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Relationship between feeding incidence and vertical and longitudinal distribution of rainbow smelt larvae (*Osmerus mordax*) in a turbid well-mixed estuary*

Jean-Claude Dauvin, Julian J. Dodson*****

Département de biologie, Université Laval, Ste-Foy, Quebec, Canada G1K 7P4

ABSTRACT: We tested the hypothesis that the active vertical migration of the larvae of anadromous rainbow smelt (*Osmerus mordax*) observed in the turbid, well-mixed portion of the St. Lawrence Estuary is an adaptation to improve feeding incidence by retaining larvae in productive, up-estuary waters. We documented the vertical distribution, diet and feeding incidence of larvae of 3 length classes over 4 tidal cycles at each of 3 stations located along the longitudinal axis of the upstream portion of the estuary. The percentage of smelt larvae with gut contents increased with larval length and with distance upstream for all 3 length classes. Vertical migrations of larvae were not related to feeding incidence in the vertical plane, except in the case of the smallest length class, indicating that active vertical migrations were not behavioral responses to vertical changes in prey availability. The predominance of calanoid copepods and freshwater cladocerans in the diets of larvae with the highest feeding frequencies and the predominance of mysids in the diets of larvae with the lowest feeding frequencies suggested that larvae were more successful feeding on copepods and cladocerans than on the larger mysids. Apparent tidal rhythmicity in diet and feeding success was largely due to the tidal displacement of water masses at fixed sampling stations. Feeding incidence at the 2 sampling stations situated within the maximum turbidity zone was greatest in larvae advected from upstream at the end of ebbing tide. We conclude that active vertical migration of smelt larvae is an adaptation to maximize the longitudinal retention of high densities of larvae in a zone of high prey biomass.

INTRODUCTION

The objective of this paper is to examine the relationship between vertical migration, estuarine retention and the feeding success of the pelagic larvae of anadromous rainbow smelt *Osmerus mordax* (Mitchill). The adaptive significance of retention of pelagic larvae in estuaries may be viewed as involving 2 ecologically distinct processes (Sinclair 1988); so-called 'energetic' processes involving favourable predator and prey conditions that contribute to improving early growth and survival (e.g. Leggett 1985) and 'spatial' processes involving sufficient larval retention to permit population persistence. The selective use of circulation to achieve landward penetration and retention in highly productive waters is well documented for a variety of aquatic organisms (Miller et al. 1985, Kimmerer & McKinnon 1987, Boehlert & Mundy 1988). In the case of smelt larvae that hatch during the latter half of May in the small rivers located along the south shore of the St. Lawrence Estuary, their subsequent distribution and retention in the St. Lawrence Estuary is related to the maintenance of other planktonic organisms in a maximum turbidity zone. This zone is a well-mixed and tidally energetic area where the concentration of suspended material is higher than in areas landward or seaward and where high densities of both micro- and macrozooplankton occur (Bousfield et al. 1975, Dodson et al. 1989). These observations suggest that the retention of smelt larvae in the maximum turbidity zone may represent an adaptation permitting the early life history stages of smelt to exploit the abundant food resources

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** Present address: Station Biologique, C.N.R.S. LP 4601 et Univ. P. et M. Curie (Paris VI), F-29211 Roscoff, France

*** Addressee for correspondence and reprint requests

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of the area. Turbid waters may also offer the advantage of refuge from predation (Bruton 1985).

Most mechanisms proposed to explain retention in well-mixed estuaries despite the net outflow of water involve some form of selective tidal stream transport whereby organisms occupy surface waters during flooding tides and deep waters during ebbing tides to minimize net downstream displacement. For example, active vertical migrations in response to tidal flow resulting in retention have been demonstrated for larvae of the crab *Rhithropanopeus harrisii* (Cronin & Forward 1979) and rainbow smelt larvae (Laprise & Dodson 1989). However, not all observations of vertical migration in the context of estuarine retention are interpreted as active responses to changes in tidal flow. In the case of Atlantic herring *Clupea harengus* larvae retained in the partially mixed section of the St. Lawrence Estuary, Fortier & Leggett (1983) concluded that the semi-diurnal vertical migrations of herring larvae were neither active responses to changes in tidal flow nor passive responses to vertical mixing, but rather behavioral responses to changes in the vertical distribution of their prey. Thus, 2 interpretations of the proximate function of vertical migrations as adaptations to estuarine retention are possible: (a) they are active (or passive) responses to changes in tidal flow that function to control the longitudinal position of larvae in relation to favourable prey conditions, or (b) they are immediate responses to changes in the vertical distribution of prey items. These 2 hypotheses are not mutually exclusive, however, as similarity in the vertical distribution of predators and their prey in a layered circulation will result in similarity in the longitudinal distribution of the 2 groups.

The retention of larval smelt in the turbid well-mixed upper estuary of the St. Lawrence River is achieved by active tidal vertical migrations (Laprise & Dodson 1989). Young larvae sampled in June 1986 (average length 12.6 mm) concentrated at the surface during floods and appeared to passively sink and disperse throughout the water column after the flooding tides attained maximum speed. Older larvae sampled in July (average length 22.6 mm) exhibited greater amplitudes of vertical migration, concentrating at the surface during floods and also concentrating closer to the bottom during ebbs. Thus, older larvae use currents more efficently as reflected by their average longitudinal position in the estuary, which is farther upstream in July than in June, and by the differential larval size distribution along the estuary, larger larvae being located further upstream than smaller larvae in July (Dodson et al. 1989, Laprise & Dodson 1989). Passive vertical transport was not responsible for the observed vertical migrations as larvae concentrated in surface and bottom layers when mixing of the water column was maximal (Laprise & Dodson 1989).

Potential food for larvae in the form of micro- and macrozooplankton is particularly abundant in the maximum turbidity zone. The density of copepods and that of *Neomysis americana*, the principal macrozooplanktonic species of the turbidity zone, are respectively 10 and 100 times greater within the turbidity zone (mean 220 000 copepods per 100 m^3; 2330 mysids per 100 m^3) than at its downstream limit (Bousfield et al. 1975, Dodson et al. 1989). In addition, Laprise & Dodson (1989) recorded a growth rate of smelt larvae of 0.33 mm d^{-1} within the turbidity zone as compared to growth rates varying from 0.10 to 0.24 mm d^{-1} reported by previous studies at the same time of year downstream of the turbidity zone (Simoneau 1986), suggesting improved growth within the turbidity zone.

