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Trophic coupling across the St. Lawrence River estuarine transition zone

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ABSTRACT: The objective of this study was to analyze the coupling between trophic levels of the frontal area of the St. Lawrence estuary transition zone, which is the site of an estuarine turbidity maximum (ETM) and is an important nursery area for the juveniles of Atlantic tomcod *Microgadus tomcod* and rainbow smelt *Osmerus mordax*. A detailed series of measurements and sampling were conducted over 6 tidal cycles within the frontal zone. An inverse relationship between the abundance of the 63 µm-net plankton and that of autotrophs indicated the impact of zooplankton grazing on autotrophic biomass, which was largely composed of diatoms. Within the 63 µm-net plankton, nauplii, copepodites and the adults of *Eurytemora affinis* appeared to be the most important grazers of autotrophs. First-order calculations illustrated that the primary production observed in the ETM is capable of supporting the biomass of this copepod and that its grazing pressure is capable of reducing autotrophic biomass in the brackish waters of the transition zone. Heterotrophic species were a small component (<20%) of total microplankton in the freshwater samples, but dominated the total community biomass at higher salinities. This shift towards heterotrophic dominance implies a spatial coupling between upstream autotrophic production and downstream consumer processes. Analysis of stomach contents showed that the calanoid copepod *E. affinis* was the primary food source for larval fishes and mysids, although the combined ingestion rates of the 2 fish species are unlikely to have any impact on copepod standing stocks. By far the most important predators of the zooplankton are *Neomysis americana* and *Mysis stenolepis*. Estuarine circulation and associated entrapment processes ultimately control the trophic relationships and gradients in community structure within the ETM.

KEY WORDS: Copepods · Estuary · Fish larvae · *Mysis* · *Neomysis* · Production · Zooplankton

INTRODUCTION

The St. Lawrence estuarine transition zone is the frontal zone where freshwater draining from the continent first meets the sea. It is characterized by sharp gradients in several environmental variables including salinity, nutrient concentrations, temperature and underwater light. It is also characterized by high concentrations of suspended sediment (turbidity) and zooplankton. This important land-margin ecosystem has been variously referred to as the entrapment or retention zone, the tidal null zone and the estuarine turbidity maximum (ETM). The key variable forcing this ETM ecosystem is likely to be discharge acting directly by controlling the position of the saltwater/freshwater front, the extent of estuarine re-circulation, and the hydraulic and particle residence times. Freshwater input will also influence temperature, the underwater light regime, and the hydrodynamic characteristics of channel versus shoal environments (Vincent & Dodson 1999).

Along the St. Lawrence ETM, a longitudinal succession of seasonally stable assemblages of zooplankton occurs whose spatial distribution is mainly a function of salinity and vertical stratification. A tidal freshwater assemblage dominated by *Bosmina longirostris* and *Gammarus* sp. reaches highest abundances at the upstream limit of saltwater intrusion. Further down-

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stream, this freshwater community grades into a true-estuarine assemblage composed of *Eurytemora affinis*, *Neomysis americana* and *Mysis stenolepis* occurring in salinities of 0.5 to 5 psu (practical salinity units). At higher salinities, the estuarine community is replaced by a euryhaline-marine assemblage composed of *Calanus* spp., *M. littoralis*, euphausiids and chaetognaths (Bousfield et al. 1975, Laprise & Dodson 1994). In June, larvae of tomcod *Microgadus tomcod* and smelt *Osmerus mordax* are associated with the true-estuarine zooplankton assemblage in waters of <5 psu. As they grow, tomcod move downstream into colder, more saline waters whereas smelt migrate upstream into warmer waters of salinity <2 psu (Laprise & Dodson 1989). The upstream migration of young-of-the-year smelt is the result of selective tidal stream transport, whereby smelt occupy surface waters on the flood tide and bottom waters on the ebb tide in order to maximize upstream displacement (Laprise & Dodson 1989). The upstream migration of smelt to the head of saltwater intrusion is associated with a significant increase in feeding incidence (Dauvin & Dodson 1990, Sirois & Dodson 2000).

The trophic processes operating in estuarine transition zones are not well understood. The downstream reaches of large rivers have been referred to as heterotrophic ecosystems in which bacterial processes dominate the carbon and energy flux (Findlay et al. 1991, Vaqué et al. 1992). A broad range of organic substrates for bacterial production is available in the St. Lawrence transition zone including marsh-derived detritus, upstream-derived dissolved and particulate carbon and urban waste discharge (Painchaud & Therriault 1989). Studies conducted at small spatial scales across the St. Lawrence transition zone have demonstrated high concentrations of zooplankton and larval fishes in the leading edge of the turbidity maximum in salinities <2 psu (Laprise & Dodson 1994). Both photosynthesis and bacterial processes appear responsible for maintaining this high standing stock. Photosynthetic rates per unit chlorophyll *a* (chl *a*) remain high across this zone, in which low light penetration is offset by a shallow mean mixing depth (Vincent et al. 1996). Bacterial concentrations and activity remain relatively constant across the transition zone, whereas chl *a* declines sharply, indicating loss of phytoplanktonic biomass to grazing. Previous estimates showed that photosynthesis contributed 34 to 66% of the total production, and freshwater phytoplankton advected from upstream contributed another 20 to 30% (Vincent et al. 1996). Work on large rivers elsewhere has similarly drawn attention to the likely importance of phytoplankton for food web energy and biomass, even within such 'heterotrophic' ecosystems (Thorp & Delong 2002).

The objective of this study was to define the coupling between trophic levels as influenced by the hydrodynamics of the frontal area of the St. Lawrence transition zone. We obtained a detailed time series of samples and measurements over 76.5 h at a fixed station, allowing us for the first time to investigate simultaneously all trophic levels from protists to fish larvae. The hypothesis that high losses of phytoplankton along the ETM are due to grazing and not simply to dilution processes was tested. To address this hypothesis, we analyzed the relationship among the abundance of autotrophic and heterotrophic protists, cladocerans, copepods, fish and mysids larvae as a function of tidally-induced fluctuations in salinity, temperature and suspended particulate matter. We then interpreted these relationships in terms of the relative importance of heterotrophs and autotrophs as potential food sources for micro- and mesocrustaceans by presenting first-order estimates of algal carbon consumption by copepods. We also addressed the importance of copepods as food for young fishes and mysids occurring in the low-salinity leading edge of the ETM.

MATERIALS AND METHODS

Sampling and laboratory procedures. In the north channel of the St. Lawrence estuary, one anchor station, located 10 km downstream of Île d'Orléans (Fig. 1), was occupied from June 22 to June 26, 1993. The daily river discharge at Québec City for this time period was in the range of 14 278.6 to 17 692.1 $m^3 s^{-1}$ (Ministère de l'Environnement Canada, Service Météorologique). This region encompasses the freshwater-saltwater transition zone and the area of maximum turbidity. The station was placed so as to obtain approximately half of the samples in freshwater (during ebb and low tides) and half in saline waters (during flood and high tides). Sampling began at spring tide and continued into neap tide. We sampled at 90 min intervals for a period of 76.5 h. Each sampling event took 45 to 50 min to complete. To obtain data on the feeding of young smelt sampled over time in the same water mass, sampling was undertaken on June 10, 1994, in the same area as the 1993 sampling. A total of 12 hourly samples was obtained during daylight hours at stations where the surface salinity was 1 psu.

For each sampling event in 1993, water samples were obtained with a 5 l GO-FLO (General Oceanics) bottle at 2 m above the bottom (bottom layer), 5 m above the bottom (middle layer), and 2 m below the surface (surface layer). The water column was approximately 10 m deep at low tide. Temperature and salinity were profiled with a Sea Bird CTD probe (Sealogger SBE-19); 1 profile was obtained at the beginning and 1 at the end of each sampling event, and we aver-

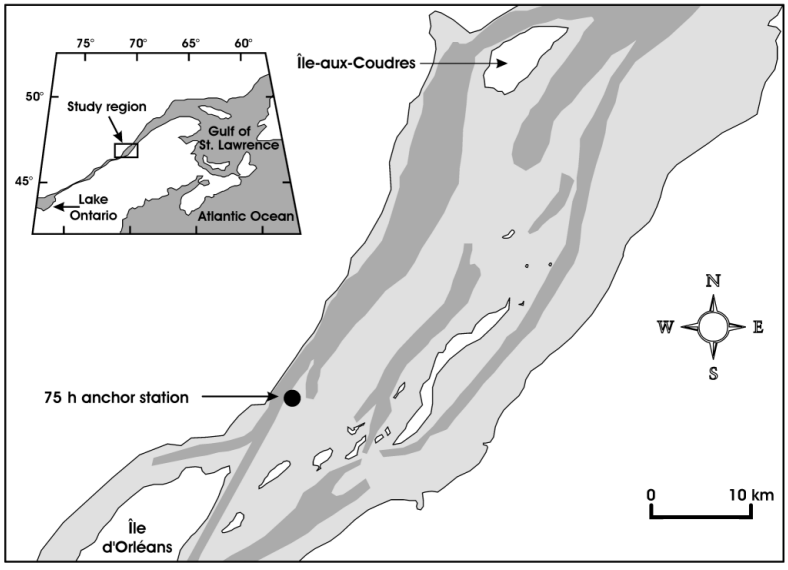

Fig. 1. Map of St. Lawrence middle estuary and location of anchor station sampled for 76.5 h in the northern channel in 1993. Shading indicates regions deeper than 10 m

aged the 2 profiles for each depth layer. Tidal height was measured with a tidal gauge moored at the anchor station during the sampling period.

