Invasion of an estuarine transition zone by *Dreissena polymorpha* veligers had no detectable effect on zooplankton community structure

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Abstract: Large numbers of the filter-feeding larval stage of zebra mussels (*Dreissena polymorpha*) (veligers) have been advected into the estuarine transition zone (ETZ) of the St. Lawrence River. In 1994, they became the dominant member of the tidal freshwater zooplankton assemblage of the ETZ (and subsequently the true estuarine assemblage) during summer months. These changes in community structure have not, however, been reflected in changes in the abundance of preinvasion taxa. Abundance of potential planktonic competitors such as rotifers and the cladoceran *Bosmina longirostris* fluctuated between years but did not decline following the invasion. Only densities of the copepod *Eurytemora affinis* declined in 2000 and 2001, but this could not be definitively associated with the invasion. Synchronous variation among different zooplankton groups suggests that environmental forcing related to or correlated with temperature anomalies is the major cause of interannual variation in the abundance of zooplankton taxa. The negative correlation between veliger abundance and salinity indicates that the ETZ acts as a sink for the larval stages of the zebra mussel. Their precise fate remains uncertain, but our study suggests that this invasion has had little or no impact on this pelagic community in spite of the numerical dominance of veligers.

Résumé : Un grand nombre de larves véligères à alimentation par filtration de la moule zébrée (*Dreissena polymorpha*) ont été entraînées par advection dans la zone de transition estuarienne (ZTE) du fleuve Saint-Laurent. En 1994, elles sont devenues l'élément dominant des peuplements intertidaux de zooplancton de la ZTE (pour former ensuite le véritable peuplement estuarien) durant les mois d'été. Cependant, ces changements de structure de communauté n'entraînent pas de changements d'abondance des taxons présents avant l'invasion. L'abondance des compétiteurs planctoniques potentiels, tels que les rotifères et le cladocère *Bosmina longirostris,* fluctue d'une année à l'autre, mais il n'y a pas eu de déclin après l'invasion. Seules les densités du copépode *Eurytemora affinis* ont diminué en 2000 et 2001, mais le déclin ne peut être clairement associé à l'invasion. L'existence de variations synchrones parmi les différents groupes du zooplancton laisse croire que le forçage environnemental associé aux anomalies de température, ou en corrélation avec elles, est la cause principale de la variation d'abondance des taxons du zooplancton. La corrélation négative entre l'abondance des véligères et la salinité indique que la ZTE agit comme un puits pour les stades larvaires de la moule zébrée. Leur sort exact reste incertain, mais notre étude laisse croire que cette invasion a eu peu ou pas d'impact sur la communauté pélagique, malgré la dominance numérique des véligères.

[Traduit par la Rédaction]

Introduction

By far the most influential invader of the Laurentian lake and river complex in recent times has been the zebra mussel (*Dreissena polymorpha*) (Griffiths et al. 1991). Since first observed in North America in the late 1980s, this invasive bivalve has successfully colonized many freshwater ecosystems (Johnson and Carlton 1996) including the entire length of the St. Lawrence River (Mellina and Rasmussen 1994*a*, 1994*b*). While human activities are responsible for much of

this secondary spread (Johnson and Carlton 1996), the rapidity of the downstream spread was largely due to the planktotrophic life cycle of this species, which includes a feeding larval stage (the veliger) that spends weeks in the water column (Martel et al. 1995). Owing to the high fecundity of this species, veligers can reach high densities (Ram and McMahon 1996) and then be transported hundreds of kilometres downstream during the planktonic period.

In contrast with the extensive research effort on the ecological impact of benthic populations of this invasive bivalve on native planktonic and benthic communities (e.g., Great Lakes (Vanderploeg et al. 2002) and the Hudson, Mississippi, and St. Lawrence rivers (Ricciardi et al. 1997; Pace et al. 1998; James et al. 2000)), little is known about the ecological impact of the planktonic phase of the life cycle. Veligers are known to filter-feed nanoplankton in a size range of 2–10 µm (Bernier 2003), and high densities of veligers could thus compete with other filter-feeders exploiting similar particle size ranges, such as rotifers (4–17 µm), cladocerans (4–28 µm), and copepods (2 to >150 µm) (Arndt 1993; Cyr and Curtis 1999; Zimmermann-Timm 2002).

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Whereas the effect of filter-feeding by veligers can be far less than that of dense populations of adult mussels in areas of shallow, rocky bottoms (e.g., western Lake Erie (MacIsaac et al. 1992)), their effects elsewhere may be substantially greater depending on levels of productivity and the abundance of competing organisms, both benthic and planktonic.

The St. Lawrence Middle Estuary includes the estuarine transition zone (ETZ) where distinct physical properties such as estuarine recirculation, semidiurnal stratification and mixing, sediment entrapment, and high turbidity act as major factors organizing the aquatic biota. Estuarine circulation and entrapment result in elevated primary production at the head of the ETZ (Vincent et al. 1994, 1996; Frenette et al. 1995), while heterotrophic processes dominate farther downstream. Both processes show strong spatial and trophic coupling (Winkler et al. 2003). The plankton community of the ETZ, including primary producers, herbivores, and planktivores, is longitudinally organized across the frontal gradient of the transition zone.

The ETZ is a key element of the estuarine ecosystem because of its unique combination of upstream and downstream properties (Vincent and Dodson 1999). For the St. Lawrence River, it is still unknown to what extent this sensitive interface between the freshwater and marine areas of this large river–estuarine ecosystem is vulnerable to environmental perturbation. Estuaries are the receiving end of lentic systems, and thus, environmental stressors can be the result of the integration and accumulation of upstream processes including chemical pollution, sediment loading, and discharge modification. Whereas some stressors might be mitigated en route (e.g., sedimentation of suspended solids), others become progressively compounded as one moves downstream. This problem is often the case for the biological pollution that results from the introduction of nonnative species, which are inevitably spread downstream.

The potential impact of veligers on the planktonic communities of the ETZ is thus difficult to predict but may depend on both the precise biological and physical conditions of the zooplankton assemblage. In the 1970s (Bousfield et al. 1973), 1980s (Laprise and Dodson 1994), and again in the 1990s (Winkler et al. 2003), three distinct assemblages of zooplankton were recognized in the ETZ that are mainly controlled by average salinity and the degree of water column stratification: (*i*) a freshwater assemblage characterized by the cladoceran *Bosmina longirostris* and the amphipod *Gammarus tigrinus* found around and upstream of Île d'Orléans in warmer, well-mixed waters of salinities <1.6 psu (practical salinity units), (*ii*) a true estuarine assemblage dominated by the copepod *Eurytemora affinis* and the mysid *Neomysis americana* that occurs downstream of Île d'Orléans in weakly stratified waters of salinities between 0.5 and 6 psu, and (*iii*) a euryhaline–marine assemblage characterized by copepods (*Calanus* spp.), the mysid *Mysis littorales*, and euphausids (*Thysanoessa* spp. and *Meganyctiphanes norvegica*), which is found farther downstream in colder and more stratified waters with salinities >6 psu. Zooplankton biomass peaks in the true estuarine assemblage (Bousfield et al. 1973; Laprise and Dodson 1994) and provides a rich food resource for larval and juvenile fish, including rainbow smelt (*Osmerus mordax*) and Atlantic tomcod (*Microgadus* tomcod) (Dauvin and Dodson 1990; Laprise and Dodson 1990; Sirois and Dodson 2000).

Normally, the higher salinities of estuarine conditions would protect this ecosystem from upstream freshwater invaders, but the combination of high discharge (sixth highest in the world), geomorphology, and extreme tides produces an estuary that extends for 540 km and thus lacks abrupt salinity changes. Moreover, the exact salinity tolerance of zebra mussels is not yet well established, but it is clear that both benthic and planktonic stages are capable of surviving in low-salinity waters (adults up to 8 psu (Mackie and Kilgour 1992; Walton 1996) and veligers up to 4 psu (Wright et al. 1996)). This concern is particularly pertinent to the ETZ where retention processes could lead to elevated densities of veligers and nanoplankton dynamics play an important role (Frenette et al. 1995; Barnard et al. 2003).