Observations of prey density, larval growth and the up-estuary movement of larvae during the retention period led us to hypothesize that the active vertical migration of smelt larvae is an adaptation permitting improved feeding in productive up-estuary waters. Given the shallowness and well-mixed nature of this part of the estuary, we also proposed that feeding success would not be dependent on the vertical position of larvae in the water column such that vertical migration could not be interpreted as a behavioral response to changes in the vertical position of prey. As tidal advection of water masses cause variations in larval smelt abundance and in zooplankton species composition at fixed stations in the St. Lawrence Middle Estuary (Dodson et al. 1989, Laprise & Dodson 1989), we also proposed that feeding incidence and prey types in gut contents of smelt larvae would be influenced by tidal advection. In order to test these hypotheses, we exploited the same 1985 sampling campaign used by Dodson et al. (1989) to demonstrate the relationship between the longitudinal distribution of smelt larvae, the macrozooplanktonic community and the maximum turbidity zone. We documented the vertical distribution, diet and feeding incidence of smelt larvae sampled along a longitudinal gradient in the upper part of the St. Lawrence Middle Estuary.

MATERIALS AND METHODS

Three stations (Stns 1, 2, 3; Fig. 1) were sampled in the Middle Channel between Ile d'Orléans and Ile aux Coudres in their numerical order between 23 and 30 July 1985. Stn 1 (mean depth: 20 m) was located at the downstream end of the maximum turbidity zone. Stns 2 and 3 (mean depths 18 m) were located 20 and 32 km upstream of Stn 1, well within the maximum turbidity zone. A detailed description of the sampling

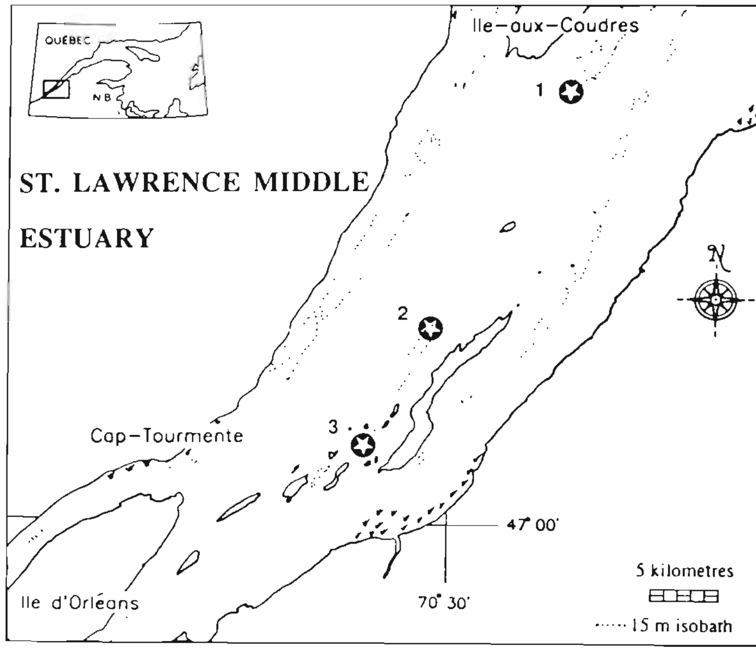

Fig. 1 Study area and location of sampling stations. Stn 1 was sampled on 23 to 24 July, Stn 2 on 26 to 28 July, and Stn 3 on 28 to 30 July, 1985

program and the physical characteristics of the stations is provided by Dodson et al. (1989). To briefly summarize, larvae were sampled using a 1 m^2 Tucker trawl fitted with an opening-closing device and a 0.5 m standard plankton net (0.500 mm mesh). A General Oceanic flowmeter fitted at the mouth of the net measured filtration rate. Towing speed varied from 2 to 3 knots. At each station, 3 discrete depth intervals were sampled hourly: a deep step-oblique tow from near the bottom to a depth of 12 m (bottom layer), a step-oblique tow from 12 to 6 m (middle layer) and a step-oblique tow from 6 m to the surface (surface layer). Each tow lasted ca 10 min and filtered on average 750 m^3 of water. The sampling program consisted of a 48 h series at each station where the surface, middle and bottom layers were successively sampled. Due to bad weather, sampling at Stn 1 was limited to 22 h from 23 to 24 July. Stn 2 was sampled for 48 h from 26 to 28 July and Stn 3 for 49 h from 28 to 30 July.

All biological samples were preserved in buffered 4 % formalin and completely sorted to calculate the density of smelt larvae. A maximum of 100 larvae were arbitrarily selected from each sample (66 samples at Stn 1, 144 samples at Stn 2, 147 samples at Stn 3) and their total length measured to the nearest 0.1 mm. All larvae were measured in samples containing less than 100 larvae. Based on the frequency distribution of the lengths measured at the 3 stations, larvae were assigned to one of 3 length classes: L1, < 25 mm, representing 27 % of the larvae measured; L2, between 25 and 29.9 mm, representing 42 % of the larvae measured; L3, > 30 mm, representing 31 % of the larvae measured.

Diet and feeding incidence were evaluated by analyzing the contents of the entire digestive tract. Only larvae with intact digestive tracts were retained for analysis. Digestive tracts were dissected and observed under a dissecting microscope and the presence or absence of prey items noted. Digestive tracts containing neither prey nor digested matter were scored as empty. Prey items were identified to species level when possible. As copepodites represented a minor fraction of all copepod stages identified, we simply classified all stages as copepods. The presence of parasites, of which the vast majority were cestodes, was also noted. At Stn 1, a total of 467 larvae were found solely at low tide, occurring in only about half of the 66 samples obtained at this station. All of these larvae were examined for gut contents. At the 2 other stations, a maximum of 50 larvae per sample were analyzed. These larvae were selected among the 3 length classes according to the proportion of each length class within the sample. As a result, the digestive tracts of 5752 larvae sampled in the 3 depth layers at Stn 2 and those of 4401 larvae from the surface and bottom depth layers at Stn 3 were analyzed.

