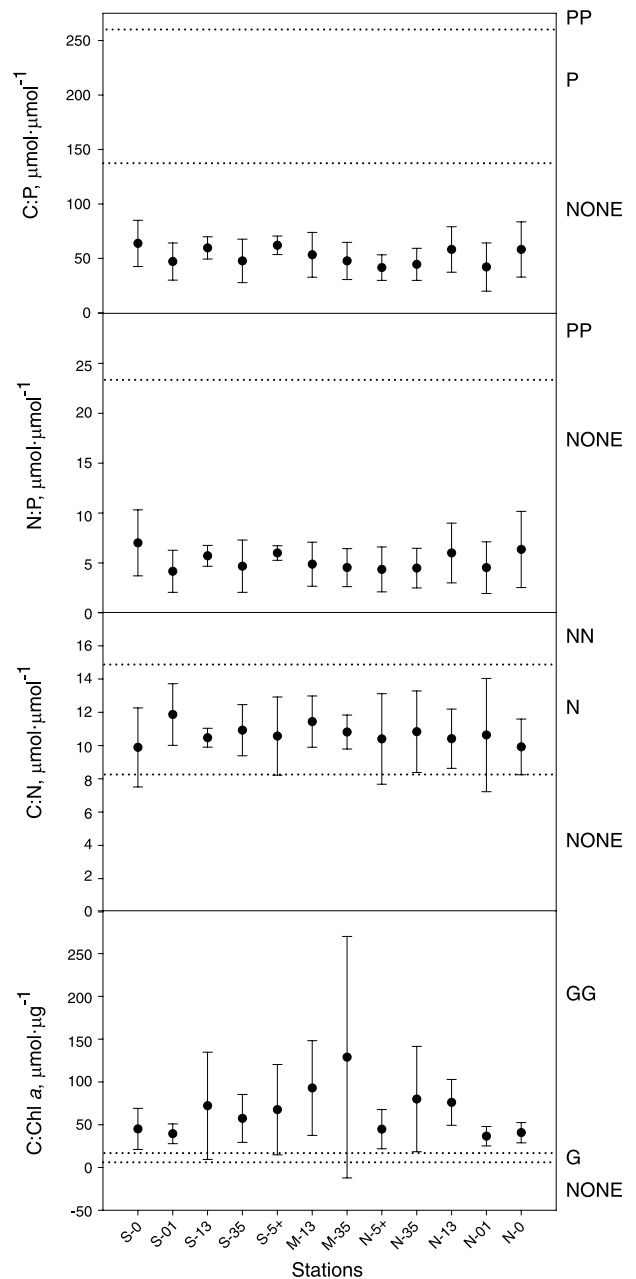
Stress due to advective transport

Horvath and Lamberti (1999) found that veligers were highly susceptible to damage by physical forces (i.e., shear and turbulence) and that mortality in high current streams (>1.0 m·s⁻¹) could limit veliger survival during downstream transport. Veliger densities from summer 2001 cruises showed a significant decline from zone 1 to zone 2, even during low tide (salinity <0.5‰). This may imply that mortality due to advective transport could have come into play. As for the effect of turbulence on the veligers, those collected in the highly mixed waters of the ETZ were active, i.e., swimming and gut filled, at salinities varying between 1‰ and 3‰ (C. Barnard, unpublished data). The physiological state of the veligers was not thoroughly examined, yet their presence or absence appears to be representative of their abundance as the abundance dropped significantly from one fixed station to the other over a fairly short distance and few empty shells were observed. The decline from zone 1 to zone 2 could be indicative of the negative impact of hydrodynamic forcing, salinity, or other factors discussed below.