In this study, we examined the impact of the zebra mussel invasion on zooplankton in the ETZ of the St. Lawrence River. We proposed that the potential for competition between veligers and other filter-feeders exploiting similar particle size ranges may have caused changes in the abundance of some zooplankton species and hence altered zooplankton community structure. The objective of this study was thus to document changes in the abundance of zebra mussel veligers and other zooplankton species at the head of the ETZ of the St. Lawrence Middle Estuary during the invasion. The distribution and abundance of *D. polymorpha* veligers and certain preinvasion species of the zooplankton community were assessed along the salinity gradient to detect changes in the three distinct zooplankton assemblages of the ETZ. Sampling cruises conducted in 1993 (preinvasion) and 1994 and 1995 (invasion) enabled us to detect the time of the massive arrival of veligers in the estuary, and further sampling was conducted in 2000 and 2001 (postinvasion) to assess if any changes have occurred since then that could be attributed to the presence of veligers in the transition zone.

Material and methods

Study site

The St. Lawrence Middle Estuary is located from 50 to 230 km downstream of the city of Québec and encompasses a salinity range of 0–25 psu (Fig. 1). Three channels (northern, middle, and southern) run through this part of the estuary. A combination of semidiurnal, lunar tides ranging from 3 to 5 m in amplitude, and freshwater discharge varying between 18 164 and 8863 $m^3 \cdot s^{-1}$ from May to August (Ministère de l'environnement Canada, Service météorologique) creates strong estuarine circulation. Because of the lateral variation in bathymetry (a deep northern channel and shallower middle and southern channels are separated by islands, sand banks, and shallow shoals), salt water intrudes farther upstream in the northern channel of the estuary, creating both along- and cross-estuary salinity gradients (Simons 2004). The water column is generally well mixed and partially stratified with stratification that varies on tidal and subtidal scales (Simons 2004). Mean current velocities exceed 0.6–3 $m \cdot s^{-1}$, and hydrodynamic trapping of inorganic and organic particles owing to estuarine circulation is responsible for high turbidity in this area (D'Anglejan 1981).

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Fig. 1. Average position of isoclines (psu) and location of stations sampled in the northern and southern channels of the St. Lawrence Middle Estuary in 1993, 1994, 1995, 2000, and 2001. Symbols represent only average positions among field surveys, as the exact location of stations was determined on each occasion according to surface salinity. Indeed, certain stations could be representative of more than one assemblage depending on the tidal conditions.
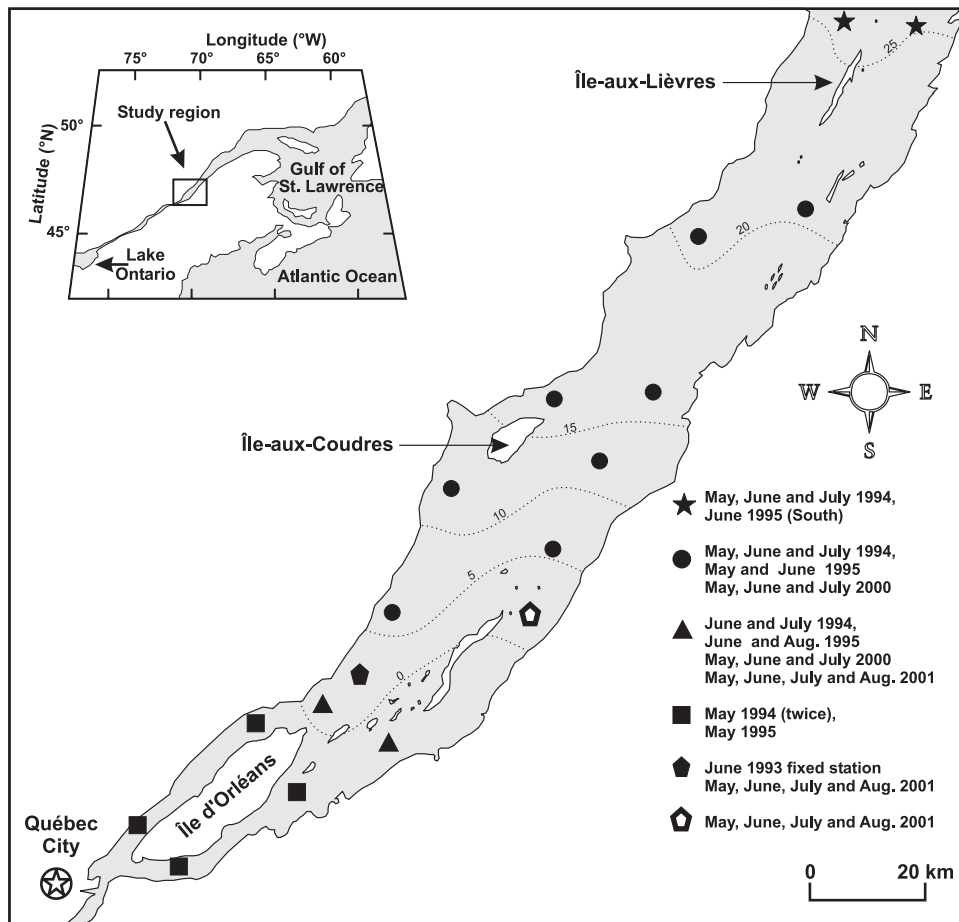
Data

The data used in this study were obtained from several studies that differed in their major objectives, and thus, sampling protocols varied between years. To render the data comparable, we imposed the well-documented preinvasion structure of zooplankton assemblages (Bousfield et al. 1973; Laprise and Dodson 1994; Winkler et al. 2003) on the data sets to form three putative zooplankton assemblages: tidal fresh water, true estuarine, and euryhaline–marine. We assessed the inter- and intra-group structure of these three assemblages with a nonmetric multidimensional scaling (MDS) analysis. Intergroup structure was analysed to test if the putative assemblages were distinct whereas intragroup structure was analysed to assess the contribution of each taxon in explaining within-assemblage similarity. To reveal the impact of veligers on the transition zone zooplankton community, we compared preinvasion (1993), invasion (1994 and 1995), and postinvasion (2000 and 2001) periods.

Preinvasion zooplankton community

To describe the preinvasion state of the zooplankton community, we used data obtained over a 76.5-h period from 22 to 26 June 1993 at a fixed sampling station located in the north channel of the St. Lawrence estuary 10 km down-

stream of Île d'Orléans (Winkler et al. 2003). Sampling was conducted every 1.5-h period covering a salinity range from 0 to 6 psu. Zooplankton samples were collected using a 0.5-m standard net (63-μm mesh size). For a detailed description of sampling and laboratory procedures, see Winkler et al. (2003). For the purposes of this paper, we only used data from surface samples taken by 5-m vertical tows in the surface layer.

Invasion (1994 and 1995) and postinvasion (2000 and 2001) periods

Field surveys were conducted in 1994 (24–26 May, 20–22 June, and 15 and 16 July), in 1995 (25–27 May, 27 and 28 June, and 14 August), and in 2000 (30 May – 4 June, 23–25 June, 11 and 12 July, and 24–26 July). A grid of 10–16 stations along the salinity gradient was sampled for each survey (Fig. 1). Stations were determined by real-time measures of surface salinity (i.e., a Lagrangian sampling design). In 2001, we sampled two stations at the head of the transition zone (freshwater <0.6 psu) and two stations in the transition zone (0.6–6 psu) each week from 22 May to 31 July. For all sampling, salinity and temperature profiles were measured using a SeaBird Seacat profiler (Sea-logger SBE-19, Sea-Bird Electronics, Inc., Bellevue, Washington). Zooplankton

were collected by 5-m vertical tows in the surface layer with a 0.5-m standard net (63-μm mesh size). In 1994 and 1995, samples were preserved in 4% buffered formaldehyde. In 2000 and 2001, 95% ethanol was used and changed once in the first week after the first preservation to prevent the solution from becoming too acidic (Butler 1992). The following species and taxa were identified: veligers of *D. polymorpha*, rotifers, *B. longirostris*, calanoid copepods *E. affinis* and *Acartia* sp. (other, rarely occurring calanoid copepods were pooled and identified as "other calanoids"), cyclopoid copepods (mainly *Cyclops* sp.), harpacticoid copepods (mainly *Ectinosoma curticorne*), and nauplii (includes all copepod species). To distinguish *D. polymorpha* veligers, we used cross-polarized light (Johnson 1995). Abundances were evaluated from subsamples, counting a minimum of 10% of the total sample volume with densities expressed per litre of filtered water.