Our 48 h sampling series were not sufficiently long to determine if the vertical migratory behavior of smelt larvae observed in 1985 was identical to that described in the same area in June and July 1986 by Laprise & Dodson (1989). However, these authors reported 2 observations characteristic of the vertical migratory behavior of smelt larvae that we tested in our data set using contingency table analyses (Legendre & Legendre 1984): (a) on average, large smelt larvae are found deeper in the water column than smaller larvae, and (b) all larvae are found near the surface during flood tide and closer to the bottom during ebbs in July.

Contingency table analyses were also performed to determine the effect of vertical distribution, length of larvae, longitudinal position within the turbidity zone and tidal state on the feeding incidence of smelt larvae. Tidal state was partitioned as high tide ± 1 h (3 hourly observations), low tide ± 1 h (3 hourly observations) and the intervening periods of flood and ebb. Feeding incidence was evaluated by calculating the percentage of larvae analyzed with gut contents (feeding coefficient). In the case of a significant chi^2 test result, we also tested a posteriori if an observed value in the tables significantly differed from the associated expected value (Legendre & Legendre 1984).

DESCRIPTION OF STUDY SITE

A description of the abiotic and biotic characteristics prevailing at the 3 stations during the sampling period is provided by Dodson et al. (1989). Briefly, surface salinities at Stn 3 during the ebb were near zero with essentially no vertical stratification. During flood, maximum salinity differences were less than 0.8 g kg^{-1} between surface and bottom layers. At Stn 2, surface layer salinities varied from 2 to less than 1 g kg^{-1} from flood to ebb tide. Mean gradient between the layers was 1.4 g kg^{-1}. At Stn 1, surface layer salinities varied from less than 7 to over 22 g kg^{-1}. Mean gradient between bottom and surface layers was 4 g kg^{-1}. No thermal stratification was observed at the 2 upstream stations. Average temperatures varied between 20 and 21 °C at Stn 3 and between 19 and 21 °C at Stn 2. Temperature variations were more important at Stn 1 where average temperatures varied between 6 and 16 °C.

Decreasing salinity and increasing water temperature with upstream distance was accompanied by increasing turbidity. At Stn 1, vertical turbidity gradients were weak with mean values in the bottom layer reaching a maximum of 10 NTU (Nephelometric Turbidity Units) at low tide. Stns 2 and 3 were situated well within the maximum turbidity zone. Surface layer turbidity values remained fairly constant over the tidal cycle at about 15 NTU whereas, in the bottom layers, turbidity values increased over the tidal cycle, being maximal (> 100 NTU) during the flood. The zone of longest average advective replacement time was situated upstream of Stn 2, retreating downstream towards Stn 2 during the sampling period. Mean bottom layer flow at Stn 1 was strongly upstream.

The turbid, warm and low salinity waters of the 2 upstream stations were characterized by *Neomysis americana*, *Gammarus* sp. (principally *G. tigrinus*), *Mysis stenolepis* and *Crangon septemspinosus*. The more stratified and less turbid waters of the downstream station were characterized by a coastal marine macrozooplanktonic community, including the potential larval fish predator, *Sagitta elegans*.

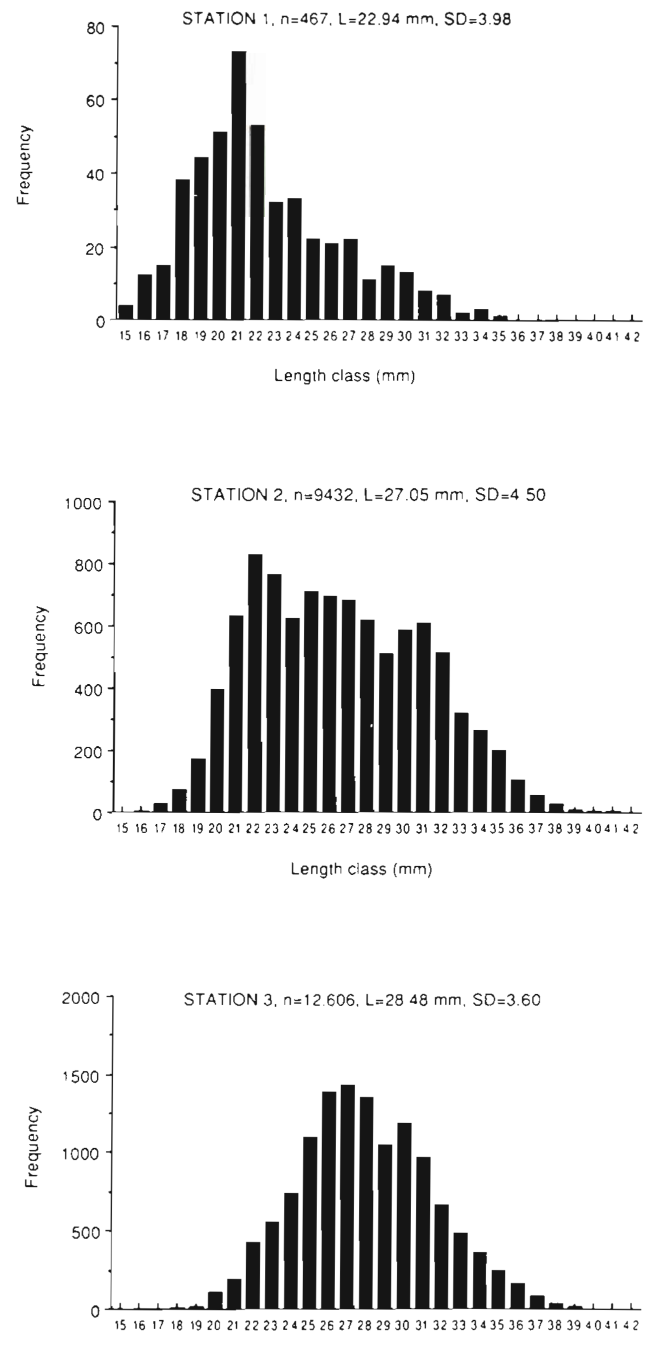

Fig. 2. *Osmerus mordax*. Length-frequency distribution of smelt larvae sampled at Stns 1, 2 and 3, St. Lawrence Estuary. n: number of larvae measured; L: mean total length; SD: standard deviation

RESULTS

Abundance, size and vertical distribution of smelt larvae

At Stn 1, smelt larvae were not abundant (mean density = 1.8 larvae 100 m^{-3}) and present only at low tide. At Stns 2 and 3, smelt larvae were more abundant, averaging 26 and 42 larvae 100 m^{-3}, respectively. Mean length of larvae increased from Stn 1 to Stn 3 with the length class frequency distribution skewed towards the smaller size classes at Stn 1 (Fig. 2). A pattern of tidal vertical migration similar to that described by Laprise & Dodson (1989) was evident. At all 3 stations, larvae of the smallest length class were significantly more abundant than expected in the surface layer and less abundant than expected in the bottom layer (Table 1). At Stns 2 and 3, larvae of all sizes pooled together were significantly more abundant than expected in the surface layer during either low or flooding tides whereas they were significantly more abundant than expected in either the middle or bottom layers during high and ebbing tides (Table 2). The absence of larvae at Stn 1 for most of the tidal cycle did not permit a similar analysis.