Turbidity was quantified as dry weight of seston filtered on preweighed Whatman GF/F glass-fiber filters. Subsamples of water for chl *a* determination were prefiltered through a Nitex 200 µm-net and then filtered onto GF/F glass-fiber filters. Chl *a* was extracted and quantified according to the procedures of Bertrand & Vincent (1994).

Subsamples of water for protist enumeration were fixed with 1% glutaraldehyde and 0.1% paraformaldehyde (final concentrations). These samples were examined using the FNU technique (fluorescence, Nomarski interference and Utermöhl sedimentation) as described by Lovejoy et al. (1993). This technique is most appropriate for visualizing plankton in turbid waters. Plankton was enumerated in 2 groups: autotrophs (with chl *a*) >5 µm and heterotrophs (without chl *a*) >5 µm. A total of at least 100 cells was counted in each sample. Cell size was measured for each group of micro-organisms using an eyepiece micrometer calibrated against a stage micrometer. Biovolume was then estimated for each taxon according to its shape. For a more accurate enumeration of microzooplankton (>40 µm; e.g. rotifers, tintinnids), we repeated the microscope examination for 300 to 500 fields at 400× (each field corresponding to a volume of 0.3 to 0.5 ml). It was important to verify the concentration of rotifers in this system because *Keratella* spp. and *Notholca* sp. were observed in mysid guts and were rarely seen in the 63 µm-net samples.

Larval fishes and zooplankton were collected with a 1.5 m^2 Tucker trawl fitted with an opening-closing device. The cod end of the trawl was equipped with 2 nets: a circular 0.56 m^2, 500 µm-mesh plankton net for sampling larval fishes and macrozooplankton and a circular 0.03 m^2, 63 µm-mesh plankton net for sampling copepods, cladocerans and rotifers. A General Oceanics flowmeter attached to each net measured flow rate. During each sampling event, a 7 min tow was conducted in each of the surface, middle and bottom layers at a towing speed of between 2 and 3 knots. The catch of each net was preserved immediately in buffered 4% formalin. The 500 µm-mesh plankton net samples were completely sorted and organisms were identified to calculate the density of fish larvae and zooplankton. Tomcod and smelt larvae were completely enumerated for each sample. Previous studies in the St. Lawrence estuary have revealed a longitudinal gradient in the size of smelt larvae, with larger larvae located further upstream than smaller larvae because of active, tidal stream transport (Laprise & Dodson 1989). Thus, a maximum of 50 smelt larvae were randomly chosen from each sample and measured to the nearest 0.1 mm with a binocular microscope linked to a video camera and image analysis system. The mean length of larvae was used to separate samples into 2 length classes. The density of smelt larvae was subsequently calculated for larvae <17.5 mm (Class L1) and larvae >17.5 mm (Class L2). In the case of mysids and amphipods, numbers were estimated volumetrically in samples containing more than 200 organisms. Densities were expressed per 100 m^3 of filtered water. The abundance of copepods and cladocerans was evaluated from subsamples, and densities were expressed per m^3 of filtered water.

Gut analyzes of tomcod and smelt larvae and mysids were conducted to establish feeding relationships among the zooplankton. The diets of fish larvae have previously been established on 2 separate occasions (Dauvin & Dodson 1990, Laprise 1991). Gut analysis of tomcod juveniles was restricted to the first tidal cycle of the sampling series, when differences in salinity and zooplankton concentrations were greatest. Gut contents were identified in a subsample of larvae sampled during the incoming tide, at high tide and at low tide. Another cruise was conducted in 1994 to get a more complete image of feeding in young-of-the-year smelt over a tidal cycle, but measured in the same water mass.

Gut contents of *Neomysis americana* and *Mysis stenolepis* were documented in 1993 on the incoming and outgoing tide as well as at high tide. No mysids were present at low tide. Stomachs were dissected under low magnification and broken open in a sedimentation chamber. The contents were examined at 100 and 400× magnification under an inverted microscope. As the stomach contents were fragmented, copepods and cladocerans were enumerated by evaluating the number of hard structures clearly diagnostic of the dominant species. The caudal rami of *Eurytemoris affinis* and *Ectinosoma curticorne* were diagnostic, as were the beak and apical spine of cladocerans. As soft-bodied prey could not be assessed and visible stomach contents were fragmented, enumeration of stomach contents is probably biased, but does provide a measure of the relative importance of the dominant zooplankton species.

Statistical analysis. Tidal periodicity, spatial organization and feeding relationship were analyzed as follows.

Tidal periodicity: Periodicity in the abundances of taxa was analyzed using a time-series analysis (Legendre & Legendre 1998). First, long-term trends were calculated for each time series using linear or polynomial (second-degree) regressions (depending on which equation gave the best fit) and removed from the original data to make the time series stationary. We considered the time series to be stationary when there was no significant difference of the intercept from zero. The residual data were then smoothed by an Order 2 unweighted moving average to reduce the white noise. Autocorrelation functions were calculated on the smoothed residuals to determine the periods of observed cyclic fluctuations. We chose this method instead of Schuster's periodogram based on Fourier series, as the latter procedure requires a time series that is at least 10 times longer than the longest hypothesized time period of importance (Legendre & Legendre 1998). The first period of cyclic fluctuation was then removed by constructing a bandpass filter using BMDP statistical software (Thrall & Engelman 1985) and residuals were analyzed for other existing periods. Correlations between the abundances of taxa were analyzed using Spearman partial correlations. Kendall correlations were used to compare biological and physical variables of the 155 samples.

Spatial organization: To describe the temporal structure of planktonic communities relative to physical characteristics of the water masses, multivariate statistical analyzes were carried out using 2 series of 6 biological variables to describe each sample. The first series of variables included the taxa collected with the 63 µm-plankton net (*Eurytemora affinis*, copepodites, nauplii, *Ectinosoma curticorne*, *Cyclops* sp. and *Bosmina longirostris*) and the second series of variables included the taxa collected with the 500 µm plankton net (*Neomysis americana*, *Mysis stenolepis*, *Gammarus tigrinus*, the larvae of tomcod and the 2 length classes of smelt larvae). These variables were used to construct a chi^2 similarity matrix (Legendre & Legendre 1998) for each series of biological variables. Using this measure of association, differences between the most abundant taxa contribute more to the similarity between samples than do differences among the rarer species. The hierarchical agglomerative clustering model of Lance & Williams (1967), as modified by Sneath & Sokal (1973) (weighted arithmetric average clustering [WPGMA] with $\alpha_j = 0.5$, $\alpha_h = 0.5$, $\beta = 0$, $\gamma = 0$) was carried out to group the data into homogenous clusters. The clustering of the samples was then superimposed on their projection in the reduced plane of the first 2 principal coordinates to separate the groups with the same planktonic composition. The principal axes were correlated (Spearman correlation) with the biological variables in order to identify those taxa contributing most to the separation of the groups. Finally, a linear canonical discriminant analysis (SAS system, Legendre & Legendre 1998) was applied to separate the groups on the basis of 4 physical variables; salinity, temperature, seston (mg l^{-1}) and tidal height (m). The average values of these variables, coincident with each biological sample, were calculated for each depth stratum.

Feeding relationships: To treat the hypothesis that losses of phytoplankton along the ETM are due to grazing rather than dilution, we established a linear dilution curve from a mean of peak concentration of chl *a* at low tides and a mean of the lowest chl *a* concentration observed at high tides. This curve was compared with curves fitted to observed declines in chl *a* with salinity using 'regular' and piecewise linear regression with breakpoint analyzes (STATISTICA '99 edn, StatSoft). To calculate the potential grazing effect of *Eurytemora affinis* on algal biomass, we used the carbon requirements for this species as determined by Heinle & Flemer (1975).