Statistical analysis

Prior to statistical analysis, we grouped our zooplankton samples into three distinct zooplankton assemblages (see above) according to salinity: (*i*) tidal freshwater from 0 to 0.5 psu, (*ii*) true estuarine from 0.6 to 6 psu, and (*iii*) euryhaline–marine waters >6 psu. We combined June and July data to represent the summer zooplankton community during the period of the highest abundance of *D. polymorpha* veligers. To visualize the distribution and variability of these three putative zooplankton communities over the sampling sites, we used MDS (Legendre and Legendre 1998; Clarke and Warwick 2001) on transformed data ($\log(x + 1)$). Data were transformed to reduce bias resulting from highly abundant species. Bray–Curtis similarities were calculated to create an MDS representation of the yearly zooplankton assemblages as a function of the three predetermined salinity categories. This technique reduces a multidimensional scatter plot into a lower number of dimensions while preserving the maximum amount of variation in the data, thus allowing relationships between individual points to be more easily visualized. Each data point represents the abundance of all taxa in the zooplankton community at one sampling site at a specific time. To test differences between zooplankton assemblages, we used analysis of similarities (ANOSIM). This analysis operates on a similarity matrix. Zooplankton assemblages are considered very different in their species composition when similarities within an assemblage are greater than those between the assemblages. The ANOSIM statistic R is based on the difference of mean ranks between assemblages and within assemblages. The ANOSIM R value shows the degree of distinctness as follows: well separated ($R > 0.75$), overlapping but clearly different ($R > 0.5$), and barely separable at all ($R < 0.25$) and value 0 indicating completely random grouping. The statistical significance of the observed R is assessed by permutation of the grouping vector to obtain the empirical distribution of R under a null model (Clarke 1993; Clarke and Warwick 2001). A similarity of percentages routine (SIMPER) was used to assess the contributions of different taxa to observed within-assemblage similarity. Nonmetric MDS, ANOSIM, and SIMPER were performed using the PRIMER v5 program (PRIMER-E Ltd., Plymouth, UK).

Even though our sampling grids are spatially structured,

spatial autocorrelation was negligible. The sampling stations for each cruise were chosen according to salinity and not to geographic position (e.g., a Langrangian sampling design). Strong tidal currents mixed the water mass from one station to another and from one day to the next. The large distances between stations further assured the sampling of different water masses. Nevertheless, to avoid any bias associated with spatial autocorrelation, we visually verified if adjacent points in the MDS plots were sampled on the same day. In such cases, data from these stations were averaged (3% of all data points).

Kendall's rank correlation coefficient τ was used to measure the best match of biotic and environmental similarity matrices for the years 1993, 1994, 1995, 2000, and 2001. Differences in the estimates of abundance of each taxon between years for the three zooplankton assemblages were tested using a Kruskal–Wallis ANOVA and Tukey's test for multiple comparisons of unequal sample sizes (Zar 1996). As abiotic factors can govern the distribution and abundance of zooplankton (Viitasalo 1992; Dippner et al. 2000), we used air temperature and discharge (Ministère de l'environnement Canada, Service météorologique) measured and estimated at Quebéc (located approximately 40 km from the ETZ) as indicators of weather conditions in the years of the study. We calculated the mean monthly temperature and mean monthly discharge of 1993–2001 to define the monthly temperature anomalies for each year that we sampled zooplankton, i.e., 1993–1995, 2000, and 2001. We did the same calculation for mean monthly zooplankton abundance of the tidal freshwater and true estuarine assemblages.

Results

Occurrence of *D. polymorpha* veligers in zooplankton assemblages

Sampling in the mid-1990s detected for the first time *D. polymorpha* veligers in the ETZ. Whereas no veligers were found in 1993, large numbers (up to 138 veligers·L^{-1}) were found starting in 1994 when the relative abundance of veligers at the head of the transition zone (i.e., in the tidal freshwater assemblage) increased from 20% to 80% of the zooplankton between May and July (Figs. 2*a*–2*c*). Similar patterns were seen over the next 7 years with the proportion of veligers reaching 75% by June in 1995 and similarly high proportions of veligers in June (80%–90%) and July (70%–90%) of 2000 and 2001 (Figs. 2*a*–2*c*). Peak abundances always occurred in June: 293 veligers·L^{-1} in 1995, 127 veligers·L^{-1} in 2000, and 353 veligers·L^{-1} in 2001. In August, the proportion of veligers diminished whereas rotifers and nauplii dominated (Fig. 2*d*). Absolute densities of veligers (30–70 veligers·L^{-1}) in the tidal freshwater zone in August were much lower than in June and July (70–235 veligers·L^{-1}). The composition of the true estuarine zooplankton assemblage was also affected by the invasion. Beginning in 1994, veligers were present in May, but only in 2001 were they the dominant component of this assemblage (Fig. 2*e*). The dominant taxa in the true estuarine zooplankton assemblage in June and July from 1993 to 1995 were copopods (especially *E. affinis* and nauplier stages). However, this pattern changed in 2000 and 2001 when veligers were numerically dominant (Figs. 2*f* and 2*g*).

Fig. 2. Seasonal and annual differences in zooplankton community structure for each assemblage. Zooplankton composition in the tidal freshwater assemblage in (*a*) May, (*b*) June, (*c*) July, and (*d*) August, in the true estuarine assemblage in (*e*) May, (*f*) June, (*g*) July, and (*h*) August, and in the euryhaline–marine assemblage in (*i*) May, (*j*) June, (*k*) July, and (*l*) August during preinvasion (1993), invasion (1994 and 1995), and postinvasion (2000 and 2001). No column indicates that data for that date were not available.
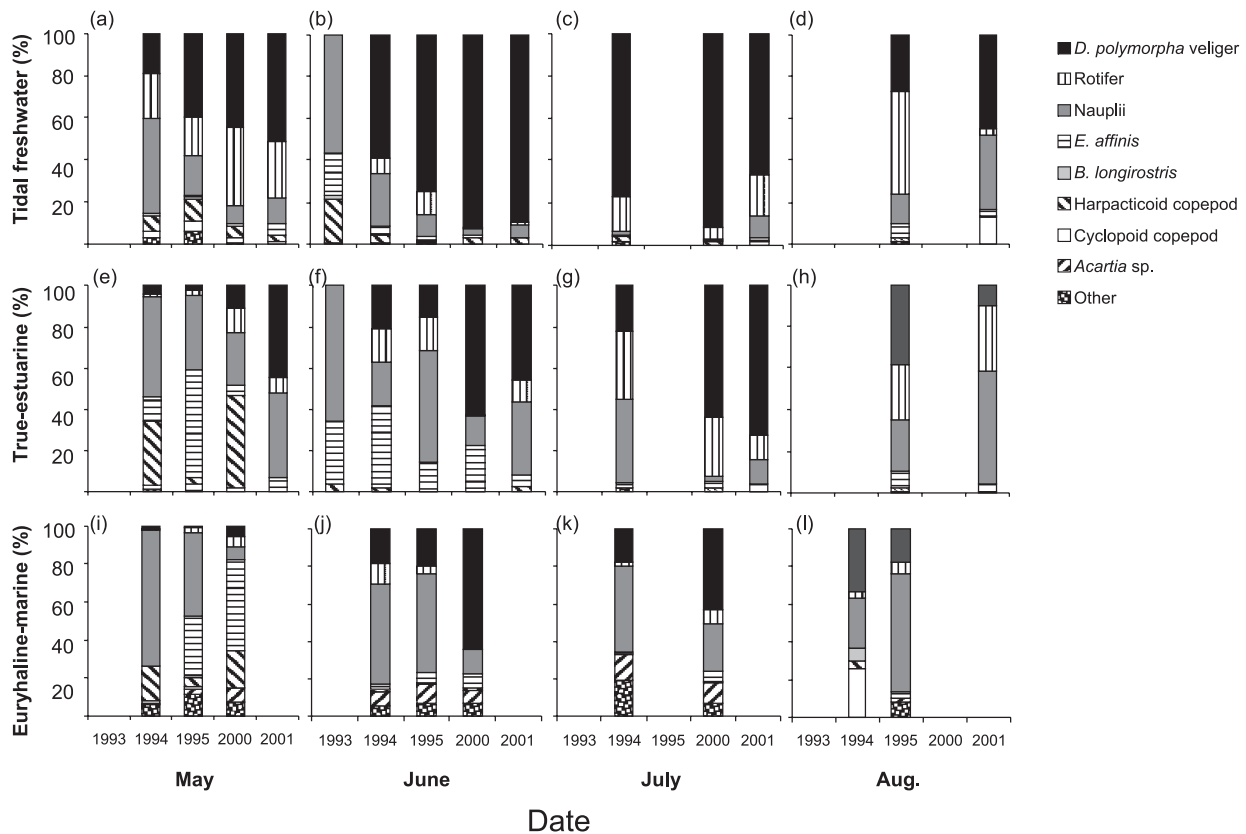
In the euryhaline–marine zooplankton assemblage, veligers contributed <20% and copepod species dominated, except in June and July 2000, when the veliger contribution was 60% and 40%, respectively. No data for 1993 and 2001 were available for this zooplankton assemblage. The rest of the assemblage consisted primarily of copepod species, especially nauplier stages. *Eurytemora affinis* was particularly abundant in May of two years (1995 and 2000) whereas *Acartia* was more common in June and July (Figs. 2*i*–2*l*), especially in 2000.