Diet

Examination of the digestive contents of 10620 larvae ranging in size from 15 to 43 mm revealed a diet of low diversity based principally on calanoid copepods, cladocerans and mysids (Table 3). The remaining prey items were relatively rare. The great majority of the calanoid copepods were adult stages of *Eurytemora affinis*, one of the most common species in this part of the estuary (Bousfield et al. 1975). The majority of cladocerans belonged to the small freshwater species, *Bosmina longirostris*. In addition, larger individuals of the freshwater genus *Daphnia* were identified. *Neomysis americana* made up the great majority of ingested mysids. Ingested gammarids were composed mainly of *Gammarus tigrinus* and the great majority of harpacticoid copepods found in gut contents were the benthic and epibenthic species, *Ectinosoma curticorne*. Finally, we noted a very high incidence of parasitism. Cestode parasites were observed in 96.8, 97.0, and 94.6 % of the larvae examined at Stns 1, 2 and 3, respectively.

Differences in diet related both to sampling station and to the length of larvae were observed (Table 3). Although copepods dominated the diet of all length classes, smelt larvae of < 25 mm and 25 to 30 mm ate significantly more copepods than expected whereas the largest length class of larvae ate significantly less than expected (Table 4). Mysids were eaten significantly more than expected by larvae measuring > 30 mm and significantly less by the smaller size classes. Finally, cladocerans were eaten principally by the intermediate length class of smelt larvae (Table 4).

Feeding incidence

The percentage of smelt larvae with gut contents increased as a function of larval length and the position of larvae along the longitudinal axis of the estuary (Table 5). For all length classes, the percentage of larvae with gut contents increased from Stn 1 to Stn 3 (Table 5).

The feeding coefficients of the 3 length classes of larvae sampled in the surface and bottom layers at each station and pooled over time were compared to detect differences in feeding incidence due to vertical position in the water column (Table 6). At all 3 stations, position in the water column had no significant effect on the feeding incidence of smelt larvae measuring from 25 to 30 mm and > 30 mm (Table 6). The feeding incidence of the smallest length class of larvae, however,

Table 1. *Osmerus mordax*. Contingency table analysis of the vertical distribution of 3 length classes of smelt larvae sampled at the 3 stations in the St. Lawrence Estuary, July 1985. Expected distribution: percentage of larvae < 25 mm (L1), 25 to 30 mm (L2) and > 30 mm (L3) sampled throughout the water column. Observed distribution: percentage of larvae (L1, L2 and L3) as a function of 3 depth layers; surface (0 to 6 m), middle layer (6 to 12 m), and bottom layer (12 to 18 m). * $p < 0.05$, ** $p < 0.001$, a posteriori. n: number of larvae sampled (per 100 m^3)

	Stn 1			Stn 2			Stn 3		
	L1	L2	L3	L1	L2	L3	L1	L2	L3
Expected distribution	80.0	14.5	5.5	36.1	35.0	28.9	16.2	52.6	31.2
Observed distribution									
Surface	95.1**	2.6**	2.2	40.2**	36.2	23.6**	21.8**	50.7*	27.4**
Middle	79.8	16.2	4.0	35.3	35.3	29.4	14.0**	53.0	33.1**
Bottom	64.1**	26.1**	9.8**	33.9**	33.9	33.2**	14.9**	53.4	31.6
	$\chi^2 = 11.81$			$\chi^2 = 23.78$			$\chi^2 = 52.80$		
	$0.01 < p < 0.05$			$p < 0.001$			$p < 0.001$		
	n = 96			n = 3813			n = 6163		

Table 2. *Osmerus mordax*. Contingency table analysis of the vertical distribution of smelt sampled as a function of tidal state at Stns 2 and 3 in the St. Lawrence Estuary, July 1985. Expected distribution: percentage of larvae sampled in 3 depth layers; surface (0 to 6 m), middle layer (6 to 12 m) and bottom layer (12 to 18 m). Observed distribution: percentage of larvae sampled in 3 depth layers during high tide, ebb tide, low tide and flood tide. * $p < 0.05$, ** $p < 0.001$, a posteriori. n: number of larvae sampled (per 100 m^3)

	Stn 2			Stn 3		
	Surface	Middle	Bottom	Surface	Middle	Bottom
Expected distribution	28.5	40.4	31.1	25.6	47.0	27.4
Observed distribution						
High tide	30.5	36.7	32.8	22.2	38.7*	39.1**
Ebb tide	16.1**	47.4*	36.5	16.7**	42.2	41.1**
Low tide	28.4	39.7	31.9	32.7**	40.0*	27.3
Flood tide	61.6**	30.3	8.1**	30.2**	58.2**	11.7**
		$\chi^2 = 22.89$, $p < 0.001$, n = 287			$\chi^2 = 46.36$, $p < 0.001$, n = 505	

Table 3. *Osmerus mordax*. Occurrence of prey items in the digestive tubes of 3 size classes of smelt larvae (L1, < 25 mm, L2, 25 to 30 mm and L3, > 30 mm) sampled at 3 stations in the St. Lawrence Estuary, July 1985

	Stn 1			Stn 2			Stn 3		
	L1	L2	L3	L1	L2	L3	L1	L2	L3
Guts with prey	82	32	19	874	1313	1413	646	1898	1323
Calanoid copepods	85.4	78.1	78.9	71.3	67.2	47.5	88.9	83.0	76.5
Harpacticoid copepods	–	–	–	–	0.2	–	–	0.1	0.2
Cladocerans	–	–	–	0.9	0.8	1.2	18.1	40.9	30.5
Mysids	14.6	25.0	26.3	29.9	35.8	60.0	3.1	7.2	30.8
Gammarus spp.	–	–	5.3	0.1	1.2	2.2	0.9	6.6	7.9
Ostracods	–	–	–	–	–	–	–	0.1	–
Insects	–	–	–	–	–	0.1	–	–	–
Bivalve larvae	–	–	–	–	–	–	0.2	–	–
Digestive matter	–	–	–	0.6	1.3	1.7	–	0.2	0.3
Detritus	–	–	–	–	0.4	0.3	0.3	0.3	0.4