Differences in the diet of mysids at flood, high and ebb tide were tested separately for each species with a Kruskal-Wallis ANOVA, followed by a non-parametric multiple post-hoc test (Tukey, after Dunn 1964, cited in Zar 1996). The null hypothesis that there were no differences in diet between *Neomysis americana* and *Mysis stenolepis* was evaluated with a Mann-Whitney *U*-test.

RESULTS

The 76.5 h anchor station straddled the upstream extent of saltwater intrusion and the upstream leading

edge of the turbidity maximum in the middle estuary (Fig. 2). At high slack tide, a maximum salinity of 5.5 psu was observed in the middle and bottom depth strata during the first 12 h of the sampling series, coincident with the spring tide. Thereafter, maximum salinities did not exceed 2 to 3 psu. The water column was slightly stratified during each high slack tide, with a mean gradient between surface and bottom waters at high tide of 1.1 psu. The tidal amplitude was between 4.3 and 5.7 m. Maximum turbidity in the middle and bottom depth strata generally occurred before high and low slack tide, with maximum values approaching 20 mg l^{-1}. Chl *a* measurements and the biovolume estimates of microplanktonic autotrophs peaked at low tides.

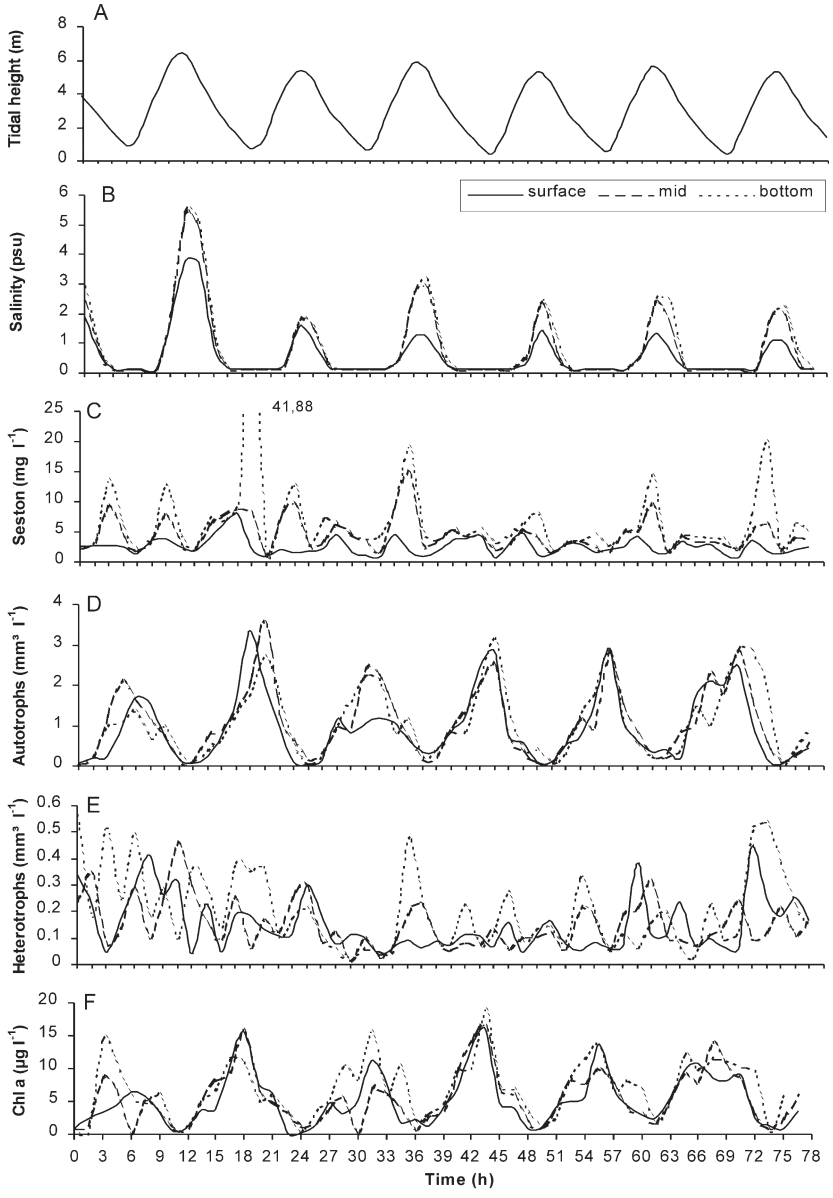

Fig. 2. Physical and biological variables in 3 depth layers at the anchor station over 76.5 h (June 22 to 26). (A) Tidal height, (B) salinity, (C) dry weight seston (D) autotrophic microplankton biovolume, (E) heterotrophic plankton biovolume, (F) chlorophyll *a* concentration

Planktonic community structure

Pooling all samples, 97% of the total protist biovolume was composed of diatoms. The 2 dominant species were *Stephanodiscus binderanus* (average diameter 16 µm) and *Skeletonema subsalsum* (4.5 µm wide, 40 µm long) which contributed 57 and 22%, respectively, of the total diatom biovolume. For the biovolume of heterotrophic microplankton, 39% was composed of tintinnids, 22% of other ciliates measuring 20 to 40 µm, 21% of flagellate measuring 5 to 15 µm, and 11% of ciliates measuring 10 to 20 µm.

Pooling all samples, the 63 µm-net plankton was dominated by *Eurytemora affinis* (27% of total numbers) and *Ectinosoma curticorne* (28%). Nauplii represented 26%, copepodites 17% and *Bosmina longirostris* 1% of the total catch. *Cyclops* sp., *Daphnia* sp. and Ostracods comprised the remaining 1%. The 500 µm-net plankton was dominated by *Neomysis americana* (81% of total numbers). *Mysis stenolepis* represented 11%, *Gammarus tigrinus* 5%, and the larvae of tomcod *Microgadus tomcod* 2% of the total catch. The larvae of smelt (*Osmerus mordax*) comprised the remaining 1%.

Periodicity in abundance of principal taxa

The abundance of all components of the plankton, with the exception of heterotrophic microplankton (Fig. 2E), *Gammarus tigrinus* and *Cyclops* sp. (Figs. 3 & 4) was highly cyclical. Fluctuations in the abundance of autotrophs (Fig. 2D) and *Bosmina longirostris* (Fig. 3) were inversely correlated with fluctuations in the abundance of *Eurytemora affinis* nauplii, copepodites and adults, *Neomysis americana*, *Mysis stenolepis* and the larvae of tomcod and smelt (Figs. 3 & 4, Table 1). These inverse correlations were clearly associated with the tidal cycle (Table 2). The abun-

dance of autotrophs and *B. longirostris* were associated with the warmer freshwaters occurring at low tide, whereas the abundance of *E. affinis* and hence nauplii, copepodites, *N. americana*, *M. stenolepis* and the larvae of tomcod and smelt were associated with the cooler, brackish waters occurring at high tide. Only the harpacticoid copepod *Ectinosoma curticorne* was correlated with the concentration of seston. The abundance of heterotrophic microplankton, *G. tigrinus* and *Cyclops* sp. were weakly or not correlated with any attribute of the tidal cycle. Autocorrelation analyzes confirmed these observations, whereby all plankton species were significatly autocorrelated with a periodicity of 12.6 h (corresponding to the tidal cycle) except for heterotrophic microplankton, *G. tigrinus*, *Cyclops* sp., small smelt larvae and *E. curticorne.* The abundance of the latter was cyclic but of irregular periodicity.