Comparison of putative zooplankton assemblages

Species contribution to similarity (SIMPER), MDS, and ANOSIM assessed both within-assemblage and between-assemblage similarity for all sampling stations in 1993, 1994, 1995, 2000, and 2001 for the three zooplankton assemblages. In 1993, before the invasion, most of the within-assemblage similarity was due to nauplii and *E. affinis* for both tidal freshwater and true estuarine assemblages (Table 1). During the invasion period, most of the within-assemblage similarity in the tidal freshwater assemblage was due to *D. polymorpha* veligers (51% and 38% in 1994 and 1995, respectively) (Table 1) whereas in the true estuarine assemblage, nauplii still accounted for much of the within-assemblage similarity (32% and 34%, respectively) (Table 1). In contrast, during the postinvasion period (2000 and

2001), both the tidal freshwater and true estuarine assemblages were dominated by *D. polymorpha* veligers, which were largely responsible for the within-assemblage similarity in both assemblages (Table 1).

General patterns in the MDS plots were similar for all years. The freshwater assemblage was adjacent to the true estuarine assemblage, which in turn was next to the euryhaline–marine assemblage (Fig. 3). However, the detailed structure of the assemblages was different between years and between analyses with and without *D. polymorpha* veligers. Overall global *R* increased when veligers were excluded from the analysis except in 2000. During the preinvasion period (1993), the tidal freshwater and true estuarine assemblages were significantly different (Table 2; Fig. 3*a*) with an average dissimilarity of 40%, mostly because of differences in mean abundance of nauplii and *E. affinis* between the two assemblages. In 1994 at the start of the invasion phase, the calculated ANOSIM *R* between the tidal freshwater and estuarine assemblages did not differ (ANOSIM *R* inferior to 0.25) in cases both with and without veligers. In contrast, ANOSIM *R* in 1995 was high (but not significant) when veligers were included in the analysis, indicating a strong difference between the assemblages. However, when veligers were excluded, the difference between these two assemblages mostly disappeared. Furthermore, none of the ANOSIM *R* for these two years were significant

Table 1. Average within-assemblage similarities (%) of the three putative zooplankton assemblages and the contribution of most important taxa (%) for all years.

Year	Tidal fresh water	%	True estuarine	%	Euryhaline–marine	%
1993	Average similarity	67	Average similarity	84		
	Nauplii	47	Nauplii	53		
	Eurytemora affinis	25	*Eurytemora affinis*	40		
	Harpacticoid copepods	21				
	Bosmina longirostris	5				
1994	Average similarity	57	Average similarity	67	Average similarity	52
	Dreissena veligers	51	Nauplii	32	Nauplii	56
	Rotifers	19	Rotifers	28	*Dreissena* veligers	15
	Harpacticoid copepods	11	*Dreissena* veligers	23	Other	14
					Acartia sp.	12
1995	Average similarity	83	Average similarity	75	Average similarity	49
	Dreissena veligers	38	Nauplii	34	Nauplii	57
	Nauplii	23	*Eurytemora affinis*	29	Other	17
	Rotifers	16	*Dreissena* veligers	23	*Dreissena* veligers	13
	Eurytemora affinis	14	Rotifers	11	*Acartia* sp.	6
2000	Average similarity	72	Average similarity	70	Average similarity	46
	Dreissena veligers	78	*Dreissena* veligers	64	*Dreissena* veligers	55
	Harpacticoid copepods	8	Nauplii	12	Nauplii	19
	Rotifers	7	*Eurytemora affinis*	10	Others	10
	Eurytemora affinis	3	Rotifers	10	*Eurytemora affinis*	10
2001	Average similarity	64	Average similarity	69		
	Dreissena veligers	40	*Dreissena* veligers	40		
	Nauplii	18	Nauplii	31		
	Rotifers	18	*Eurytemora affinis*	14		
	Hapacticoid copepods	8	Rotifers	11		

owing to small sample sizes (*n* = 4 in 1994 and *n* = 2 in 1995). During the postinvasion phase, we found the tidal freshwater and true estuarine assemblages to be different in 2000 but not in 2001 because of high variability within both assemblages in 2001 (Figs. 3*c* and 3*d*; Table 2) (ANOSIM *R* < 0.25). When veligers were excluded, ANOSIM *R* decreased and there were no differences between the two assemblages in 2000 whereas ANOSIM *R* slightly increased. in 2001. The euryhaline–marine assemblage always showed significant differences from the two upstream assemblages whether veligers were included or not in the calculations (Figs. 3*b*–3*d*; Table 2).

Kendall's rank correlations between the similarity matrices for biotic and environmental patterns revealed that salinity seemed to be far more important in determining zooplankton distribution than temperature (Table 3). These correlations appear to be due to patterns of abundance of *D. polymorpha* veligers, rotifers, *B. longirostris*, and cyclopoid copepods, which reached the highest levels in the freshwater assemblage and were negatively correlated with salinity and positively correlated with temperature (Table 4). The abundance of *E. affinis*, the characteristic species of the true estuarine assemblage, was positively correlated with temperature but not with salinity, as it reached maximum abundance at midrange salinities. Nauplii were weakly correlated with temperature (positive) and salinity (negative) because of the fact that this group included several copepod species distributed throughout the estuary. *Acartia* sp. was strongly positively correlated with salinity and negatively correlated with temperature, reflecting its strong affinity to

the euryhaline–marine assemblage (Table 4).

Interannual variation in the abundance of individual groups of zooplankton

Mean abundances of the invader (*D. polymorpha* veligers) and most of the preinvasion taxa (rotifers, nauplii, *E. affinis*, and cyclopoid copepods) varied significantly between years mostly in the tidal freshwater and true estuarine assemblages. In contrast, mean abundances of harpacticoid copepods did not differ between years in either zooplankton assemblage (Table 5). For *D. polymorpha* veligers, there was no increasing trend with time after the initial invasion (Fig. 4*a*), and in fact, a significantly lower mean abundance was found in the tidal freshwater group in 2000. In the true estuarine group, mean abundance of veligers was always lower but generally showed a trend in interannual variation similar to that observed in the tidal freshwater group (Fig. 4*b*). No interannual variation in mean abundance of veligers occurred in the euryhaline–marine assemblage (Table 5).

No rotifers were found in 1993 whereas they were abundant in all subsequent years. Their mean abundance varied significantly between years and paralleled the pattern of veliger abundance in the tidal freshwater and true estuarine assemblages, with their abundance in 2000 being the lowest of the postinvasion years (Figs. 4*c* and 4*d*; Table 5).

