Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt *Osmerus mordax*

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ABSTRACT: We investigated the link between hatch date, growth trajectory, estuarine retention and survival of rainbow smelt larvae *Osmerus mordax* in the St. Lawrence Middle Estuary. Young smelt were collected over their entire distributional range across the salinity gradient of the Middle Estuary (0 to 25 psu) during 2 growing seasons. Individual growth trajectories and hatch-date distributions were reconstructed from otolith microstructure. High abundances of larvae were observed in the upstream region (0 to 10 psu) corresponding to the estuarine turbidity maximum (ETM). Larval rainbow smelt hatched in May during a period of 26 to 27 d, and mortality rates were variable among hatch dates. These variations were related to the feeding conditions experienced by first-feeding larvae (3 to 5 d after hatching) that fluctuated from day to day according to a predictable cycle of 15 d associated with photoperiod and tide. Comparison of growth trajectories of larvae at various ages indicated that older individuals, i.e. survivors, grew faster. Furthermore, smelt larvae collected within the ETM exhibited significantly higher growth rates than those sampled in the downstream area of the Middle Estuary, suggesting that larvae collected in the latter region represented dispersal from the ETM. We concluded that inter-annual variations in year-class strength might not be generally affected by early starvation, as larvae will experience recurrently good, medium and bad first-feeding conditions each year because of the length of the hatching period. However, any factor that reduces growth rate during the larval stage, including parasitism, has the potential to affect interannual variability in year-class strength.

KEY WORDS: Hatch date · Growth rate · Survival · Estuarine turbidity maximum · Otolith microstructure · Rainbow smelt larvae

INTRODUCTION

Variable mortalities during the early life history of fishes are largely responsible for interannual fluctuations in the abundance of fish populations (Houde 1987). Predation, starvation and dispersion are the most important factors likely to contribute to the mortality of fish larvae (Hjort 1914, May 1974, Cushing 1975, 1990, Lasker 1978, Parrish et al. 1981, Anderson 1988, Sinclair 1988, Bailey & Houde 1989). Body size or growth during early life history is frequently suggested

to have an impact on survival and subsequent recruitment. Recently, Campana (1996) demonstrated that recruitment of Atlantic cod on Georges Bank between 1984 and 1988 was positively and highly correlated with body size of juvenile cod aged 90 d. Size-dependent and growth-dependent mortality have been studied on various species experimentally (e.g. Rosenberg & Haugen 1982), in the field (e.g. Rice et al. 1987, Hovenkamp 1992, Meekan & Fortier 1996), and through modeling (e.g. Pepin 1989, Rice et al. 1993, Cowan et al. 1996). Most of these studies concluded that fast growth enhances survival. However, selection for slow growth in sole *Solea solea* larvae (Amara et al. 1994),

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and silversides *Menidia beryllina* (Gleason & Bengtson 1996) have been reported.

The different causes of mortality during the early life history of fishes implies different selective processes acting on the phenotype within generations (Houde 1997). For instance, if survival is governed by predation, larger larvae should be less susceptible to predation (the 'bigger is better' hypothesis; Miller et al. 1988), while faster-growing larvae should be available to predators for a shorter period of time before metamorphosis to the juvenile stage (the 'stage duration' hypothesis; Anderson 1988, Cushing 1990). In the case where starvation is the principal cause of mortality, larger and faster-growing larvae are expected to exhibit the highest feeding rates, and to be less sensitive to starvation (Beyer & Laurence 1980, Rosenberg & Haugen 1982). Finally, if dispersion is mainly responsible for mortality, larger and faster-growing larvae should exhibit better swimming capabilities for retention in favourable nursery areas. However, it is unlikely that only 1 mechanism regulates mortality (Leggett & DeBlois 1994).

Examination and analysis of otolith microstructure provides a means of studying growth and survival of the early life stages of fish. Daily increment counts provide age estimates (see reviews by Campana & Neilson 1985 and Geffen 1992), and increment widths may be used to determine previous size-at-age using appropriate back-calculation procedures (Campana 1990, Secor & Dean 1992, Sirois et al. 1998). Distributions of hatch dates can be estimated from ages of larvae and dates of sampling (Campana & Jones 1992). These distributions have been used to examine periods of successful hatch dates (Methot 1983, Yoklavich & Bailey 1990, Fortier & Quiñonez-Velazquez 1998).