Table 4. *Osmerus mordax*. Contingency table analysis of the occurrence of the 3 major prey items of smelt larvae (copepods, mysids and cladocerans) as a function of the length of larvae. Prey items pooled for all stations, with the exception of cladocerans that occurred only at Stn 3. Expected distribution: percentage of all larvae with or without each prey item in the digestive tube. Observed distribution: percentage of larvae of 3 length classes (L1, < 25 mm, L2, 25 to 30 mm and L3, > 30 mm) with and without each prey item. * $p < 0.05$, ** $p < 0.001$, a posteriori. n: number of larvae analyzed

	With copepods	Without copepods	With mysids	Without mysids	With cladocerans	Without cladocerans
Expected distribution	71.7	28.3	28.5	71.5	33.6	6.4
Observed distribution						
L1	79.0**	21.0**	18.3**	81.7**	18.1**	81.9**
L2	76.6**	23.4**	18.9**	81.0**	40.9**	59.1**
L3	61.6**	38.4**	45.6**	54.2**	30.5**	69.5**
	$\chi^2 = 218.22$, $p < 0.001$, n = 7600		$\chi^2 = 630.15$, $p < 0.001$, n = 7600		$\chi^2 = 295.51$, $p < 0.01$, n = 3867	

appeared to be greater in the surface layer at 2 of the 3 stations. At Stn 1, significantly more small larvae with gut contents were observed in the surface layer than expected whereas, at Stn 3, significantly more small larvae without gut contents were observed in the bottom layer than expected (Table 6).

Sampling series at Stns 2 and 3 were sufficiently long to subdivide the observations into 4 periods (high,

Table 5. *Osmerus mordax*. Percentage of smelt larvae with digestive contents as a function of larval size and sampling station, St. Lawrence Estuary, July 1985. L1, < 25 mm, L2, 25 to 30 mm and L3, > 30 mm. n: number of larvae analyzed. Larvae were obtained from the 3 depth layers sampled at Stns 1 and 2 and from the surface and bottom layer sampled at Stn 3

	Stn 1	Stn 2	Stn 3
All larvae	28.5	62.6	87.8
L1 larvae	23.7	40.7	76.1
L2 larvae	35.1	68.9	88.3
L3 larvae	61.3	83.1	94.3
n	467	5752	4401

ebbing, low and flooding tide) to test if the relationship between feeding incidence and vertical distribution of the 3 length classes of smelt larvae was influenced by tidal state. Of the 24 contingency table analyses performed (2 stations, 3 length classes, 4 tidal states), only 3 revealed a significant effect of vertical distribution on feeding incidence. These 3 tests all involved the smallest larvae with gut contents being less abundant in the bottom layer than expected during high or flooding tide.

Feeding rhythms

Temporal variations in the feeding incidence of larvae of each length class were examined at Stns 2 and 3. As little evidence existed to demonstrate a significant effect of vertical distribution on feeding incidence, observations in the 3 depth layers for each length class were pooled and presented as a function of time for each station (Figs. 3 and 4). At Stn 2, the percentage of larvae with gut contents fluctuated in concert with the tidal cycle (Fig. 3). Generally speaking, the feeding coefficients of all 3 length classes were maximal at low tide, declining to minimal values during high tide. At Stn 3, the percentage of larvae of all length classes with gut contents was greater than that observed downstream at Stn 2. However, feeding coefficients fluctuated in the same manner as at Stn 2, being maximal at low tide and declining to minimal values at high tide (Fig. 4). Temporal fluctuations were most pronounced for the smallest length class of larvae. Temporal fluctuations in the feeding coefficients of larvae measuring > 30 mm were minor as feeding coefficients exceeded 77 % at all times (Fig. 4).

The tidal rhythmicity of feeding incidence was con-

Table 6. *Osmerus mordax*. Contingency table analysis of the vertical distribution of smelt larvae with and without digestive contents as a function of larval length at the 3 stations sampled in the St. Lawrence Estuary, July 1985. Expected distribution: percentage of larvae with and without digestive contents sampled throughout the water column at the 3 stations. Observed distribution: percentage of larvae with and without digestive contents in the surface (0 to 6 m) and bottom (12 to 18 m) layers at each of the 3 stations. * $p < 0.05$, ** $p < 0.001$, a posteriori, ns: not significant. n: number of larvae analyzed

	L1		L2		L3	
	With	Without	With	Without	With	Without
Stn 1						
Expected distribution	27.2	72.8	35.3	64.6	54.5	55.5
Observed distribution						
Surface	46.5**	53.5**	75.0	25.0	50.0	50.0
Bottom	11.8**	88.2**	32.8	67.2	55.0	45.0
	$\chi^2 = 34.34$		$\chi^2 = 2.98$		$\chi^2 = 0.014$	
	$p < 0.001$		ns		ns	
	n = 228		n = 65		n = 22	
Stn 2						
Expected distribution	40.4	59.6	68.2	31.8	81.5	18.5
Observed distribution						
Surface	41.7	58.3	69.3	30.7	84.4	15.6
Bottom	37.9	62.1	66.7	33.3	78.8	21.2
	$\chi^2 = 1.84$		$\chi^2 = 0.54$		$\chi^2 = 5.29$	
	ns		ns		ns	
	n = 1422		n = 1242		n = 1074	
Stn 3						
Expected distribution	76.1	23.9	88.3	11.7	94.3	5.7
Observed distribution						
Surface	79.6	20.4**	88.1	11.9	93.3	6.7
Bottom	70.0**	30.0**	88.4	11.6	94.8	5.2
	$\chi^2 = 9.76$		$\chi^2 = 0.04$		$\chi^2 = 1.34$	
	$0.01 < p < 0.001$		ns		ns	
	n = 849		n = 2149		n = 1403	