Retention and turbidity

Retention by hydrodynamic trapping can explain the high densities observed at stations N-0 and N-01. Frenette et al. (1995) documented a prolonged residence time for cells (2–200 µm) in the ETZ and pathways that favour retention of larger particles (>20 µm). Veligers could then be subjected to this hydrodynamic trapping, a consequence of opposing currents in stratified estuaries that position the organisms to be moved upstream on flooding tides and retained during ebbing tides (Frenette et al. 1995). This recirculation mecha-

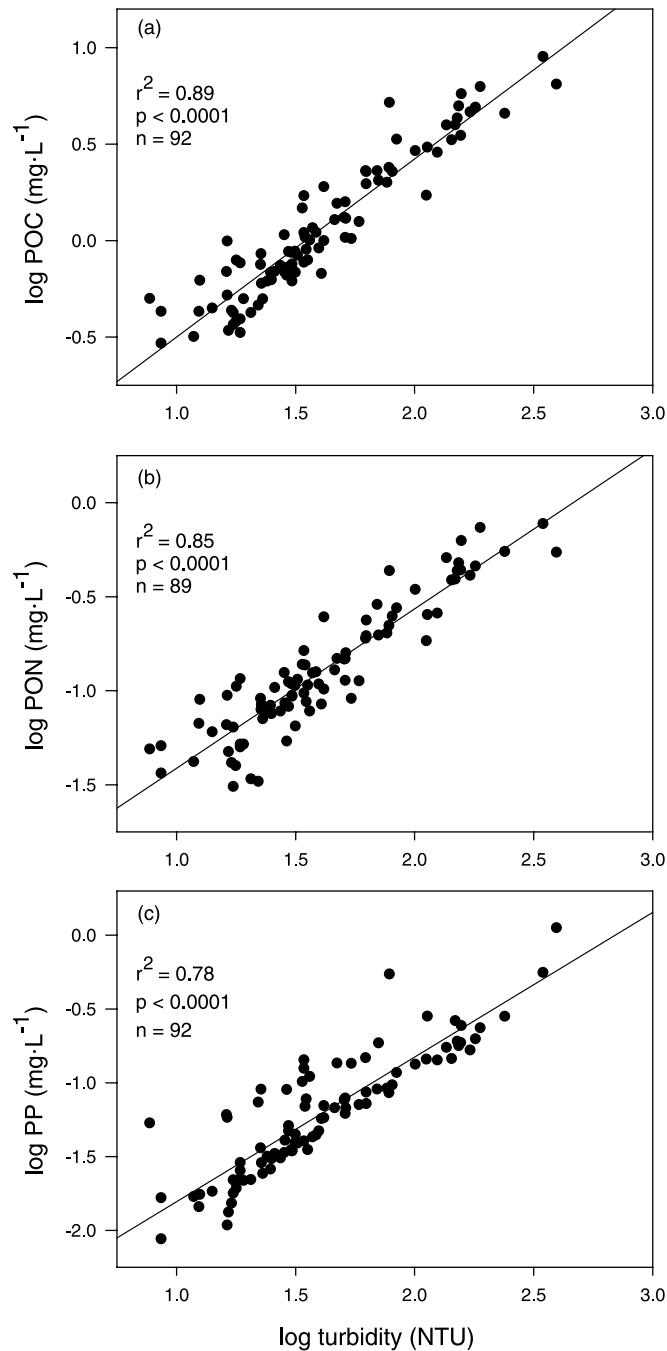
Fig. 5. Particulate nutrient stoichiometry and the C:Chl *a* ratio of the seston in the St. Lawrence estuarine transition zone (ETZ) during summer 2000. Samples were taken from the surface (0–2 m). Indication of nutrient deficiency according to Healey and Hendzel (1980) and Hecky et al. (1993): P, P deficiency; N, N deficiency; G, general nutrient deficiency; single symbol indicates moderate deficiency; double symbols indicate severe deficiency. Stations are indicated by a letter representing the channel (N, north; S, south; M, middle) followed by numbers indicating the salinity (0, 0‰; 01, 0–1‰; 13, 1–3‰; 35, 3–5‰; 5+, 5+‰).



nism would tend to lower downstream advective losses in this stratified estuary.

The veligers were positively correlated with turbidity, implying that turbidity can be used as an approximate guide to their distribution in the ETZ. The turbidity maximum present in this part of the estuary is the result of the recirculation

Fig. 6. Relationship between the log of (a) particulate organic carbon (POC), (b) nitrogen (PON), and (c) phosphorus (PP) as a function of turbidity (nephelometric turbidity units (NTU)) in the St. Lawrence estuarine transition zone (ETZ).



and retention mechanisms of suspended matter (Vincent and Dodson 1999). The stations where high veliger densities were found (N-0 and N-01) were situated directly in this maximum turbidity zone. Along with the potential accumulation of veligers due to vertical circulation and entrapment, these high densities could also be favoured by Coriolis effects and horizontal recirculation. These stations could also be receiving individuals originating from adult populations colonising the shores of Île d'Orléans.