A wide variety of fish species spend their early life in estuarine environments. Estuaries such as that of the St. Lawrence River are characterised by an estuarine turbidity maximum (ETM) which is the dynamic frontal region where freshwater from the river first mixes with saltwater from the sea. The St. Lawrence ETM is characterised by sharp gradients in several physical variables and high concentrations of suspended sediment (turbidity) and zooplankton. Highly turbid estuarine environments may provide a refuge from predation (Bruton 1985, Miller et al. 1985, Miner & Stein 1996). It also has been demonstrated that turbidity does not adversely affect feeding of estuarine fish larvae (Boehlert & Morgan 1985, Chesney 1989, Sirois & Dodson 2000), and entails lower energetic costs for larval rainbow smelt *Osmerus mordax* (Sirois & Dodson 2000).

Larvae of the anadromous rainbow smelt are a major component of the ichthyoplankton community in the St. Lawrence Middle Estuary (Able 1978), especially in the ETM (Dodson et al. 1989, Laprise & Dodson 1989b). Larval smelt achieve retention in the ETM by active tidal vertical migration (Laprise & Dodson 1989a). No predator of smelt larvae is known within the ETM. Therefore, mortality of larval smelt is believed to be controlled by starvation, or dispersion, or both. Fast-growing smelt larvae are expected to exhibit high feeding rates, to be more resistant to starvation, and to be in a better condition to carry out the vertical migration necessary to achieve estuarine retention. The presence of parasites in the gut may also affect survival, because parasitised larval smelt were found to ingest half the amount of food and to be significantly smaller than non-parasitised larvae in the St. Lawrence ETM (Sirois & Dodson 2000). The same study also showed that larval smelt feed only during the coincidence of daylight hours with flood tide. We use the term 'feeding window' to describe such periods. The feeding window varies from 5 to 9 h d^{-1} during a 15 d tidal cycle in the ETM during the growing season. The duration of the feeding window is expected to substantially influence the feeding success of larval smelt, especially during the few days after hatching when larvae start to feed on exogenous food sources for the first time.

The objectives of this study were to verify that survival of rainbow smelt larvae in the St. Lawrence Middle Estuary was related to hatch date, growth trajectory, and ETM retention. We first evaluated the influence of food availability during the hatching period on the survival of smelt larvae. Second, we examined the survival among larvae exhibiting variable growth trajectories during early life, and third, we compared these trajectories from larvae collected within the ETM with those sampled downstream. Smelt larvae were collected across the salinity gradient of the St. Lawrence Middle Estuary during 2 growing seasons. Individual growth trajectories and hatch-date distributions were reconstructed from otolith microstructure. The use of otolith microstructure to determine the age and growth of rainbow smelt larvae has been validated (Sirois et al. 1998).

Several studies have shown the existence of 2 genetically distinct sympatric populations of smelt in the St. Lawrence Middle Estuary (Baby et al. 1991, Bernatchez & Martin 1996). However recent work suggests that larvae exhibiting active tidal migration to exploit the pelagic estuarine environment originate mostly from 1 genetic population (Pigeon et al. 1998). Our data were collected in the channels of the St. Lawrence Middle Estuary across the salinity gradient, and encompass the entire larval distributional range (Laprise & Dodson 1989b) of only 1 of the 2 genetic populations—the population that is largely associated with the north shore of the estuary (Pigeon et al. 1998).

MATERIALS AND METHODS

Study site. The St. Lawrence Middle Estuary is located between 50 and 230 km downstream of Québec City (Canada) and encompasses the salinity range 0 to 25 psu (Fig. 1). The area receives an annual mean discharge of 12 600 m^3 s^{-1} from the river, and the circulation is dominated by semi-diurnal lunar tides (M2 type) ranging from 3 to 6 m in height. The estuary has 3 main channels (Northern, Middle and Southern), and is characterised by a partially mixed zone downstream of Île-aux-Coudres and a well-mixed zone in the upstream section corresponding to the ETM (salinity ca <10 psu). Rainbow smelt larvae are found throughout the St. Lawrence Middle Estuary, but mainly within the ETM.

Field surveys. Young rainbow smelt *Osmerus mordax* were collected across the salinity gradient in the St. Lawrence Middle Estuary on 3 occasions in 1994 (24 to 26 May, 20 to 22 June and 15 to 16 July), and 3 in 1995 (25 to 27 May, 27 to 28 June and 14 August). On

each occasion, stations were determined according to surface salinity. Six salinity strata (0, 5, 10, 15, 20, and 25 psu) were sampled in the Northern Channel and in the Southern Channel of the Estuary (Fig. 1). The 25 psu salinity stratum was not sampled in 1995, except in June in the Southern Channel. In May 1994 and 1995, 4 stations were sampled in the 0 psu salinity stratum, 2 in the Northern Channel and 2 in the Southern Channel (Fig. 1). These 4 stations around Île d'Orléans (0 psu) were sampled twice in 1994 (24 and 31 May).