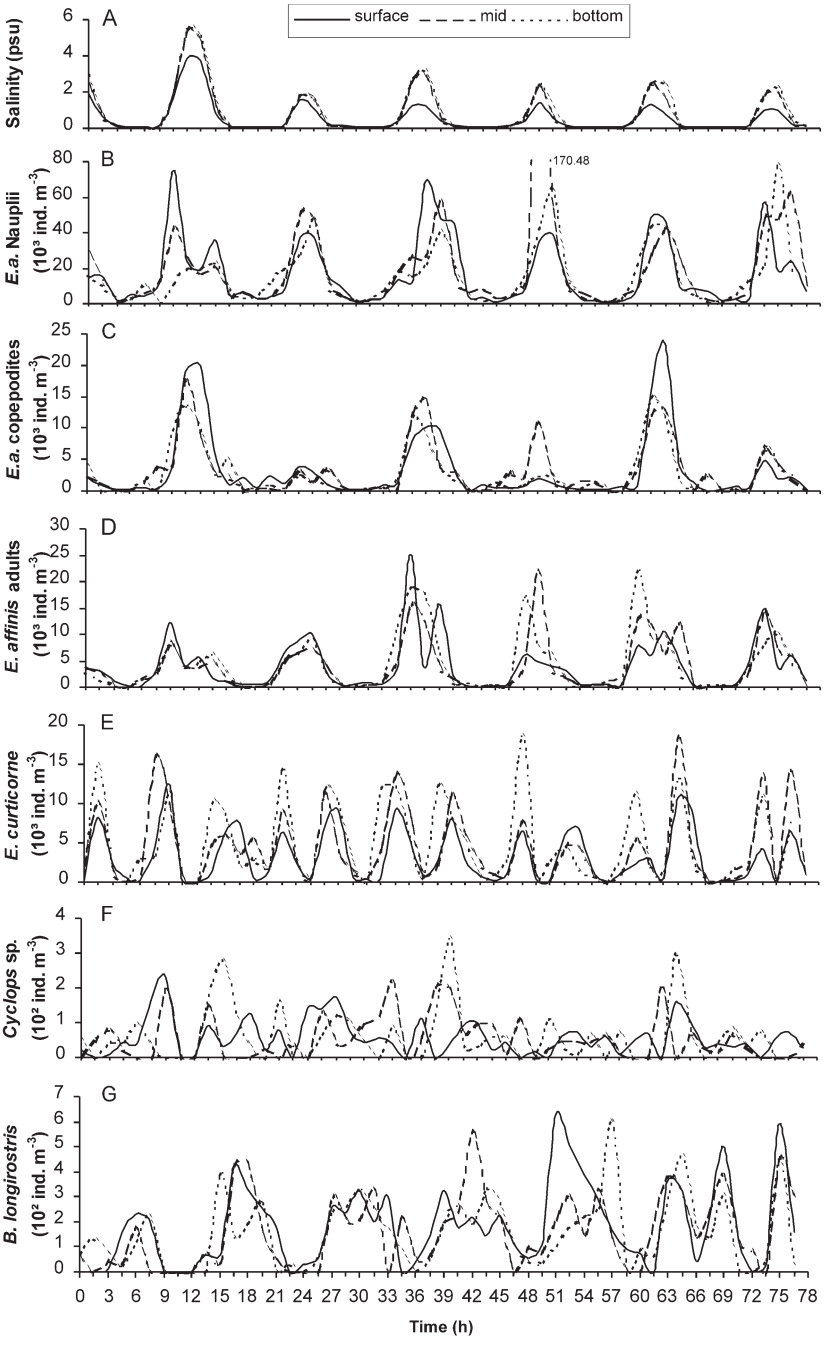

Fig. 3. Temporal series of 63 µm-net plankton organisms in 3 depth layers at the anchor station over 76.5 h (June 22 to 26). (A) Salinity, (B) abundance of *Eurytemora affins* nauplii, (C) abundance of *E. affinis* copepodites, (D) abundance of *E. affinis* adults, (E) abundance of *Ectinosoma curticorne*, (F) abundance of *Cyclops* sp., (G) abundance of *Bosmina longirostris*

Spatial organization of planktonic community

Plankton: 63 µm-net

The clustering of the 155 samples resulted in 3 groups: Group 1 was composed of 54 samples, Group 2 of 90 samples, and Group 3 of only 11 samples. Principal coordinate analysis revealed that 78.5% of the total variance was explained by the 2 first principal axes (Axis 1 = 44.9, Axis 2 = 33.6). The first axis was positively correlated with the density of *Eurytemora affinis*, nauplii and copepodites and negatively correlated with that of *Bosmina longirostris* and *Cyclops* sp. (Table 3), and contributed to separating Group 1 from Groups 2 and 3. The second axis was negatively correlated with the density of *Ectinosoma curticorne* and *Cyclops* sp. but was not positively correlated with any plankton species, and it contributed to separating Group 3 from Groups 1 and 2.

The first function of the discriminant analysis carried out to separate the groups on the basis of the physical characteristics of the environment (Wilk's lambda = −0.38; p = 0.0001) explained 95% of intergroup variance and was correlated with tidal height, salinity and temperature (Table 4).

Plankton: 500 µm-net

The clustering of the 155 samples resulted in 3 groups: Group 1 was com-

posed of 64 samples, Group 2 of 49 samples and Group 3 of 42. Principal coordinate analysis revealed that 88% of the total variance was explained by the 2 first principal axes (Axis 1 = 52.6, Axis 2 = 35.4). The first axis was positively correlated with the density of *Neomysis americana*, *Mysis stenolepis* and the larvae of tomcod and both size classes of smelt, and negatively correlated with that of *Gammarus tigrinus* (Table 3), and contributed to separating the 3 groups. The second axis was negatively correlated with tomcod, and positively correlated with smelt and *G. tigrinus*, and contributed to separating Group 3 from Groups 1 and 2.

The first function of the discriminant analysis carried out to separate the groups on the basis of the physical characteristics of the environment (Wilk's lambda = −0,31; p = 0.0001) explained 97% of intergroup variance and was correlated with depth, salinity and temperature (Table 4).

In summary, temporal variations in the density of the pelagic organisms were clearly associated with the tidal cycle. In the case of 63 µm-net plankton, nauplii, copepodites and *Eurytemora affinis* (Group 1) dominated the highest-salinity water masses occurring at high tides; *Ectinosoma curticorne* (Group 2) was characteristic of the lowest-salinity water masses occurring on the ebb and flood tides and was correlated with seston, whereas *Bosmina longirostris* (Group 3) characterized freshwaters that occurred at low tides (Tables 4 & 5).

In the case of the 500 µm-net plankton, high concentrations of all species except for *Gammarus tigrinus* (Group 1) characterized the water masses of highest salinities occurring at high tides; low densities of mysids and smelt larvae and moderate concentrations of *G. tigrinus* and tomcod larvae (Group 2) characterized water masses of lowest salinities occurring on ebb and flood tides; and low densities of smelt and tomcod larvae and the highest concentrations of *G. tigrinus* (Group 3) characterized freshwaters occurring at low tides (Tables 4 & 5).