Mean abundance of nauplii varied significantly between years and zooplankton assemblages (Table 5). Mean abundance of nauplii was highest in 1995 and lowest in 2000 as was the case for other taxa of the tidal freshwater and true estuarine assemblages (Figs. 4*e* and 4*f*; Table 5). The abun-

Fig. 3. Nonmetric multidimensional scaling (MDS) plots for three zooplankton assemblages (tidal fresh water (▲), true estuarine (▼), and euryhaline–marine (■)) in the St. Lawrence Middle Estuary (June and July data pooled) during (*a*) preinvasion in 1993, invasion from (*b*) 1994 to (*c*) 1995, and postinvasion from (*d*) 2000 to (*e*) 2001. The stress of the MDS plots varied between years: 0.04 (1995), 0.08 (1993, 1994, and 2000), and 0.16 (2001).
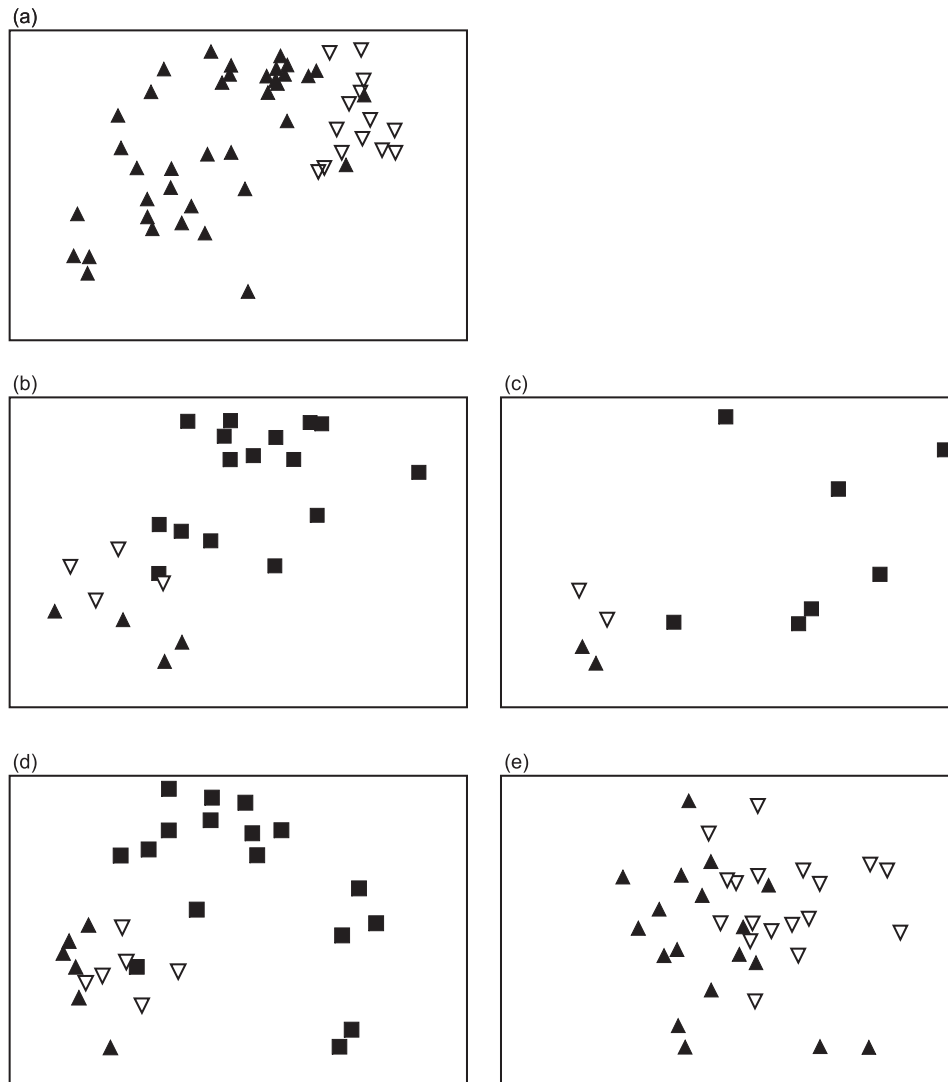
dance of *E. affinis* declined progressively after the invasion of *D. polymorpha* in the tidal freshwater and true estuarine assemblages, with the lowest abundance in the true estuarine assemblage occurring in 2000 (Figs. 4*g* and 4*h*; Table 5). Mean abundance of *B. longirostris* in the tidal freshwater assemblage did not differ significantly between years (Table 5) owing largely to high variability between replicates in each year. In the true estuarine group, mean abundance was significantly higher in 1994 than in all other years. Harpacticoid copepods did not show any significant difference in mean abundance between years in any assemblage (Table 5). Abundance of cyclopoid copepods was highly variable between years, and maximum abundance occurred in the tidal freshwater group in 2001 (Table 5). *Acartia* sp. occurred only in the euryhaline–marine group and its mean abundance was significantly lowest in 2000 (Table 5). In general, the abundance patterns observed over time all showed broadly similar trends, although they differed in amplitude: elevated

from 1993 to 1995, down in 2000, and then up again in 2001 (Fig. 4). This alone suggests that there was no major impact of the veliger invasion on interannual variation.

Interannual variability: air temperature and discharge

In all years of the study, mean air temperature varied between months and years (Fig. 5*a*). Relatively warm temperatures in June 1994 and 1995 coincided with relatively high zooplankton abundances in this month whereas relatively low temperatures in June 1993 and 2000 and July 2000 coincided with relatively low abundances (Figs. 5*c*–5*j*). In the other months and years, this pattern was not so evident, suggesting that temperature is not the only factor in explaining interannual variability in abundance. Variability in mean discharge between years and months was also high, characterizing 1993 and 1994 as high-flow years and 1995 and 2001 as low-flow years (Fig. 5*b*). In high-flow year 1994, veliger abundance was below the overall mean, and in low-flow year

Table 2. Results of ANOSIM including and excluding veligers from the analysis.

| Year | ANOSIM global R (p level) | | Pairwise test assemblages | ANOSIM R (p level) | |
	Veligers included in the analysis	Veligers excluded from the analysis		Veligers included in the analysis	Veligers excluded from the analysis
1993		**0.319 (0.001)**	Fresh water – estuarine		**0.319 (0.001)**
1994	**0.512 (0.001)**	**0.525 (0.001)**	Fresh water – estuarine	0.188 (0.171)	0.094 (0.23)
			Fresh water – marine	**0.691 (0.002)**	**0.654 (0.001)**
			Estuarine–marine	**0.504 (0.001)**	**0.548 (0.003)**
1995	**0.443 (0.013)**	**0.522 (0.013)**	Fresh water – estuarine	0.75 (0.33)	0.25 (0.667)
			Fresh water – marine	**0.656 (0.028)**	**0.727 (0.028)**
			Estuarine–marine	**0.532 (0.023)**	**0.643 (0.028)**
2000	**0.346 (0.001)**	**0.285 (0.001)**	Fresh water – estuarine	**0.413 (0.002)**	0.091 (0.21)
			Fresh water – marine	**0.521 (0.002)**	**0.377 (0.001)**
			Estuarine–marine	**0.337 (0.009)**	**0.288 (0.009)**
2001	**0.208 (0.001)**	**0.249 (0.001)**	Fresh water – estuarine	**0.208 (0.001)**	**0.249 (0.001)**

Note: ANOSIM R varies from –1 to +1, with a value of 0 indicating completely random grouping. Statistical significance of the observed R is assessed by permutation and shown in parentheses. Significant R values are shown in boldface.

Table 3. Environmental variables yielding the best match of biotic and abiotic similarity matrices as measured by Kendall's rank correlation coefficient τ for the years 1993, 1994, 1995, 2000, and 2001.

| Year | τ | |
	Salinity	Temperature
1993	0.453	0.144
1994	0.538	0.364
1995	0.517	0.546
2000	0.584	0.381
2001	0.146	0.233

Table 4. Kendall's correlation coefficients τ between zooplankton abundance and physical variables of all 165 samples collected in the estuarine transition zone (ETZ) in 1993, 1994, 1995, 2000, and 2001.

| | τ | |
	Water temperature	Salinity
Dreissena polymorpha veligers	**0.6**	**–0.52**
Rotifers	**0.25**	**–0.18**
Nauplii	**0.16**	**–0.17**
Eurytemora affinis	**0.17**	–0.15
Bosmina longirostris	**0.29**	**–0.24**
Harpacticoid copepods	0.03	**–0.20**
Cyclopoid copepods	**0.17**	**–0.22**
Acartia sp.	**–0.32**	**0.44**

Note: All values greater than 0.15 or less than –0.15 (boldface) represent significant correlations at the $p < 0.05$ level.

2001, veliger abundance in both the tidal freshwater and true estuarine groups was higher than average in all three months. However, in the other taxa, no consistent pattern between abundance and discharge occurred (Figs. 5*e*–5*j*).

Discussion

Data limitation

The mining of data sets collected over many years that were initially collected to meet objectives at times quite different from those of this study inevitably involves a disparate collection of sampling strategies and techniques. Thus, not all previous data sets were appropriate for the present analysis and the interpretation of those that were appropriate was complicated by the limitations of specific data sets. Data from the preinvasion phase are limited to sampling at a fixed station in June 1993. Nevertheless, sampling at a fixed station in this highly dynamic estuary permitted the intensive sampling of water masses varying between 0 and 6 psu, which is equivalent to the spatial sampling of stations deployed over approximately 15 km of the middle estuary. Earlier work in the middle estuary is not quantitatively comparable with the data that we present here. In 1971, Bousfield et al. (1973) sampled the ETZ, but with a bigger mesh size (158 µm instead of 63 µm), thus missing potential nauplii and rotifers. The study by Laprise and Dodson (1994)

from the late 1980s only examined *E. affinis* and *B. longirostris* and abundances were estimated semiquantitatively; smaller zooplankton were not counted. These data sets were thus unsuitable for integration into our analysis.