Table 3. Molar ratios of particulate organic carbon to nitrogen to phosphorus (C:N:P) for the seston (0–2 m) at the 12 stations sampled during summer 2000.

Station	Cruise 2	Cruise 3	Cruise 4	Cruise 5
S-0	43:3:1	87:91:1	48:5:1	77:10:1
S-01	46:4:1	70:6:1	58:6:1	64:6:1
S-13	74:5:1	58:7:1	54:6:1	62:6:1
S-35	23:2:1	53:5:1	56:6:1	45:5:1
S-5+	16:1:1	50:6:1	34:5:1	68:6:1
M-13	28:2:1	61:6:1	54:6:1	NA
M-35	40:3:1	30:3:1	54:7:1	NA
N-5+	44:4:1	34:3:1	63:7:1	92:11:1
N-35	37:3:1	45:4:1	69:9:1	82:8:1
N-13	23:2:1	66:5:1	61:6:1	63:7:1
N-01	24:2:1	40:3:1	56:6:1	70:8:1
N-0	24:2:1	50:3:1	66:7:1	49:4:1

Note: Stations are indicated by a letter representing the channel (N, north; S, south; M, middle) followed by numbers indicating the salinity (0, 0‰; 01, 0–1‰; 13, 1–3‰; 35, 3–5‰; 5+, 5+‰). NA, not available.

Bioavailability of the veligers' prey

Kranck (1979) found that the particle size spectra of organisms in the maximum turbidity zone increases drastically from zone 1 to zone 2. According to this author, the majority of particles in the turbidity maxima (zone 2) appear to be $>10\ \mu\text{m}$ because of flocculation processes. Indeed, preliminary microscopic results on the protist community of the ETZ revealed that the veligers' prey become unavailable to them because of the formation of aggregates, thus causing mechanical interference. This sharp decrease in prey bioavailability at salinity $>2\text{‰}$ may be an important stressor to the veligers, in addition to salinity.

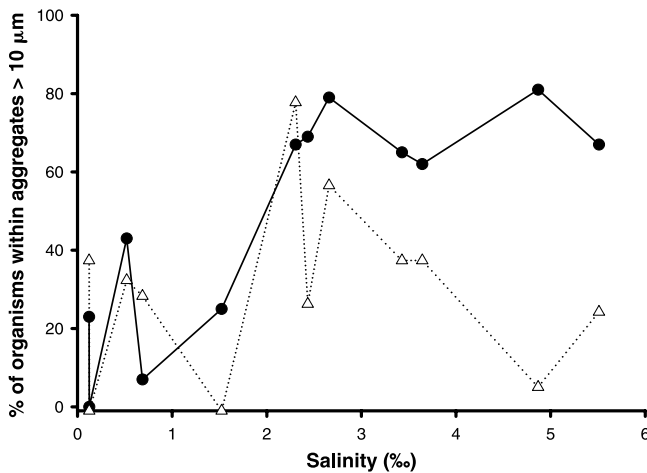
Predation

Previous studies conducted in the St. Lawrence ETZ observed sharp declines in Chl *a*, photosynthetic picoplankton, and protist concentrations between zones 1 and 2 (Lovejoy et al. 1993; Frenette et al. 1995). The authors attributed this effect to zooplankton grazing, as there is a large standing stock of zooplankton in the ETZ (Vincent and Dodson 1999; Winkler et al. 2003). Predation pressures could then also be partially responsible for the decrease in veliger abundance. Wright et al. (1996) observed that rotifer predation caused high mortality rates of their zebra mussel larvae culture. Mills et al. (1995) observed that alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) prey upon veligers but concluded that predation did not substantially reduce the number of veligers because they were either resistant to predation pressures and (or) the predation rate was not high enough. In contrast, other authors have stressed the importance of predation on veligers by fish larvae (*Osmerus esperlanus*, *Lucioperca lucioperca*, *Acerina arnua*, and *Rutilus rutilus*) (Sprung 1993).