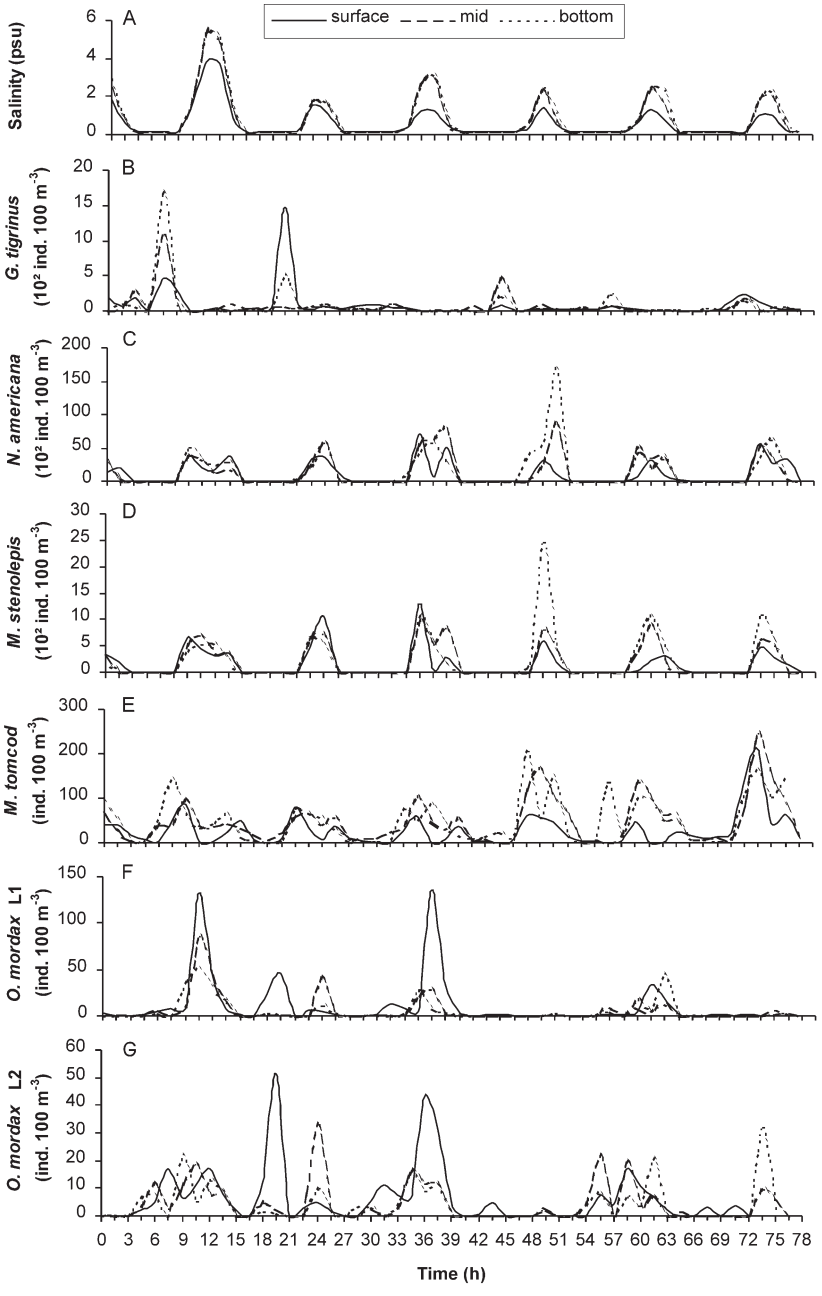

Fig. 4. Temporal series of 500 µm-net plankton organisms in 3 depth layers at the anchor station over 76.5 h (June 22 to 26). (A) Salinity, (B) abundance of *Gammarus tigrinus*, (C) abundance of *Neomysis americana*, (D) abundance of *Mysis stenolepis*, (E) abundance of *Microgadus tomcod*, (F) abundance of *Osmerus mordax* (L1 = small), (G) abundance of *O. mordax* (L2 = large)

Feeding relationships

There was a significant inverse relationship between autotrophic biomass and the abundance of all stages of the dominant copepod *Eurytemora affinis* (Table 2). Chl *a* showed a significant inverse relationship to salinity, while zooplankton (63 µm-net) and mysids were

Table 1. Spearman correlation matrix between biological variables measured over 76.5 h at anchor station in the St. Lawrence estuarine transition zone. *Aut*: autotrophs; *Het*: heterotrophic microplankton; *Naup*: nauplii; *Cop*: copepodites; *E.a*: *Eurytemora affinis*; *E.c*: *Ectinosoma curticorne*; *Cyc*: *Cyclops* sp.; *B.l*: *Bosmina longirostris*; *G.t*: *Gammarus tigrinus*; *N.a*: *Neomysis americana*; *M.s*: *Mysis stenolepis*; *M.t*: *Microgadus tomcod*; *O.m*1: *Osmerus mordax* <17.5 mm, *O.m*2: *O. mordax* >17.5 mm. All shown correlation coefficients are significant ($p < 0.05$); ns: not significant

	Het	*Naup*	*Cop*	*E.a*	*E.c*	*Cyc*	*B.l*	*G.t*	*N.a*	*M.s*	*M.t*	*O.m*1	*O.m*2
Aut	ns	−0.71	−0.70	−0.64	ns	ns	0.52	ns	−0.74	−0.72	−0.45	ns	ns
Het		ns	ns	ns	ns	ns	0.26	ns	ns	ns	ns	ns	ns
Naup			0.73	0.78	0.26	ns	−0.50	−0.31	0.82	0.80	0.57	0.36	0.28
Cop				0.73	ns	ns	−0.42	−0.36	0.75	0.75	0.43	0.54	0.45
E.a					0.29	−0.26	−0.52	ns	0.82	0.83	0.70	0.42	−0.37
E.c						ns	ns	ns	ns	ns	0.37	ns	ns
Cyc							0.26	ns	ns	−0.30	ns	ns	ns
B.l								ns	−0.60	−0.65	−0.40	−0.34	−0.29
G.t									−0.34	−0.30	ns	ns	ns
N.a										0.95	0.56	0.45	0.39
M.s											0.57	0.46	0.39
M.t												ns	ns
*Om*1													0.95

Table 2. Kendall correlation coefficients between biological and physical variables of 155 samples collected at leading edge of St. Lawrence estuarine transition zone in 1993. ns: not significant; ***$p < 0.001$.

Biological variables	Salinity (psu)	Tide level (m)	Temperature (°C)	Seston (mg l^{-1})
Autotrophs	−0.77***	−0.65***	0.49***	ns
Heterotrophic microplankton	ns	ns	ns	ns
Chlorophyll *a*	−0.51***	−0.67***	0.40***	ns
Eurytemora affinis	0.83***	0.87***	−0.59***	ns
Ectinosoma curticorne	ns	ns	ns	0.52***
Cyclops sp.	−0.27***	−0.26***	ns	ns
Zooplankton (63 µm-net sample)	0.51***	0.73***	−0.37***	ns
Gammarus tigrinus	−0.28***	ns	0.26***	ns
Mysids	0.55***	0.73***	−0.45***	ns

positively correlated with salinity (Table 2, Fig. 5). The decline in chl *a* was steep in all layers and showed a good fit, with an exponential function that explained 57 to 70% of the variance. The values deviated substantially from the linear curves (R^2 only = 0.26 to 0.37) that would describe the dilution of a conservative property. This deviation was further confirmed by a piecewise linear regression with breakpoint analysis that gave the best fit; chl *a* declined by a factor of 2 at salinities of 0.23 and 0.24 psu in the surface and the mid-water layers, respectively. For example, in the surface layer the equations were: chl $a = 14.78 - 42.12 \times$ salinity (chl $a > 5.2$ mg m^{-3} and salinity < 0.23 psu); chl $a = 3.56 - 1.05 \times$ salinity (chl $a < 5.2$ mg m^{-3} and salinity > 0.23 psu). In the bottom layer the patterns were less obvious and the breakpoint was at 3 psu. This implies that the phytoplankton produced *in situ* and advected from the upstream freshwater section of the river provided a major food supply for the zooplankton in the upstream section of the ETM.

Neomysis americana, *Mysis stenolepis*, and the larvae of tomcod consumed mainly *Eurytemora affinis* (Fig. 6). Both mysid species exploit a wide variety of foods and feed on the same plankton taxa, but significant differences were found in numbers and at different tidal states (Table 6). The diet of *M. stenolepis* was characterized by *E. affinis*, *Ectinosoma curticorne* and diatoms as the most important food items, while *Bosmina longirostris*, rotifers and pollen were less abundant. *N. americana* showed a more balanced diet in terms of abundance of food items; only diatoms

Table 3. Spearman correlation coefficients between biological variables and first 2 principal axes (C1, C2) of principal coordinate analyzes of the 155 samples. L1, L2: 2 length classes (<17.5 and > 17.5 mm, respectively) of smelt larvae. ***$p < 0.001$; **$p < 0.01$; ns: not significant

Biological variables	C1	C2
63 µm-net plankton		
Nauplii	0.83***	ns
Copepodites	0.75***	ns
Eurytemora affinis	0.86***	ns
Ectinosoma curticorne	ns	−0.83***
Cyclops sp.	−0.30***	−0.20**
Bosmina longirostris	−0.66***	ns
500 µm-net plankton		
Neomysis americana	0.88**	ns
Mysis stenolepis	0.86***	ns
Microgadus tomcod	0.54	−0.47***
Osmerus mordax L1	0.46***	0.29***
O. mordax L2	0.38***	0.32
Gammarus tigrinus	−0.58***	0.39***

Table 4. Means and (standard deviations) for physical variables characterizing the 3 sample groups (Groups 1, 2 and 3) for 2 categories of organisms (63 and 500 µm-net plankton) and their contribution (standardized canonical coefficients) to the formation of the first canonical axis (FCA). Percentage of samples of each group correctly classified in their group of origin is also indicated (% class)

Variable	Group 1	Group 2	Group 3	FCA
63 µm-net plankton				
Salinity (psu)	1.8 (1.4)	0.3 (0.3)	0.1 (0.0)	0.86
Temperature (°C)	17.4 (0.8)	18.2 (0.2)	18.3 (0.3)	−0.79
Depth (m)	11 (1.1)	8.6 (1.3)	7.4 (0.7)	0.95
Seston (mg l^{-1})	43 (40)	48 (30)	23 (11)	−0.07
% class	82	61	100	
500 µm-net plankton				
Salinity (psu)	1.7 (1.3)	0.2 (0.2)	0.1 (0.0)	0.81
Temperature (°C)	17.4 (0.8)	18.2 (0.2)	18.2 (0.2)	−0.73
Depth (m)	10.9 (1.0)	8.7 (1.3)	7.7 (0.8)	0.98
Seston (mg l^{-1})	48 (43)	45 (18)	39 (33)	0.13
% class	81	61	69	