Veliger invasion

Although the distribution of adult zebra mussels had reached at least into the intertidal zone of the St. Lawrence Estuary at Levis as early as 1992 (Mellina and Rasmussen 1994*a*), veligers were not detected in our sampling of the ETZ of the St. Lawrence River in 1993 and were only first observed there in 1994, at which time and thereafter they occurred in great numbers. Despite the spatial limitation of the 1993 sampling, we are confident in our observation of the absence of veligers in 1993. Although adult zebra mussels had already been documented along the St. Lawrence River down to the western tip of the Île d'Orléans in 1992, their abundance was very low (a maximum of 1631 individuals·m^{-2} at Port de Bécancour and 287 individuals·m^{-2} at Île d'Orléans (Costan and de Lafontaine 2000). The combination of low adult densities throughout the St. Lawrence River with the dilution of larvae by high river outflow proba-

Table 5. Kruskal–Wallis ANOVA calculated for the abundance of each taxon for factor "years" and post hoc multiples comparisons (Tukey's test after Dunn for unequal sample size) for each taxon in each salinity group.

Taxon	Salinity group	df	N	H	p	Multiple comparisons test (years)				
Dreissena polymorpha veliger	Tidal fresh water	4	61	56.9	<0.001	1995	2001	1994	2000	1993
	True estuarine	4	40	29.2	<0.001	2001	1995	2000	1994	1993
	Euryhaline–marine	2	40	1.3	0.513					
Rotifer	Tidal fresh water	4	61	54.8	0.000	1995	1994	2001	2000	1993
	True estuarine	4	40	29.7	<0.001	1995	1994	2001	2000	1993
	Euryhaline–marine	2	40	4.2	0.118					
Nauplii	Tidal fresh water	4	61	16.8	0.002	1995	2001	1993	1994	2000
	True estuarine	4	40	20.7	<0.001	1995	1993	1994	2001	2000
	Euryhaline–marine	2	40	19.3	<0.001			1995	1994	2000
Eurytemora affinis	Tidal fresh water	4	61	16.6	0.002	1995	1993	2001	1994	2000
	True estuarine	4	40	21.4	<0.001	1995	1993	1994	2001	2000
	Euryhaline–marine	2	40	14.3	0.002			2000	1995	1994
Bosmina longirostris	Tidal fresh water	4	61	8.1	0.085					
	True estuarine	4	40	14.6	0.005	1994	2000	1993	2001	1995
	Euryhaline–marine	2	40	1.0	0.600					
Harpacticoid copepods	Tidal fresh water	4	61	4.1	0.389					
	True estuarine	4	40	7.2	0.126					
	Euryhaline–marine	2	40	0.1	0.955					
Cyclopoid copepods	Tidal fresh water	4	61	34.0	<0.001	2001	1994	1993	1995	2000
	True estuarine	4	40	6.5	0.165					
	Euryhaline–marine	2	40	12.7	0.002			1994	1995	2000
Acartia sp.	Tidal fresh water	4	61	0.0	1.000					
	True estuarine	4	40	0.0	1.000					
	Euryhaline–marine	2	40	7.0	0.029			1994	1995	2000

Note: Post hoc multiples comparisons were not conducted in the case of nonsignificance (multiple comparisons test column left blank). The degrees of freedom (df), number of samples (*N*), *H* statistic, and significance levels (*p*) are shown. In multiple comparisons tests, years are ordered by decreasing ranks from left to right and nonsignificant differences among years are underlined.

bly left veliger densities below our ability to detect them until 1994. The data for all years after 1993 always indicated that maximum abundances of veligers occurred in June and July in the tidal freshwater region of the middle estuary. Thus, even if present in 1993, the abundance of veligers must have been very low. Otherwise, veligers would have been easily detectable in the June 1993 samples.

Densities of veligers were much higher than at upstream sites in the fluvial part of the river where the peak abundance in early July was 40 veligers·L^{-1} (de Lafontaine et al. 1995). Veligers are estimated to drift at a rate of 250–500 km·week^{-1} in the fluvial part of the St. Lawrence River (Costan and de Lafontaine 2000), suggesting a high advective loss from these fluvial habitats. In contrast, tidal influence farther downstream could prolong residence time, and net drift distance could be shortened (i.e., the concept of persistence (Speirs and Gurney 2001)). This combination of advection and retention may explain the high observed veliger abundance at the head of the transition zone and may thus reflect the reproduction from the ensemble of established upstream populations. In contrast, local production in the ETZ is likely to be relatively small because of limited