At each station, temperature and salinity profiles were monitored using a SeaBird Seacat profiler. Zooplankton concentration was estimated by a vertical tow of a 0.5 m standard plankton net (63 µm) from 2 m above the bottom to the surface (mostly 12 m within the ETM). Zooplankton samples were preserved in 4% buffered formaldehyde. Concentration estimates and identification of zooplankton were done in the laboratory.

Larval sampling consisted of step-oblique tows from the bottom to the surface using a 1 m standard plank-
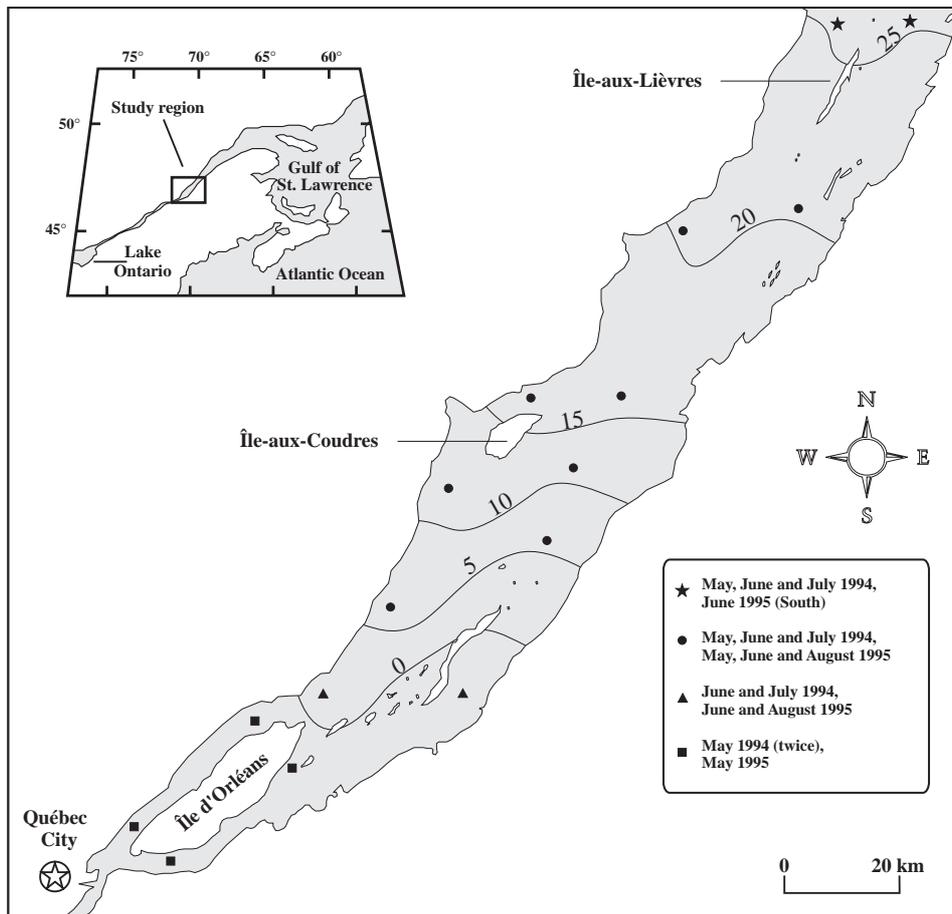
Fig. 1. Isolines of salinity (psu) and location of stations sampled in Northern and Southern Channels of St. Lawrence Middle Estuary in 1994 and 1995. While exact location of stations was determined on each occasion according to surface salinity, symbols represent average positions among field surveys
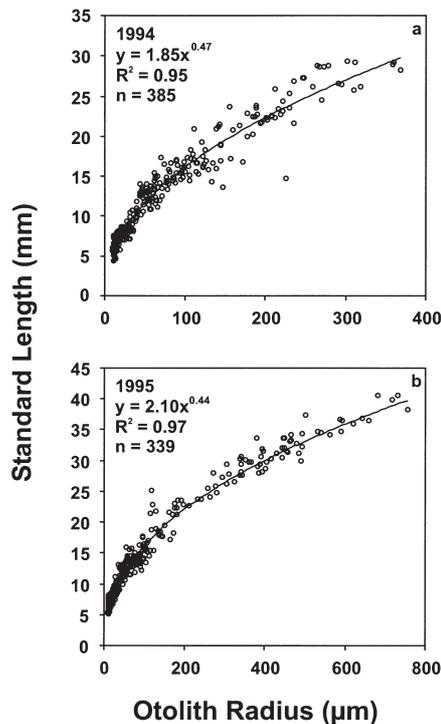
Fig. 2. *Osmerus mordax.* Relationships between standard length and otolith radius of smelt larvae sampled from (a) May to July 1994, and (b) May to August 1995 in St. Lawrence Middle Estuary. Regression equations, R^2 values, and sample size (n) are shown in each graph