Table 5. Mean density and (standard deviation) of 63 µm-net plankton m^{-3} and 500 µm-net plankton 100 m^{-3} of the 3 groups of samples revealed by principal coordinate analyzes. L1, L2: 2 length classes (<17.5 and >17.5 mm, respectively) of smelt larvae

Species	Group 1	Group 2	Group 3
63 µm-net plankton			
Nauplii	10416 (11243)	576 (843)	56 (65)
Copepodites	6256 (5795)	588 (590)	299 (241)
Eurytemora affinis	8048 (5560)	2208 (3166)	620 (305)
Ectinosoma curticorne	2556 (3138)	5595 (4886)	261 (184)
Cyclops sp.	39 (62)	68 (68)	40 (20)
Bosmina longirostris	62 (97)	211 (148)	301 (93)
500 µm-net plankton			
Neomysis americana	3494 (2654)	0.5 (1.4)	0 (0)
Mysis stenolepis	477 (407)	0.3 (1.0)	0 (0)
Microgadus tomcod	68 (53)	39 (41)	9 (13)
Osmerus mordax L1	16 (28)	0.6 (1.4)	3 (8)
O. mordax L2	8 (9)	1 (2)	4 (9)
Gammarus tigrinus	32 (36)	42 (57)	194 (362)

were present in higher numbers in its diet during flood tide. Comparing the 2 mysid species, *M. stenolepis* had significantly higher numbers of *Eurytemora affinis* in its stomach than *N. americana*, while the opposite was true for much smaller prey such as rotifers and pollen (Mann-Whitney *U*-test, $p < 0.05$). *Ectinsoma curticorne* (12 to 15%) and *B. longirostris* (11 to 12%) were a significant component of the diet of mysids but were rare or absent from the diets of tomcod and smelt larvae, respectively. There were no differences in abundance of the cladocerean *B. longirostris* in the stomachs of the 2 mysid species. Differences in abundance of *E. curticorne*, diatoms and pollen in the stomachs of the 2 mysids occured only during certain tidal states. *M. stenolepis* consumed significantly more harpacticoids during flood tide than *N. americana*, while no significant differences were found during high and ebb tides (Mann-Whitney *U*-test, $p < 0.05$). For diatoms, significant differences were seen at ebb tide, when *M. stenolepis* consumed more than *N. americana*. The numbers of diatoms in the stomachs showed the same decline in abundance on high tide as in the corresponding water samples. The most abundant component of the zooplankton, the copepod nauplii, were not found in any of the gut contents. In contrast, rotifers did occur in the stomachs, but a total of only 6 rotifers as observed in 5 of the 155 water samples. The highest incidence of copepods was in the stomachs of tomcod. In contrast, the incidence of copepods was surprisingly low in guts of smelt larvae relative to previous observations (Dauvin & Dodson 1990). Among the 546 smelt larvae (mean length of 20.0 ± 3.3 mm) sampled in June of 1994 at a mean surface salinity of 1.1 psu, *E. affinis* was the only prey consumed, but was found in only 43.6% of stomachs, with an average of 1.5 prey items per stomach (SD = 2.2), whereas tomcod exploited a wider prey spectrum by feeding on *N. americana* and *Gammarus tigrinus* also.

DISCUSSION

Periodicity and spatial organization

The temporal distribution of the plankton groups at the leading edge of the St. Lawrence River ETM was directly associated with the salinity of the water masses which, in turn, was a function of the tidal cycle. Autotrophs and chl *a* showed a significant inverse correlation with salinity and water level, whereas heterotrophs maintained similar densities. Similar relations were found in the San Francisco Bay estuary for phytoplankton and bacterioplankton (Hollibaugh & Wong 1999). Although the strong correlation between salinity and chl *a* indicates that physical processes are important in controlling phytoplankton distribution, the exponential shape of the chl *a* decline implies that other factors are also involved. Vincent et al. (1996) previously demonstrated that the decline in autotrophic biomass at the leading edge of the ETM was not associated with a decline in physiological condition potentially caused by light limitation or osmotic stress, as had been previously hypothesized (Ther-riault et al. 1990). In the present study, variations in autotrophic biomass were

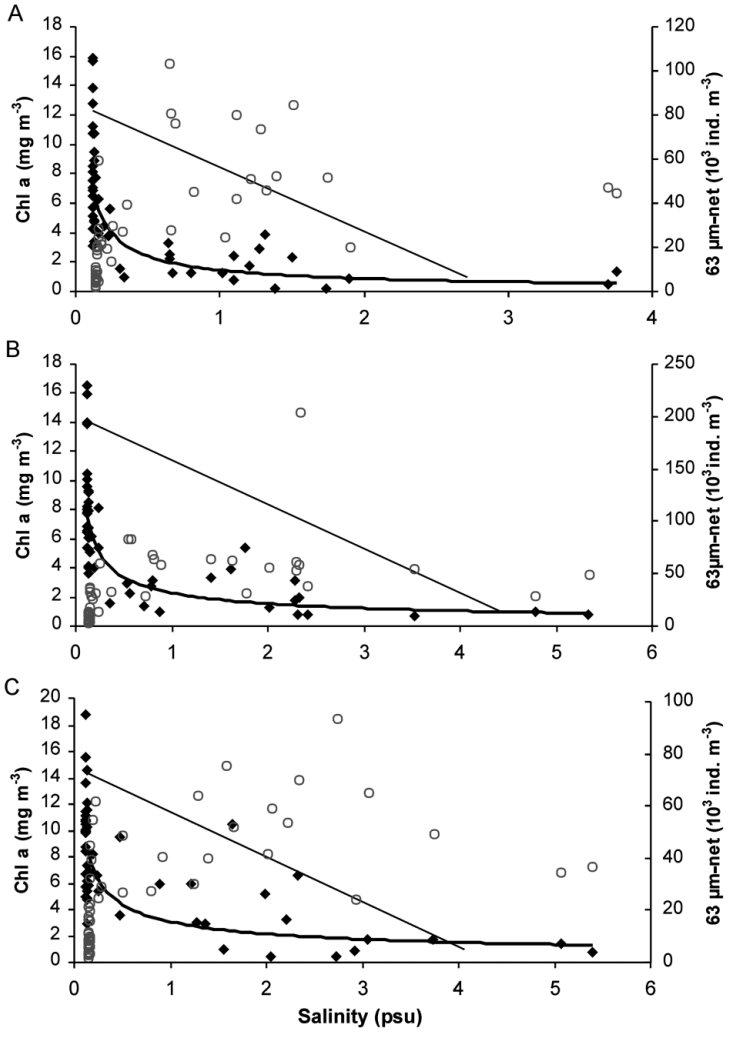

Fig. 5. Chlorophyll *a* (♦) and 63 µm-net plankton abundance (○) as a function of salinity in 3 depth layers. Thin line: conservative linear dilution curve; thick line: best fit to decline in chl *a* concentration. (A) surface layer R^2 = 0.65, (B) middle layer R^2 = 0.70, (C) bottom layer R^2 = 0.57

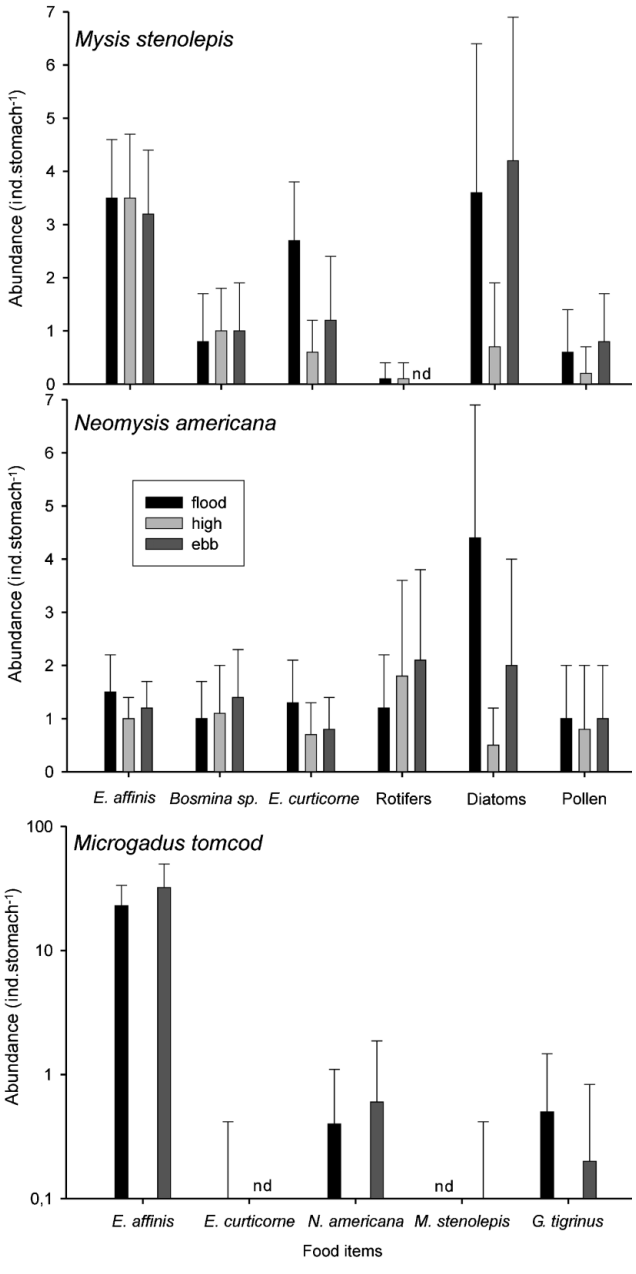

Fig. 6. Stomach contents of 2 mysid species, *Neomysis americana* and *Mysis stenolepis*, and of tomcod larvae *Microgadus tomcod*. Logarithmic scale used for stomach content of *M. tomcod*. nd: not detected