Fig. 4. Interannual variation in mean summer abundance (June and July pooled) in the tidal freshwater group of (*a*) *Dreissena polymorpha*, (*c*) rotifers, (*e*) nauplii, and (*g*) *Eurytemora affinis* and the true estuarine group of (*b*) *D. polymorpha*, (*d*) rotifers, (*f*) nauplii, and (*h*) *E. affinis* during preinvasion (1993), invasion (1994 and 1995), and postinvasion (2000 and 2001). Bars represent standard errors, and letters above the bars indicate significant differences from multiple comparisons.
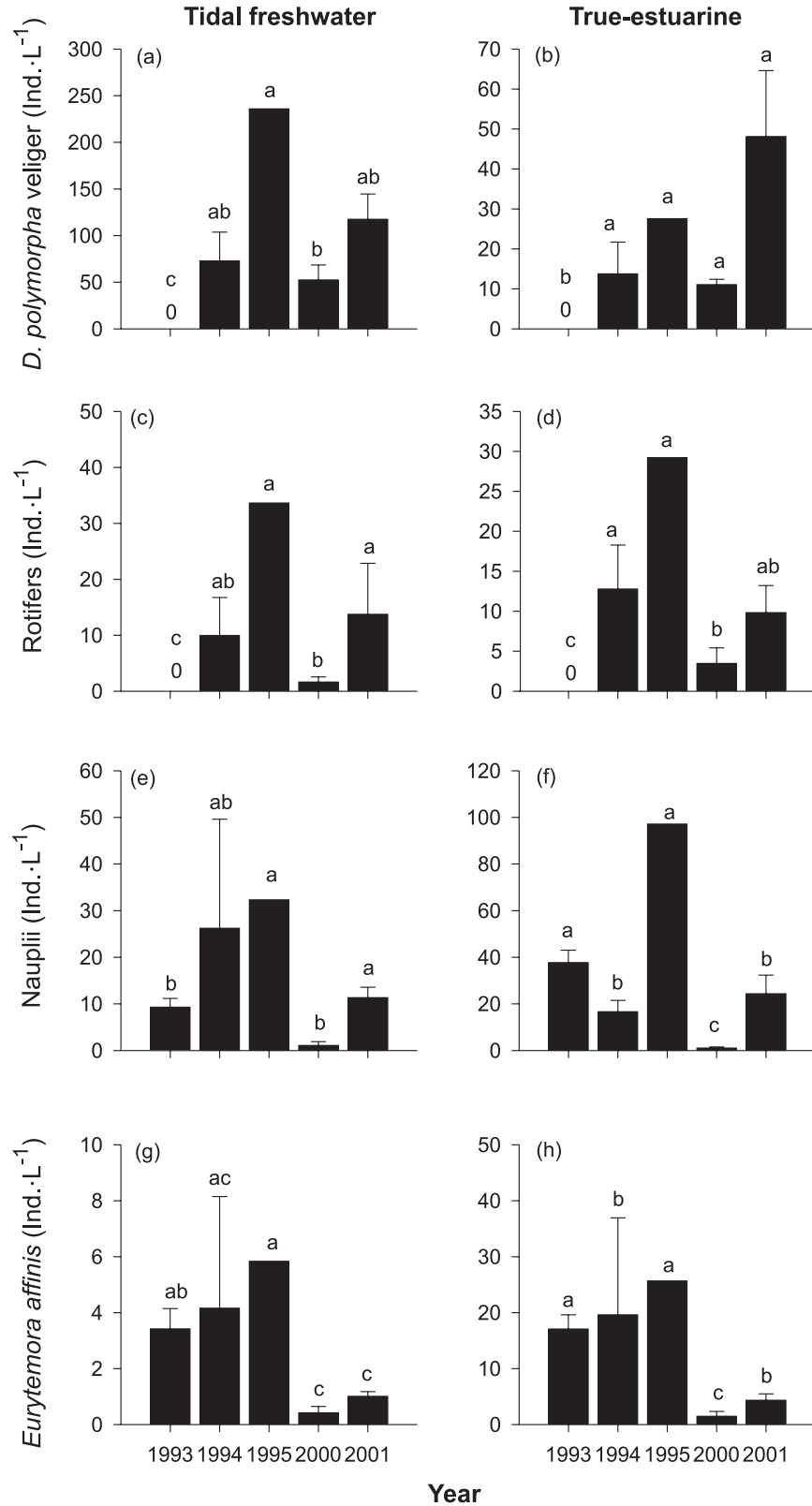
Fig. 5. Monthly air temperature, discharge anomalies at Québec, and monthly zooplankton abundance anomalies in the tidal freshwater and true estuarine groups for the years 1993–1995, 2000, and 2001. An asterisk indicates that data for that month were not available.
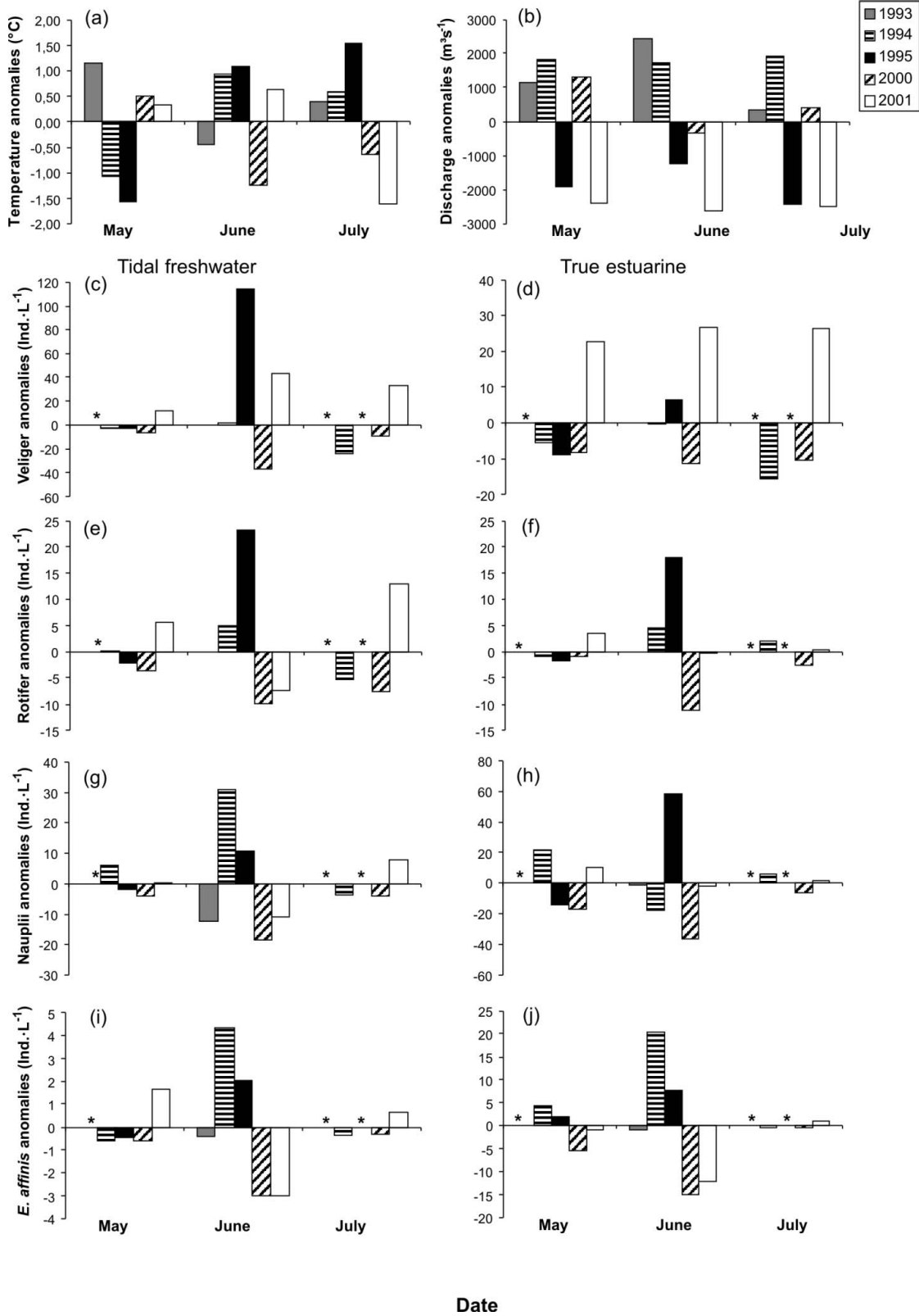
distribution and low population densities at the head of the ETZ (Costan and de Lafontaine 2000; A. Casper, Québec–Océan, Pavillon Vachon, Université Laval, Québec, QC G1K 7P4, Canada, unpublished data). Mean veliger abundance in 1994, 1995, 2000, and 2001 did not show any consistent trend with time of invasion, and the high interannual

variability in veliger abundance may be simply due to changes in reproduction of upstream populations as well as in the river discharge controlling advection of veligers (see below).

Effect of the invasion on individual zooplankton species

Interannual variation in the abundance of the preinvasion zooplankton in the tidal freshwater and true estuarine assemblages did not appear to be related to the invasion of veligers in the ETZ. Abundance patterns of preinvasion taxa were more or less rising and falling in synchrony, with changes in relative amplitude that suggested that other factors are responsible for the interannual variation (see below). An exception might be the copepod *E. affinis* where abundance in the postinvasion phase (2000 and 2001) was lower than in the preinvasion and invasion periods, but it is unclear if this decline in abundance was directly or indirectly caused by the invasion. Density variation found in this study corresponded to the density range (0.01–3 *E. affinis*·L^{-1}) found in the early 1970s (Bousfield et al. 1973) and 1980s (Laprise and Dodson 1994). Although both species are filter-feeders, exploitative competition for food between *E. affinis* and *D. polymorpha* veligers is highly unlikely, as their ability to ingest particles differs. Veligers appear to be limited to particles sizes ≤10 μm (Bernier 2003) whereas *Eurytemora* spp. ingest particles ranging from 1 to 200 μm, including free-living and attached bacteria (Boak and Goulder 1983), phytoplankton (Uitto 1996), seston (Poulet 1978), and micro- and macro-aggregates (Zimmermann-Timm 2002). In the middle estuary, a high percentage of free-living autotrophs form aggregates with increases in salinity >2 psu, suggesting that food availability is reduced for veligers (Barnard et al. 2003). In contrast, food resources for *E. affinis* are probably unlimited because of their omnivorous behaviour and ability to exploit a vast size range of prey.

In contrast, the abundance of rotifers (e.g., *Keratella* sp.) closely paralleled that of the veligers, including their absence in samples from 1993. Rotifers, feeding most efficiently on protists in the 4- to 17-μm size range (Arndt 1993), seem to have very similar food requirements to *D. polymorpha* veligers (Bernier 2003), and isotopic (δ^{15}N) studies indicate that both taxa occupy the same trophic level (Martineau et al. 2004). The invasion by the veligers did not, however, appear to have any negative effect on rotifers, as there was no obvious decline in their abundance. Competition for food resources may not exist in the ETZ because of its high primary production (Frenette et al. 1995; Vincent et al. 1996) and the relatively low abundance of rotifers (260 rotifers·L^{-1} compared with 900–1000 rotifers·L^{-1} reported from upstream sites (Thorp and Casper 2002, 2003)). Furthermore, veliger abundance in the ETZ was positively correlated with Chl *a* and protist abundance, suggesting that food limitation is unlikely (Barnard et al. 2003).

The total absence of rotifers in the 1993 samples should be interpreted with caution. Winkler et al. (2003) could not find rotifers in these samples in spite of the fact that they occurred in the digestive tracts of mysids collected at the same time. Thus, we are certain that rotifers were present in the ETZ in 1993 but suspect that they were not detectable owing to very low densities. In addition, sampling efforts in 1993 were focussed on a 3-day period in June and thus are not representative of the entire summer.