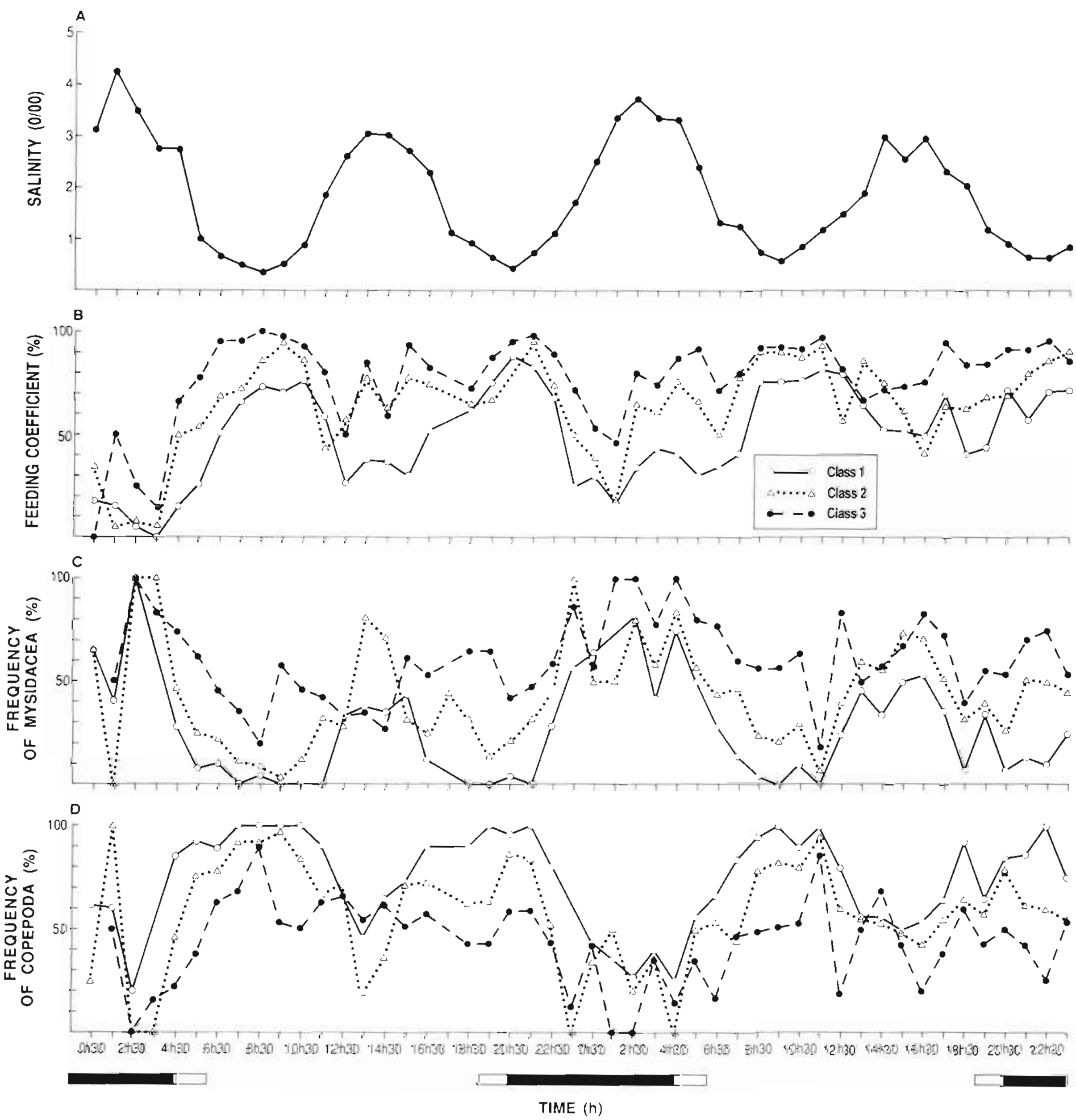

Fig. 3. *Osmerus mordax*. Tidal rhythms in feeding coefficient (percentage of larvae with gut contents) and diet of smelt larvae at Stn 2. (A) Tidal cycle as illustrated by salinity measured in the middle depth stratum (6 to 12 m). (B) Feeding coefficient of 3 length classes of smelt larvae (Class 1, < 25 mm; Class 2, 25 to 30 mm; Class 3, > 30 mm). (C) Percentage of 3 length classes of smelt larvae with gut contents containing Mysidacae as prey items. (D) Percentage of 3 length classes of smelt larvae with gut contents containing copepods as prey items

firmed by contingency table analysis of the influence of tidal state on the proportion of larvae of all 3 length classes with and without gut contents. The proportion of larvae measuring < 25 mm and 25 to 30 mm with gut contents was significantly more abundant than expected during low and flooding tide and significantly less abundant than expected during high and ebbing tide at Stns 2 and 3 (Table 7). Similar results were obtained for larvae measuring > 30 mm, although fewer significant differences were observed in accordance with the overall higher feeding coefficients exhibited by large larvae.

Marked temporal cycles were also observed in the taxonomic identity of gut contents of all larval size classes at Stns 2 and 3 (Figs. 3 and 4). At Stn 2, the proportion of small and intermediate size larvae containing mysids was greatest during high tide when the overall feeding coefficient and the proportion of