not correlated with seston concentrations and, hence, do not appear to be related to light conditions. Although inversely correlated with salinity, autotrophic biovolume and chl *a* began declining before the arrival of saline water masses at the sampling station (Fig. 2). The major loss in chl *a* was seen between 0 and 0.24 psu in the surface and mid-water column. In the bottom layer, the chl *a* values were much more variable, with higher salinities due to resuspension from the sediment during high ebb and flood currents. Zooplankton grazing is likely to be the primary cause of the decline in chl *a*, and is examined in more detail in the following subsection on food-web structure.

The zooplanktonic communities associated with low and high tides seen in 1993 were identical to the tidal freshwater and true-estuarine communities, respectively, previously described by Laprise & Dodson (1994) based on the 1987 sampling of the middle estuary. These observations thus confirm the annual stability of zooplankton structure throughout the transition zone, and illustrate the importance of tidal advection. However, during the greatest current speeds during both tidal states, concentrations of suspended particulate matter and high densities of the harpacticoid copepod *Ectino-*

Table 6. *Mysis stenolepis* and *Neomysis americana*. Comparison of food items in stomachs during different tidal states. Kruskal-Wallis rang ANOVA; post-hoc test Tukey-type after Dunn (1964) cited in Zar (1996); $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; ns: not significant

Predator Food item	Kruskal-Wallis ANOVA *H*	Post-hoc test Tukey-type Contrast	 *Q*
M. stenolepis			
Eurytemora affins	1.66 ns		
Ectinosoma curticorne	34.22 ***	flood—high	9.07***
		flood—ebb	6.39
		high—ebb	2.68
Bosmina longirostris	1.22 ns		
Rotifers	2.96 ns		
Diatoms	28.06 ***	flood—high	6.63***
		flood—ebb	1.34 ns
		high—ebb	7.97***
Pollen	7.76 *	flood—high	2.74*
		flood—ebb	1.19 ns
		high—ebb	3.92***
N. americana			
Eurytemora affins	8.205 **	flood—high	3.7 ***
		flood—ebb	1.5 ns
		high—ebb	2.1 ns
Ectinosoma curticorne	9.492 **	flood—high	4.42 ***
		flood—ebb	3.35 **
		high—ebb	1.08 ns
Bosmina longirostris	4.118 ns		
Rotifer	3.416 ns		
Diatoms	38.04 ***	flood—high	9.94 ***
		flood—ebb	5.16 ***
		high—ebb	4.78 ***
Pollen	1.184 ns		

soma curticorne increased in the water column as a result of bottom scouring and resuspension. This defined the third zooplankton assemblage seen in this study. The distribution of *E. curticorne* observed in this study is identical to that of another harpacticoid copepod, *Coullana canadensis*, observed in the Columbia River ETM (Morgan et al. 1997). Densities of these 2 copepod species mirrored those of turbidity, suggesting that in both estuaries the harpacticoid copepod populations are retained by the same near-bottom circulation that traps particulate matter in the ETM. This suggests a passive population-maintenance strategy for *E. curticorne*. In contrast, we did not see similar distribution patterns or any correlation with seston for *Eurytemora affinis*. The distribution of *E. affinis* observed in the St. Lawrence estuary and elsewhere confirms that the maximum abundance of *E. affinis* is associated with the ETM (Laprise & Dodson 1989, 1994, Simenstad et al. 1994), and the 2 psu isohaline (Jassby et al. 1995, Kimmerer et al. 1998). However, no differences in vertical distribution were found in the present study. Thus there is no evidence of vertical migration by this species as a strategy to minimize downstream transport, in contrast to reports for the Columbia River ETM (Morgan et al. 1997), the Conwy estuary (Hough & Naylor 1991) and the Seine estuary (Mouny 1998). Our observations are, however, consistent with those of other authors who found equal abundances of *Eurytemora* sp. in the water column (Girond estuary: Castel & Veiga 1990; Chesapeake Bay: Roman et al. 2001; San Francisco estuary: Kimmerer et al. 1998). These authors all proposed that the migration capacity of this species is insufficient for effective displacement against the direction of general circulation. The occurrence of several estuarine *Neomysis* species in ETMs and low-salinity waters (< 5 psu) is associated with the interaction between vertical distribution and estuarine circulation (*N. americana*: Hulburt 1957, Siegfried et al. 1979, Orsi 1986). Finally, the larvae of rainbow smelt are retained in the St. Lawrence ETM by tidal stream transport (Laprise & Dodson 1989), whereas tomcod in the same estuary are retained by remaining in the deep, upstream, residual circulation (Laprise & Dodson 1990).

The observed discontinuity in the relative proportions of autotrophs and heterotrophs along the leading edge of the transition zone is due to a variety of mechanisms. Physical retention associated with prolonged hydraulic residence time, estuarine recirculation and tidal stream transport retain advected and autochthonous phytoplankton as well as brackish water zooplankton dominated by *Eurytemora affinis* and *Neomysis americana*. Pace et al. (1992) showed that increasing hydraulic residence time across rivers to estuaries to lakes is accompanied by a trend of increasing zooplankton biomass across these habitats. The shift to a heterotrophic-dominated community probably occurs because of large standing stocks of zooplankton across the saltwater-freshwater edge that graze down the phytoplankton in this region.

Food web structure

Heterotrophic species were a small component (< 20 %) of the total protists in the freshwater samples, but dominated the total community biomass at higher salinities. This community showed no significant relationship with zooplankton biomass, suggesting that these species were little grazed relative to the autotrophs, or that their growth rates were able to keep pace with grazing losses. The shift in protist community structure from autotroph to heterotroph dominance underscores the hydrodynamic coupling between upstream producer and downstream consumer processes.

Effect of grazing

The inverse relationship between the abundance of the 63 µm-net plankton and the biovolume of autotrophs and chl *a* illustrates the impact of zooplankton grazing on autotrophic biomass, which was largely composed of diatoms. Within the 63 µm-net plankton, nauplii, copepodites and adult *Eurytemora affinis* appear to be the most important grazers of autotrophs as seen in various estuaries elsewhere (Heinle & Flemer 1975, Burkill & Kendrall 1982, Peitsch 1995). Copepods are known to feed heavily on diatoms, the dominant phytoplankton group in our study, and phytoplankton is known to be the more nutritious food source compared to detritus and bacteria (Mayzaud et al. 1992, Mauchline 1996, Lehman 2000, Thoumelin et al. 2000). Some simple calculations illustrate that the primary production observed in the ETM is capable of supporting the biomass of this copepod, and that the grazing pressure is capable of significantly reducing autotrophic biomass. The major inputs of phytoplankton biomass to the water column of the ETM are *in situ* primary production and the advection of phytoplankton from upstream. Based on the measurements and calculations provided by Vincent et al. (1996), we can calculate these inputs for a 10 nautical mile section of the middle estuary downstream of Île d'Orléans (Fig. 1), a region that encompasses the greater part of the ETM. In July, at water temperatures of approximately 20°C, *in situ* production is 412 mg C m^{-2} d^{-1}, representing 187 t C d^{-1}. Net advective transport (input minus output) contributes an additional 86 t of algal C d^{-1} (Vincent et al. 1996). Thus, 273 t of algal carbon are lost from the ETM on a daily basis. Respiration losses must be incorporated in these calculations, because phytoplankton production was measured during daytime (continuous light) incubations and was not corrected for nighttime respiration (Vincent et al. 1996). However, respiratory correction to obtain net primary production remains a major source of uncertainty in turbid systems. If we adopt Kromkamp & Peene's (1995) estimate that respiratory losses represent 1.5% of the maximum photosynthetic rate (P_{max}) in turbid waters then this represents 34 t C d^{-1}, leaving approximately 239 t of algal C d^{-1} lost through grazing, sedimentation and other loss processes such as cellular lysis. The latter factor is unlikely to play a major role in the decline of chl *a*, given the absence of any evidence of physiological stress (Vincent et al 1996).