ton net (500 µm mesh) in May (1994 and 1995), and a Tucker trawl (1.09 × 1.19 m) in June (1994 and 1995), July (1994), and August (1995). The Tucker trawl was composed of a 0.5 m standard plankton net (500 µm mesh) attached to a metal frame with a 5 mm mesh net 1.5 m in length. A General Oceanic flowmeter was fitted at the mouth of the gear to measure filtration rate. Each tow lasted ca 15 min and filtered on average 600 m^3 of water with the 1 m plankton net and 1500 m^3 of water with the Tucker trawl. All samples were preserved in 95% ethanol. The total volume of ethanol was changed 1 d after the first preservation to prevent the solution from becoming too acidic (Butler 1992). Samples were sorted in the laboratory, and the total number of smelt was determined. Samples containing more than 250 larvae were subsampled with a Motoda splitter (van Guelpen et al. 1982).

Otolith procedure. When available, 15 larvae were randomly chosen from each sample and standard length was measured using a camera connected to an image-analysis system. No correction for shrinkage resulting from preservation in ethanol was made (Sirois et al. 1998). Sagittal otoliths were removed with fine needles and mounted on a microscope slide with thermoplastic glue (Crystal Bond). Otoliths were mea-

sured using an image-analysis system connected to a light microscope at 630 to 1000× magnification. Three measurements were taken along the growth axis: core radius (µm), otolith radius (µm), and width of every increment (µm). The number of increments was automatically compiled using the number of widths measured. All otoliths were examined twice by the same reader at an interval of >3 mo. A total of 411 otoliths were examined from the 1994 survey; 26 were not retained in the analysis because of discrepancies exceeding 10% in number of increments between counts. In the 1995 survey, 42 of 381 otoliths were discarded for the same reason.

Biases in back-calculations caused by variations of somatic growth rate over time and by the 'growth effect' (*R*) were accounted for by the time-varying growth method (Sirois et al. 1998). *R* is the impact of somatic growth rate on the fish size:otolith size ratio, which results in relatively large otoliths in slow-growing fish (Secor & Dean 1989, Campana 1990). The time-varying growth method (Sirois et al. 1998) weighs the contribution of each increment in the length calculation using a growth-effect factor. Thus, a small growth increment contributes less to the length increase of larvae than its relative importance in total otolith growth. On the other hand, a large growth increment contributes more to the length increase of larvae in comparison to its relative importance in total otolith growth. Therefore, standard lengths (L_t) at Age *t* were back-calculated from increment widths (W_t) as:

$$L_t = L_0 + \sum_{i=1}^{t}(W_t + R[W_t - W])(L_c - L_0)(O_c - O_0)^{-1} \quad (1)$$

where L = fish length at the biological intercept (L_0), and at capture (L_c), O = otolith radius at biological intercept (O_0), and at capture (O_c), and W = stage-specific mean increment width. A hatching length of 5.81 mm and the observed individual core radius were used as the biological intercept (Sirois et al. 1998). *R* was calculated using each fish as an independent observation (Campana 1990, Sirois et al. 1998), and was estimated to be 0.6 for wild-caught rainbow smelt larvae. The mean increment widths (*W*) vary during ontogeny and were calculated for each fish during the yolk-sac stage (0 to 7 d), the pre-flexion stage (8 to 25 d), the post-flexion stage (26 to 90 d) and the juvenile stage (>90 d). Development stages were determined from observations of larvae collected in the field and from the description of larval rainbow smelt development (Cooper 1978).