Vertical distribution (summer 2001)

The veligers were evenly distributed throughout the water column, regardless of tidal state and zone. Even when the water column was stratified, no significant difference in abundance between surface, mid-column, and bottom samples was observed. Kern et al. (1994) also observed homoge-

Fig. 7. Protists within aggregates $>10\ \mu\text{m}$ as a function of salinity in the St. Lawrence estuarine transition zone (ETZ). The protist community was grouped into two functional groups: autotrophs, solid circles and solid line; heterotrophs, open triangles and dotted line. Samples were collected on 15 July 2000.



neous vertical distribution in the Rhine River, which most likely had higher mixing rates than lakes in which stratified distribution was observed under low wind conditions (Fraleigh et al. 1993; Garton and Haag 1993). With current speeds at ca. $2.5\ \text{m}\cdot\text{s}^{-1}$ and horizontal and vertical mixing, the ETZ hydrodynamics are much more complex and intense than in lakes. The veligers are most likely undergoing passive transport under these conditions. The elevated current speed and mixing rates of the ETZ throughout the water column and the constant influence of the salinity front on the hydrodynamics most probably does not allow the veligers to actively maintain their position in a density gradient or to passively settle. In this regard, veligers are also unlikely to have the capacity to actively move to areas of high productivity to feed.

Temporal distribution

Certain authors have documented that a single massive explosion of individuals during the summer characterizes veliger larvae abundance in the plankton, whereas other authors have observed several pulses of high abundances over the summer (Stoeckel et al. 1997). These authors suggested that upriver source populations spawned in frequent distinct bursts throughout the summer rather than just once or twice. Of the four cruises undertaken during summer 2000, our data revealed that veliger abundance was significantly higher during cruise 2 than during cruises 3, 4, and 5. Our data were not collected on a daily basis but show evidence of sporadic and distinct peaks in veliger abundance. This was consistent with the results obtained during the fixed station sampling of summer 2001, which showed large variation in veliger abundance between samples. Stoeckel et al. (1997) also observed the continual passage of pulses of individuals in a large river.

Food quality

Herbivores with high nutrient demands, such as the veligers, are frequently limited not by food quantity or available energy but by the quantity of mineral elements in their

food, i.e., seston food quality (Sterner and Hessen 1994). It has been illustrated that food quality has a highly significant effect on the survival rates of *Dreissena veligers* (Wacker et al. 2002). Seston ratios have proven to be effective physiological indicators of the nutritional state of phytoplankton (Healey and Hendzel 1980). Veliger densities were weakly but positively correlated with the PP/TP ratio as well as with PP, indicating their association with good quality seston. The ratio PP/TP represents the amount of phosphorus within the particulate material (and potential prey items) relative to the total phosphorus. Under nutrient-poor or resource-limited conditions, organisms tend to have a high particulate carbon content relative to other nutrients (Sterner 1997). The seston throughout the ETZ has relatively low C:P, C:N, and N:P ratios, indicative of its good overall nutritional quality, and in this aspect is a favourable environment for veliger growth. According to pre-established criteria, the ratios suggest no severe limitation of single N or P of plankton in the water column (Healey and Hendzel 1980; Hecky et al. 1993), and SRP and nitrate were always at detectable levels, suggesting adequate nutrient supply for the algae. The C:N:P ratios were generally in agreement, suggesting no simultaneous deficiencies. In general, however, these did not correspond to the traditional Redfield ratio of 106:16:1. The concentrations of particulate matter in this dynamic estuary are presumably much higher and more variable than in typical oceanic environments. Redfield ratios tend to be an exception rather than the rule in fresh water (Hecky et al. 1993), and studies have shown that although this ratio is found in the ocean and large lakes, it can vary greatly according to transient effects on cellular physiology (Falkowski 2000).