The proportion of algal carbon grazed by the standing stock of *Eurytemora affinis* observed in the ETM can be roughly estimated from the carbon requirements calculated for *E. affinis* in the Patuxent River estuary (Maryland) by Heinle & Flemer (1975). The average total concentration of nauplii, copepodites and adult *E. affinis* in the ETM in late June is approximately 25 000 m^{-3}, based on the concentrations observed in Group 1 (Table 4). The carbon-specific ingestion rate of this copepod is 8.10^{-2} kg (kg body $carbon^{-1}$ d^{-1}). Based on an average individual dry weight of 8.1 µg and assuming that carbon content is 50% of dry weight, the ETM *E. affinis* population consumes 17 t of algal C d^{-1} to maintain its biomass, and another 33 t of algal C d^{-1} to meet egg production (based on a ratio of egg biomass produced per day to female biomass of 0.03: Heinle & Flemer 1975). Thus, the *E. affinis* population consumes approximately 50 t algal C d^{-1} in late June and early July, representing about 20% of the net algal production in the ETM, or about 38% of the net advective loss of phytoplankton biomass across the region. If algal respiration rates achieve higher values (for example they are often approximated to represent 5% of P_{max} in the oceanic systems), then the consumption by *E. affinis* grazing could represent an even more substantial fraction of net algal production. Although only first-order estimates, these calculations illustrate the potential impact of copepod grazing on phytoplankton biomass in the ETM. Furthermore, our calculations represent a lower boundary of the total grazing pressure, given that they are for only 1 zooplankton taxon. Other taxa such as *Ectinosoma curticorne* and *Neomysis americana* will contribute to the overall grazing impact; however we lack appropriate data to extend our calculations to these populations. Our values for *E. affinis* are of a similar magnitude to the estimates of grazing impacts of estuarine copepods on phytoplankton biomass in the Newport River estuary, North Carolina (Stearns et al. 1987). In addition to phytoplankton, *E. affinis* is known to feed on detrital particles enriched with bacteria and ciliates (Heinle et al. 1977), which may affect phytoplankton ingestion. Studies of the *in situ* grazing of *E. affinis* in the Gironde Estuary have shown that the concentration of suspended particulate matter had no effect on phytoplankton ingestion in this species (Irigoien et al. 1993). Several studies which support our hypothesis have shown that microzooplankton herbivory represents from 50 to 80% of potential phytoplankton primary production and is an important sink for estuarine phytoplankton production (McManus & Ederington 1992, Froneman & McQuaid 1997, Ruiz et al. 1998, Lehrter et al. 1999).

Benthic communities may also play a role in diminishing phytoplankton concentration, as seen in the San Francisco Bay estuary, where the Asian clam *Potamocorbula amurensis* is responsible for an overall decline in chl *a* in the area (Alpine & Cloern 1992). In the St. Lawrence transition zone, mussel abundances (mainly the introduced zebra mussel *Dreissena polymorpha*) were too low to suggest a major effect of benthic grazing on phytoplankton (A. Casper, Department of Biology, Université Laval, unpubl. data).

Feeding relationships at higher trophic levels

Gut analysis demonstrated that larval fishes and mysids are important predators of adult *Eurytemora affinis*. The studies of Dauvin & Dodson (1990) and Laprise (1991) also demonstrated the preponderance of *E. affinis* in the gut contents of larval fishes. In the case of smelt, Sirois & Dodson (2000) calculated an ingestion rate of 30 µg prey dry wt per 100 µg larva dry wt d^{-1} for larvae measuring on average 20 mm and weighing 1.5 mg. Given the densities of 24 smelt larvae 100 m^{-3} observed in Group 1, the larval smelt population ingests approximately 14 adult copepods m^{-3} d^{-1} or a trivial 0.0017% of adult copepod standing stock on a daily basis. Although the ingestion rates of tomcod larvae are unknown, the combined ingestion rate of the 2 species are unlikely to have any impact on copepod standing stocks. This would be the case even if the larval fish concentrations in the ETM were to increase by an order of magnitude. Thus on average, larval fishes have little impact on copepod dynamics in the St. Lawrence middle estuary.

By far the most important predators of the zooplankton are the mysids. Most mysids prey on all sizes of rotifers, cladocerans and copepods (Hanazato 1990). However, we are unaware of any published rates of ingestion of *Eurytemora affinis* or *Bosmina longirostris* by *Neomysis americana* and *Mysis stenolepis*. Freshwater mysids are known to be voracious predators of zooplankton. For example, the introduction of *M. relicta* to lakes to improve salmonid fisheries is often accompanied by major declines in cladocerans (including *B. longirostris*) and sometimes also copepods (Spencer et al. 1991). Cladocera are typically eaten in preference to copepods and nauplii probably due to differences in their escape behavior (Cooper & Goldman 1980, Murtaugh 1981a, Bowers & Vanderploeg 1982, Grossnickle 1982). The inverse relationship between the abundance of *B. longirostris* and mysids and the occurrence of the former in the stomachs of both mysids observed in this study may reflect this predation pressure. On a seasonal time scale, the abundance of *B. longirostris* in the St. Lawrence ETM declined from early June to late July 1987 by 1 order of magnitude, possibly reflecting predation pressure (Laprise & Dodson 1994).

Predation rates of *Neomysis americana* on various copepod species other than *Eurytemora affinis* vary between 30 to 40 prey $mysid^{-1}$ d^{-1} at densities of 50 prey l^{-1} (Fulton 1982). The predation rates of *N. integer* (measuring between 2 and 17 mm) on all stages of *E. affinis* vary from 6 to 52 prey $mysid^{-1}$ d^{-1}, depending on development stage and prey density (Aaser et al. 1995). Predation rates of *Mysis stenolepis* are unknown, but given the large size of this mysid (range = 15 to 35 mm; mean = 23.2 mm; SD = 5.44; n = 25 in June in the St. Lawrence estuary), it is probably a major predator of adult copepods. Stomach-content analysis suggests that *M. stenolepis* feeds more efficiently on *E. affinis* than does *N. americana*, the latter showing a more homogenous distribution of various prey. Despite the predatory potential of mysids, their abundance was positively correlated with that of *E. affinis*, demonstrating that predation pressure was not sufficient to reduce prey numbers at the time of sampling. Irvine et al. (1993) argued that there was no control of the population of *E. affinis* by *N. integer* because of rapid reproduction by the copepod. However, seasonal patterns in the abundance of zooplankton in the St. Lawrence estuary do suggest such a predator-prey relationship (Laprise & Dodson 1994). Laprise & Dodson reported that in 1987 the abundance of *E. affinis* was reduced by 72% at the end of July compared to previous abundances in early June. In contrast, *N. americana* was 2.5 times more abundant at the end of July than at the beginning of June. *M. stenolepis* diminished in abundance over the same time period, and thus did not follow the same pattern as *N. americana*. The magnitude of the impact of mysid predation on zooplankton prey can only be assessed after determining the production rates *in situ* of both prey and predator.

Conclusions

In summary, hydrodynamic processes within the St. Lawrence ETM appear to promote both passive and active mechanisms of estuarine retention of zooplankton as well of early life-history stages of fishes, and to control the high production and availability of their food resources. Phytoplankton biomass entering the region by advection and by *in situ* photosynthetic production appears to play an important role as a direct carbon and energy source for the micro- and mesocrustaceans. These crustacean populations are in turn the food supply for mysids and fish larvae. These findings support the revised riverine productivity model (Thorp & Delong 2002) that emphasizes the overriding importance of autochthonous carbon for supporting metazoan production, even within so-called heterotrophic ecosystems. In the St. Lawrence River, and probably in many estuaries elsewhere, the populations of primary producers, herbivores and planktivores are longitudinally organized across the frontal gradient of the freshwater-saltwater transition zone. This pronounced gradient of communities ensures a strong spatial coupling between upstream autotrophic production and downstream trophic processes that ultimately sustain the region as an important nursery site for larval fishes.

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