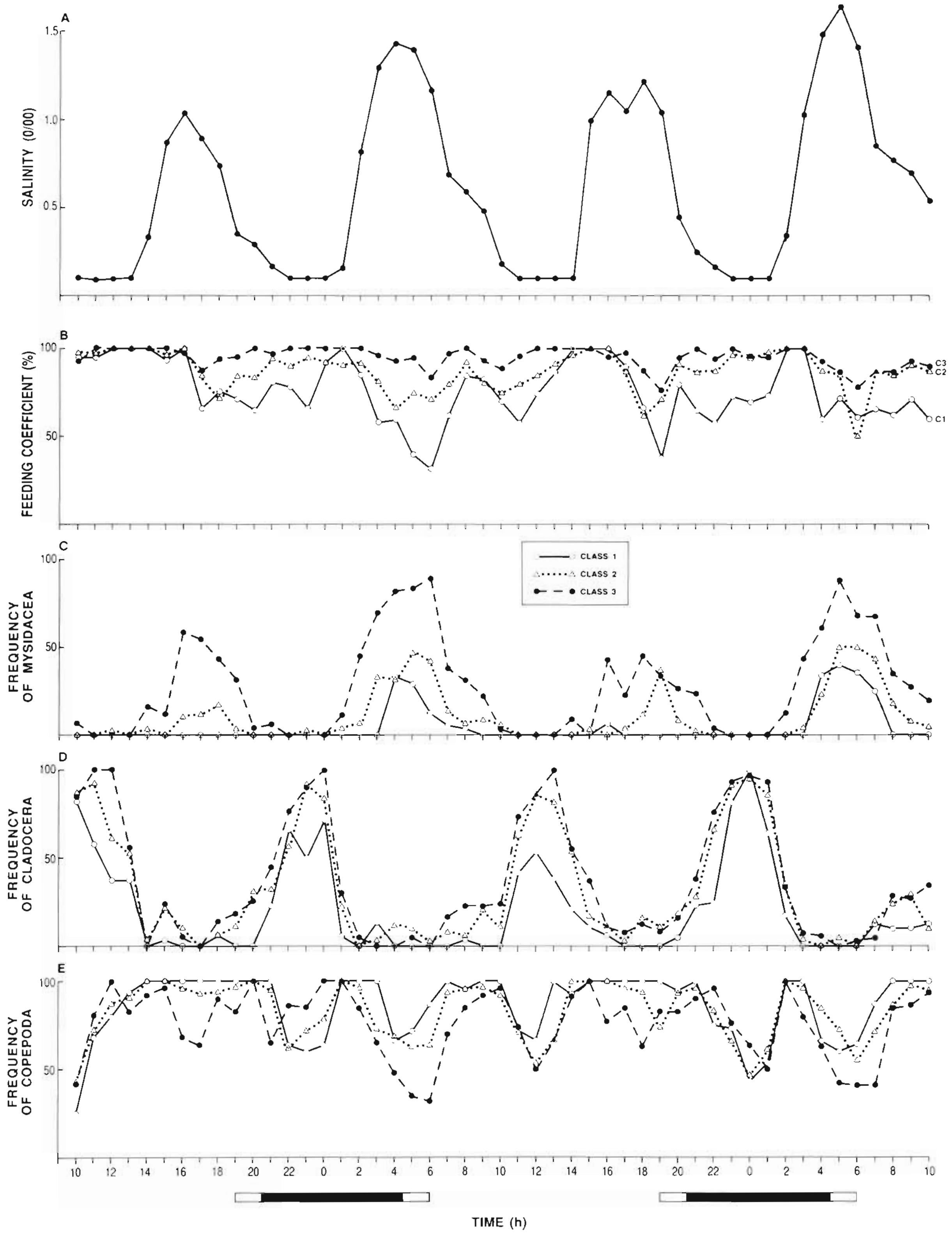

Fig. 4. *Osmerus mordax*. Tidal rhythms in feeding coefficient (percentage of larvae with gut contents) and diet of smelt larvae at Stn 3. (A) Tidal cycle as illustrated by salinity measured in the middle depth stratum (6 to 12 m). (B) Feeding coefficient of 3 length classes of smelt larvae (Class 1, < 25 mm; Class 2, 25 to 30 mm; Class 3, > 30 mm). (C) Percentage of 3 length classes of smelt larvae with gut contents containing Mysidacae as prey items. (D) Percentage of 3 length classes of smelt larvae with gut contents containing Cladocera as prey items. (E) Percentage of 3 length classes of smelt larvae with gut contents containing copepods as prey items

copepods in gut contents were low (Fig. 3). Conversely, the proportion of larvae containing mysids was lowest during low tide at which time the overall feeding coefficient and the proportion of larvae containing copepods were greatest (Fig. 3). Large larvae (> 30 mm) exhibited a greater feeding incidence on mysids characterized by more erratic temporal fluctuations. Nevertheless, the proportion of large larvae containing mysids in their gut contents also appeared greatest during high tides. At Stn 3, small and intermediate-size larvae contained mainly copepods and cladocerans whereas larger larvae also contained mysids in their gut contents (Fig. 4). As at Stn 2, the proportion of larvae containing mysids was greatest during high tide when feeding coefficients of the smaller larvae were lowest. However, mysids were absent from gut contents during low tide. Conversely, the proportion of larvae with cladocerans in their gut contents was greatest during low tide and lowest during high tide.

DISCUSSION

The vertical and longitudinal distribution of smelt larvae observed during the 1985 sampling campaign conformed to the mechanism of retention based on active tidal vertical migrations as proposed by Laprise & Dodson (1989) for smelt larvae. Larvae were found nearer the surface during floods and closer to the bottom during ebb tides. Larger larvae were on average deeper in the water column and located farther upstream than smaller larvae.

The diet of smelt larvae varied according to larval length and longitudinal position in the estuary (Table 3). Calanoid copepods were the major prey item of all length classes at all stations. Mysids, principally *Neomysis americana*, were important prey items of larvae sampled at Stn 2 and freshwater cladocerans were important at Stn 3. Whereas mysids were proportionately more abundant in the gut contents of larvae measuring > 30 mm, cladocerans were proportionately more abundant in the gut contents of the intermediate length class of larvae. These results illustrate that although prey size increases with larval length, smaller prey continued to be consumed by larger larvae such that larger larvae occupied a wider feeding niche. Similar observations were reported for a landlocked population of smelt by McCullough & Stanley (1981) and for Atlantic herring by Courtois & Dodson (1986).

The predominance of copepods and freshwater cladocerans in the diets of larvae with the highest feeding coefficients and the predominance of mysids in the diets of larvae with the lowest feeding coefficients suggest that smelt larvae are less successful feeding on mysids than on copepods and cladocerans. This may be

Table 7 *Osmerus mordax*. Contingency table analysis of the distribution of larval smelt with and without digestive contents at Stns 2 and 3 as a function of the length of larvae and tidal state. Expected distribution. percentage of 3 length classes (L1, < 25 mm, L2, 25 to 30 mm and L3, > 30 mm) of smelt larvae with and without digestive contents at Stns 2 and 3. Observed distribution: percentage of 3 length classes of smelt larvae with and without digestive contents sampled at high tide, ebb tide, low tide and flood tide at Stns 2 and 3. * $p < 0.05$, ** $p < 0.001$, a posteriori. n: number of larvae analyzed