All length back-calculations were executed on natural log-transformed standard length and otolith radius (Fig. 2). Regression slopes of the relationship between standard length and otolith radius differed between 1994 and 1995 (ANCOVA, $F_{1,720} = 15.37$, p <

0.0001) supporting the inclusion of *R* in the back-calculation procedure (Sirois et al. 1998).

Computations and statistical analyses. Trends of zooplankton and smelt abundance across the salinity gradient were described using a smoothing spline. The spline fit uses a set of smoothly spliced 3rd-degree polynomial segments (Simonoff 1996, JMP Software: SAS Institute Inc., Cary, North Carolina, USA).

Mortality rates (*Z*) of the 1994 and 1995 cohorts were estimated from the catch curves (Essig & Cole 1986, Campana & Jones 1992). Abundance-at-age estimates were plotted with time, and *Z* was the instantaneous rate of decreasing abundance of the negative exponential equation. Abundance-at-age estimates were determined in 2 steps. First, for each sampling month, the contribution to the abundance observed at each sampling station was calculated for each aged larva, as smelt densities varied among stations. Second, the contribution values of larvae of the same age were summed across stations to obtain the abundance-at-age estimates of smelt larvae within the whole estuary. In these computations, Salinity Strata 20 and 25 psu were pooled together as were the stations in Salinity Stratum 0 psu in May of both years to insure uniformity between sampling periods and between years.

Hatch-date frequency distributions were constructed for each sampling month using the abundance of each daily cohort. The abundance of a daily cohort was the sum of the contribution values (see preceeding paragraph) of all larvae hatched on the same day. Mortality rate of a daily cohort was the instantaneous rate of decrease in cohort abundance across the 3 sampling months. Daily-cohort mortality rates were analysed by time-series analysis (Legendre & Legendre 1984). First, 1 mortality rate was linearly interpolated on 19 May 1994 to replace a missing data point. Second, raw mortality rates were filtered using the smoothing spline (see 1st paragraph above). Autocorrelation functions were calculated on the raw and the filtered data to find the periods of observed cyclic variations. Cross-correlation functions were used to describe the temporal relations between daily-cohort mortality rates and the duration of the feeding window in May, when smelt larvae start to feed on exogenous food sources for the first time.

Growth trajectories of all larvae were reconstructed at 5 d intervals. Measurements of multiple otolith increments that constitute the longitudinal record of growth of a fish larva are not independent within an individual (Chambers & Miller 1995). For this reason, growth trajectories required repeated-measures multivariate analysis of variance (RM-MANOVA) for comparison among months of capture and among zones. The multivariate approach was preferred to the univariate test because our data did not meet the assumptions of sphericity and compound symmetry. Wilk's Λ of the age-by-group interaction was used as the test statistic. All RM-MANOVAs were executed on natural log-transformed standard lengths.

The intensity of phenotypic selection for fast growth can be estimated by comparing the frequency distributions of growth rates of 2 groups of fish during different growth intervals (Healey 1982, Hovenkamp 1992, Meekan & Fortier 1996). Larvae were divided into 'survivors' and 'population' in each year. Survivors represent larvae aged between 51 and 71 d in 1994 (n = 78), and between 79 and 102 d in 1995 (n = 78). Ideally, the back-calculated growth of survivors during a given growth interval should be compared to the population's larvae collected immediately at the end of this growth interval. However, there were not enough larvae of this precise age available for appropriate analysis. Thus, to represent the population, larvae aged 1 to 10 d older than the upper limit of the growth interval were selected. For example, larvae aged 11 to 20 d represented the population during the growth interval 1 to 10 d, larvae aged 21 to 30 d represented the population during the growth interval 11 to 20 d, and so on. One exception to this rule was made in 1995. Larvae aged 21 to 40 d were chosen to represent the population during the growth interval 11 to 20 d. As discussed by Meekan & Fortier (1996), this procedure provided conservative estimates of the magnitude of selection for fast growth because the selection had already operated in the reference population. Larvae were assigned into 9 growth-rate classes and relative frequency distributions were calculated for survivors and the population separately for each growth interval. A survival ratio (*SR*) was calculated for each growth-rate class using the relative frequency of the survivors (F_s) and the relative frequency of the population (F_p) in the growth-rate class:

$$SR = \frac{F_s}{F_p} \tag{2}$$

This ratio represents the probability of survival of fast-growing fish in comparison to slow-growing fish (Hovenkamp 1992).