The high C:Chl *a* ratios observed in the ETZ could potentially be interpreted as indicating a high general nutrient deficiency or as a substantial detrital influence (Healey and Hendzel 1980; Hecky et al. 1993). The first scenario is highly unlikely considering the values of seston elemental ratios. In the second scenario, some authors attempt to correct for the influence of detritus on particulate C, N, and P on the basis of a standard C:Chl *a* ratio (Hecky et al. 1993). Estimating the latter is difficult for the St. Lawrence ETZ where physical gradients are pronounced. Even the C:Chl *a* ratio of algae grown in culture varies significantly with varying degrees of nutrient stress and light conditions (Healey and Hendzel 1980). If detritus had an overriding influence on the ratios, we would expect to find an increase of particulate C in the ratios with an increase in turbidity, but this was not the case. Moreover, there were no differences between the surface and bottom ratios, despite higher turbidities near the bottom (C. Barnard, unpublished data).

Järvinen et al. (1999) also observed high C:Chl *a* ratios in large, turbid Lake Tanganyika, which is characterized by low Chl *a* concentrations. In the ETZ, Chl *a* concentrations are tidally variable, with lows occurring during high tide (Vincent and Dodson 1999). It has been shown that the phytoplankton in the ETZ are adapted to intermittent light rather than low light conditions (Vincent et al. 1994), which could result in lower cellular requirement for Chl *a* and thus a higher C:Chl *a* ratio.

Chl *a* biomass, veliger abundance, and particulate C, N, and P were all positively correlated with turbidity. It is interesting to note that the turbidity does not seem to negatively

affect Chl *a* biomass or seston quality. The positive relationship between turbidity and the biological variables is likely the result of the common influence of hydrodynamic retention on biotic particles, as well as on abiotic particles (Frenette et al. 1995). A similar peak in phytoplankton biomass, coincident with the turbidity maximum, has also been observed in the ETZ of the James River, U.S.A. (Moon and Dunstan 1990).

Impacts of veligers on the food web

The positive correlations between Chl *a*, PC picoplankton, and veliger concentrations imply that the veligers have no severe negative impacts on these food sources and that phytoplankton resources are not limiting for the veligers in the ETZ. These associations also suggest that veligers are subject to the same physical and chemical forces in the water column as the other biological variables. These biological variables had a negative relationship with salinity and TP but a positive relationship with temperature and turbidity. As shown with variance partitioning, the spatial component did not have a strong influence on the biological community. On the other hand, the environmental variables were highly significant explanatory variables, underlying the pivotal role that the salinity front plays in structuring the biological community. The zone of high veliger abundance, the upstream portion of the ETZ, seems to be a favourable environment (low salinity and abundant food resources) for their growth. Bertrand and Vincent (1994) observed that picoplankton could contribute from 6% to 56% of the total Chl *a* in the water column of the ETZ. This may imply that a high proportion of the Chl *a* biomass is edible by the veligers (prey size spectrum 1–9 µm) (Sprung 1993; Wright et al. 1996). In the present study, the mean photosynthetic picoplankton densities at <2‰ was 5.09 (standard deviation = 1.9) × 10⁶ individuals·L⁻¹. This is similar to the photosynthetic picoplankton densities previously documented by Bertrand and Vincent (1994) before the invasion. No decrease in the photosynthetic picoplankton densities of the ETZ has thus been observed since the arrival of this new species.

In summary, we found that the larval veligers of *Dreissena polymorpha* were abundant in the low salinity waters of the St. Lawrence ETZ. Their concentrations decreased exponentially with increasing salinity, with the maximum decrease observed at 2‰, suggesting salinity-induced mortality, grazer, or other loss processes. The veligers were homogeneously distributed throughout the water column, under all tidal regimes, even when the water column was stratified. Despite their dominance in the ETZ plankton, the veligers have no severe effects on the lower food web because they are positively correlated with Chl *a* biomass, picoplankton densities, and good quality seston. The high productivity of the ETZ may explain why the ecosystem does not appear to be negatively impacted by their invasion, i.e., the ETZ may have a sufficient surplus of food resources to support the high population of zebra mussel veligers in addition to the usual zooplankton residents. The high abundance of veligers may have an impact on higher trophic levels, but this was not assessed in our analysis. The low salinity waters (<2‰) of the upper reaches of the St. Lawrence ETZ therefore provide a favourable environment for their survival. Future perspectives should investigate their impact on the biomass size

spectrum of the microbial community and on higher trophic levels of this important larval fish nursery.

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