	L1		L2		L3	
	With	Without	With	Without	With	Without
Stn 2						
Expected distribution	40.7	59.3	68.9	31.1	83.1	16.9
Observed distribution						
High tide	31.9**	68.1*	53.6**	46.4**	66.7**	33.3**
Ebb tide	33.4**	66.6**	59.2**	40.8**	80.6**	19.4**
Low tide	73.6**	26.4**	83.7**	16.3**	94.0**	6.0**
Flood tide	65.2**	34.8**	76.4**	23.6**	87.7	12.3**
	$\chi^2 = 253.86$		$\chi^2 = 137.97$		$\chi^2 = 104.78$	
	$p < 0.001$		$p < 0.001$		$p < 0.001$	
	n = 2146		n = 1905		n = 1701	
Stn 3						
Expected distribution	76.1	23.9	88.3	11.7	94.3	5.7
Observed distribution						
High tide	64.8**	35.2**	75.4**	24.6**	89.0	11.0
Ebb tide	70.6**	29.4**	85.9	14.1**	94.0	6.0
Low tide	84.1**	15.9**	94.4**	5.6**	98.6	1.4
Flood tide	92.9**	7.1**	95.4**	4.6**	97.8	2.2
	$\chi^2 = 52.95$		$\chi^2 = 110.11$		$\chi^2 = 36.98$	
	$p < 0.001$		$p < 0.001$		$p < 0.001$	
	n = 849		n = 2149		n = 1403	

largely due to their size, as suggested by the increased incidence of mysids in the gut contents of large larvae and the concomitant higher feeding incidence of large larvae. As mysids were most abundant in the vicinity of Stn 2 (Dodson et al. 1989), upstream migration into fresher water where copepod and freshwater cladoceran resources are exploited may be particularly advantageous for all but the largest length classes of larvae.

The observation that feeding coefficient increased with distance upstream for all 3 length classes (Table 5) supports the hypothesis that retention of larvae in the maximum turbidity zone by active tidal vertical migration improves the feeding incidence of larvae. The feeding coefficient of the smallest length class of larvae nearly tripled from 28 % at Stn 1 to 76 % at Stn 3. The feeding coefficients of larvae measuring > 30 mm increased from 61 % at Stn 1 to 94 % at Stn 3. The feeding coefficients observed within the turbidity zone are among the highest reported in the literature for a variety of species (Courtois & Dodson 1986). McCullough & Stanley (1981) reported maximum feeding coefficients of 77.8 % for the largest smelt larvae captured in their study. In the St. Lawrence, the low feeding incidence observed at the downstream end of the maximum turbidity zone (Stn 1) is consistent with the observations of Courtois & Dodson (1986) who noted a feeding incidence of only 27 % among 11 smelt larvae (mean standard length = 12.9 mm) sampled ca 20 km downstream of Ile aux Coudres in July 1979.

The active vertical migrations of smelt larvae were not clearly related to feeding incidence in the vertical plane, except in the case of the smallest larval length class (Table 6). Although the amplitude and precision of active vertical migration increases with larval length (Laprise & Dodson 1989), feeding incidence of smelt larvae measuring > 25 mm was independent of vertical distribution. Although we did not measure the vertical distribution of prey, the homogeneous distribution throughout the water column of vertically migrating larvae with gut contents strongly suggests that the active vertical migrations of smelt larvae do not represent behavioral responses to changes in the availability of their prey in the vertical plane.

Apparent tidal rhythmicity in diet and feeding incidence of smelt larvae observed in this study was largely due to tidal displacement of water masses at fixed sampling stations. The analysis of the same data set by Dodson et al. (1989) revealed the advection at Stn 2 of high densities of large smelt larvae from upstream during the stronger, daytime ebbs. High tides were associated with the advection of smaller larvae from downstream. These observations led to the conclusion that larger larvae were upstream of Stn 2 with smaller larvae predominantly distributed downstream. Thus, the predominantly large and intermediate length classes of larvae advected from upstream at the end of ebbs were feeding mainly on copepods and were characterized by elevated feeding coefficients. The predominantly smaller length classes of larvae advected from downstream at the end of floods were feeding mainly on mysids and were characterized by lower feeding coefficients (Fig. 3). At Stn 3, smelt larvae of all size classes were most abundant at maximum values of both ebb and flood currents (Dodson et al. 1989). However, larvae advected past the station at the end of ebbs and beginning of floods fed uniquely on cladocerans and copepods and were characterized by elevated feeding coefficients whereas the larvae advected from downstream at the end of floods fed mainly on mysids and copepods and were characterized by lower feeding coefficients, particularly within the smallest length class.

Semi-diurnal cycles in the feeding incidence of larval capelin and Atlantic herring in the partially-mixed section of the St. Lawrence Estuary are also a function of the tidal displacement of water masses (Courtois & Dodson 1986). However, these authors suggested that changes in feeding success were mainly related to changes in the swimming activity of larvae in water masses of different temperatures, such that colder water masses occurring at high tide resulted in lower feeding coefficients. In the present study, such a phenomenon is unlikely as the minor temperature differences observed during the tidal cycle, particularly at Stns 2 and 3, cannot be considered great enough to have a major impact on swimming activity. Rather, we propose that the differences in feeding incidence of smelt larvae observed in different water masses are a result of the co-occurrence of larvae and their dominant prey items (copepods and freshwater cladocerans) in the fresher upstream water masses of the maximum turbidity zone.

In conclusion, the retention of the early life-history stages of anadromous rainbow smelt in the turbid, well-mixed part of the St. Lawrence Middle Estuary contributes to maximizing their feeding incidence. We propose that increased feeding incidence is largely a result of the increased availability of dominant prey items encountered in the maximum turbidity zone. The positive relationship between prey consumed and prey density has been experimentally demonstrated for smelt larvae in Lake Superior (Balcer 1983). As growth rates of larval fishes are known to increase with prey densities (Houde & Schekter 1981), the elevated growth rate of larvae observed in the turbidity zone may be directly associated with the increased feeding incidence afforded by retention in the turbidity zone. As such, the active tidal vertical migration of smelt larvae acting in concert with the cyclonic circulation of the middle estuary represents an adaptation to regulate the longitudinal position of larvae within the estuary. The occurrence of potential predators of larval fish (Chaetognatha) and the very low abundance of smelt larvae sampled downstream of the turbidity zone, and the low feeding coefficients and poor growth rates of these larvae, all suggest that failure to remain within the turbidity zone diminishes the probability of recruitment to the adult population of rainbow smelt.

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