Bosmina longirostris also showed no decline with the invasion of *D. polymorpha* veligers in the system. Abundance ranged between 0.1 and 3.6 individuals·L^{-1} depending on sampling site, month, and year. In earlier sampling campaigns in the 1970s, 2 individuals·L^{-1} were found in the tidal freshwater region but declined with increasing salinity in the true estuarine zone (0.2 individual·L^{-1}) (Bousfield et al. 1973), and in the 1980s, Laprise and Dodson (1994) found 0.1–1 individual·L^{-1} in the tidal freshwater assemblage. In terms of possible trophic interactions with veligers and rotifers, *B. longirostris* is potentially a superior competitor for protists. Their feeding size spectrum (4–45 μm) is broader and completely encompassed the feeding range of the latter taxa (Bogdan and Gilbert 1982; Cyr and Curtis 1999). Moreover, stable isotope analysis indicates that *B. longirostris* is situated on a higher trophic level than either rotifers or veligers (Martineau et al. 2004), suggesting that there is little overlap in food resources between them.

Overall, then, there is little evidence for competitive interactions between zooplankton species, and we suggest that the ETZ is still able to support a high level of zooplankton standing stock despite the invasion of *D. polymorpha* veligers in this ecosystem. There was nevertheless substantial interannual variation in the abundance of preinvasion taxa, but we assert that this variation is more likely due to forcing by the physical environment (e.g., discharge and weather) and biological properties of the zooplankton taxa (food conditions, reproduction, predation, and mortality) than to the massive occurrence of *D. polymorpha* veligers in the system. For example, all taxa, including *D. polymorpha* veligers, showed the highest abundance in 1995 and the lowest abundance in 2000 compared with all other years. These extremes coincided with negative temperature anomalies in 2000 and positive ones in 1995 measured at Québec. Furthermore, cumulative degree-days in the tidal freshwater section in May, June, and July reflected the same patterns (data not shown). Without a longer time series of data from the ETZ, it is not possible to more rigorously evaluate changes in the preinvasion and invasion communities. However, in the Baltic Sea, interannual variability during spring and summer of small copepods (*Acartia* spp. and *E. affinis*) was controlled by climate variability (Viitasalo 1992; Dippner et al. 2000).

Weak relationships between monthly discharge and abundance of preinvasion species suggest that discharge is a minor factor driving interannual variation. In contrast, the negative correlations between the abundance of veligers and discharge support the idea that discharge may affect veligers directly by controlling advective losses (and thus the persistence of veliger populations), the position of the saltwater–freshwater front, the extent of estuarine recirculation, and the hydraulic and particle residence times (Pace et al. 1992; Jassby et al. 1995; Speirs and Gurney 2001). Thus, the higher discharge may lead to a lower residence time of veligers owing to high net advective outflow.

Biotic factors are also likely to influence zooplankton dynamics and may be partly responsible for interannual variation in abundance. Population growth and egg production in copepods are dependent on food resources, and population size may be impaired by mortality (i.e., predation) (Heinle et

al. 1977; Plourde and Runge 1993; Peitsch et al. 2000).

Effect of the veliger invasion on zooplankton assemblages

Relative dominance of *D. polymorpha* veligers showed a tendency to increase in all zooplankton assemblages from the initial to the postinvasion phase. Whereas there was no evidence that the arrival of veligers in the ETZ has affected the abundance of zooplankton species living there, they have changed the statistical characteristics and distinctiveness of the three zooplankton assemblages (tidal fresh water, true estuarine, and euryhaline–marine) distributed longitudinally along the ETZ of the St. Lawrence Middle Estuary. During the initial stages of the invasion (1994 and 1995), the tidal freshwater assemblage was dominated by *D. polymorpha* veligers whereas copepods were mostly responsible for the within-assemblage structure of the true estuarine and euryhaline–marine assemblages. Statistically, these two assemblages could not be discriminated, but this is most likely due to the low numbers of sampling sites in both assemblages. During the postinvasion phase, veligers made the greatest contribution to the within-group similarity in all assemblages, and by 2001, the tidal freshwater assemblage could not be discriminated from the true estuarine assemblage. Furthermore, the exclusion of veligers from the analysis revealed a random distribution between the tidal freshwater and true estuarine assemblages in all years, except 2001 in which a slight difference between the two assemblages occurred. Our results suggest that the distinction between the tidal freshwater and true estuarine assemblages is highly dependent on sample size, abundance of contributing taxa, and within-assemblage variability. In consequence, to reveal finer differences between zooplankton assemblages, it is necessary to increase the resolution of community structure by documenting the abundance of separate species instead of multispecies groups such as nauplii and rotifers, cyclopoid copepods, and harpacticoid copepods. Different species integrated in these taxa may have obscured differences in community structure.

The strong correlations between biotic and abiotic patterns suggest that the physical environment controls the longitudinal distribution and composition of the zooplankton assemblages in the middle estuary. Both temperature and salinity play a role, but the high correlations between zooplankton abundance and salinity suggest that it is the primary factor explaining the distribution of zooplankton, supporting the conclusions of previous studies of the ETZ of this estuary (Laprise and Dodson 1994; Barnard et al. 2003; Winkler et al. 2003).

The ETZ as a sink for *D. polymorpha* veligers

Veliger densities decreased significantly from the tidal freshwater to the euryhaline–marine assemblage, illustrating that the ETZ acts as a sink for the larval stage. As adult densities are quite low (maximum of 670 mussels·m^{-2}, occurring in patches on hard substrate) in the ETZ (A. Casper, Québec–Océan, Pavillon Vachon, Université Laval, Québec, QC G1K 7P4, Canada, unpublished data), this pattern is undoubtedly the result of high rates of mortality rather than high settlement. The strong negative correlation with salinity suggests that osmotic stress is an important mortality factor,

and this conclusion is consistent with other laboratory and field studies. A parallel field survey in the ETZ found that the greatest decrease in veliger density in the ETZ occurred at around 2 psu (Barnard et al. 2003). Feeding rates in the laboratory declined linearly between 0 and 5 psu (Bernier 2003), and lethal salinity levels have been estimated at 4–4.5 psu (Kilgour et al. 1994; Wright et al. 1996). Alternatively, the high discharge and tides of the ETZ produce strong currents (up to 3 m·s^{-1}) and high turbulent mixing (1 m^2·s^{-1}) (Laprise and Dodson 1989), resulting in shear forces and turbulence that can increase mortality of veligers (Horvath and Lamberti 1999). The strong estuarine circulation also creates high turbidity (up to 400 nephelometric turbidity units), but veliger feeding activity is much less affected by turbidity relative to salinity in laboratory studies (Bernier 2003). Finally, there is also the possibility that predation rates might be high. Larval fish, however, do not appear to feed on veligers (H. Yonekama, Québec–Océan, Pavillon Vachon, Université Laval, Québec, QC G1K 7P4, Canada, unpublished data). Predation by the dominant mysid *N. americana* has been observed on veligers in the ETZ (G. Winkler, unpublished data), but it remains unknown if this predation is sufficient to limit veliger abundance.

In summary, the veligers of the zebra mussel have seasonally dominated the zooplankton communities of the ETZ of the St. Lawrence Estuary, especially in the tidal freshwater portion, since 1994. This invasion appears, however, to have had little impact on individual zooplankton species. Comparisons of the interannual variation in abundance of potential competitors such as rotifers, *E. affinis*, and *B. longirostris* showed little indirect evidence of any competitive effect, (e.g., declines in abundance over time or a negative relationship with the abundance of veligers). Much interannual variation was observed in the abundance of individual species but appears to reflect variation in the abiotic environment such as temperature rather than the *D. polymorpha* invasion. The addition of this invader has, however, changed the statistical characterization of zooplankton community structure in the tidal freshwater and true estuarine assemblages because of its numerical dominance. Although the functioning of this ecosystem seems not to have been impaired by this invasion and it is still able to support the zooplankton community, the veligers have changed its nature by playing a numerically dominant but noninteractive role. In effect, their presence is transitory, as the abundance of veligers is both temporally limited by the reproduction of upstream populations and spatially limited by the strong salinity gradient that appears to be largely responsible for the decline downstream of veliger abundance in the ETZ. Thus, the ETZ of the St. Lawrence Estuary acts as a veliger sink.

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