RESULTS

Abundance of smelt larvae in St. Lawrence Middle Estuary

High abundances of smelt larvae *Osmerus mordax* were generally observed within the ETM (average salinity ca <10 psu) and were associated with higher concentrations of zooplankton and higher tempera-
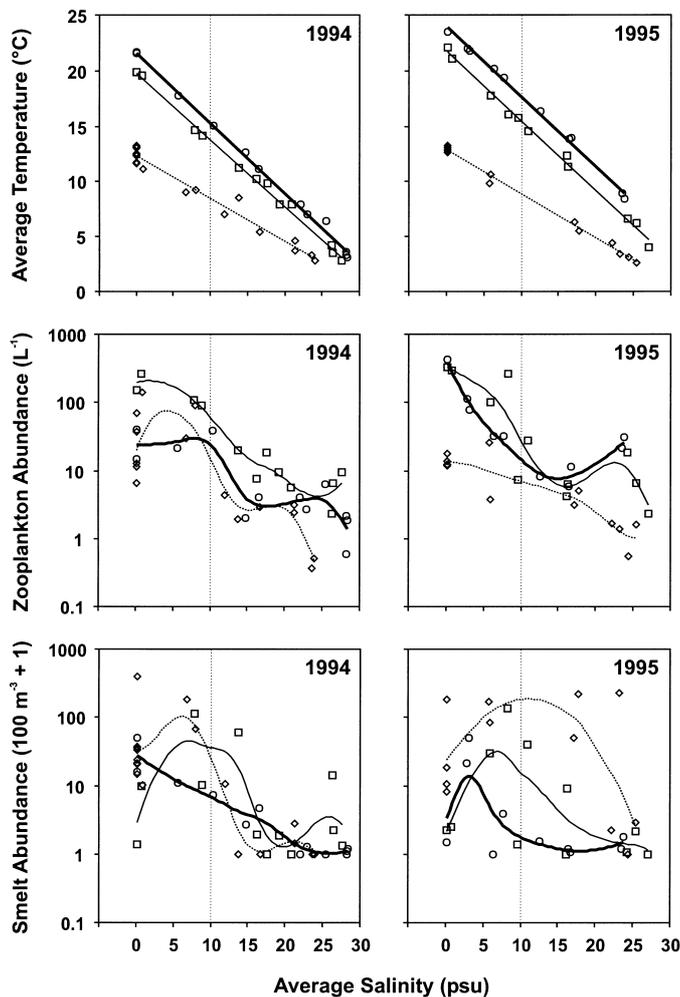
Fig. 3. Average temperature of water column, abundance of zooplankton, and abundance of smelt larvae *Osmerus mordax* (ind. 100 m^{-3} + 1) as a function of average salinity of water column in May (◊), June (□), and July or August (○) 1994 and 1995 in St. Lawrence Middle Estuary. Trend lines are illustrated for May (dotted lines), June (continuous thin line), and July or August (continuous thick line) in each panel. Average downstream limit of estuarine turbidity maximum (ETM) was set at 10 psu (vertical dotted line). Equations and statistical details of the trend lines are given in Table 1

tures than were observed downstream of the ETM (Fig. 3, Table 1). Peak abundances of larvae tended to concentrate at the head of the estuary (Salinity Strata 0 to 5 psu) during the growing season in 1994 and 1995 (Fig. 3).

Abundance-at-age estimates were calculated for the entire study region and were plotted to estimate instantaneous mortality rates (Z) in 1994 and 1995 (Fig. 4). Values of Z computed by the regression analysis were 0.032 and 0.036 for the 1994 and the 1995 cohorts, respectively. Z did not differ significantly between the 2 years (ANCOVA, $F_{1,137}$ = 0.302, p =

0.583), but abundance of larvae at hatching (intercept) was higher in 1995 than in 1994 (ANCOVA, $F_{1,138}$ = 4.068, p = 0.046).

Hatch date

Frequency distributions of back-calculated hatch date of smelt larvae were compared among sampling months in 1994 and 1995 (Fig. 5). Examination of the range of hatch dates (6 May to 1 June in 1994, 3 to 28 May in 1995) and of median hatch dates indicated that smelt larvae hatched on average 3 to 4 d earlier in 1995 (Fig. 5). Hatch-date frequencies tended to become increasingly jagged during the sampling season.

The fluctuations in hatch-date relative abundances among months indicated variable mortality rates of daily cohorts (Fig. 6). The time-series of mortality rates displayed a pattern related to the feeding conditions in the ETM during the hatching period. Autocorrelation functions calculated on the daily cohort mortality rate revealed a cycle of 14 d in 1994 and 16 d in 1995
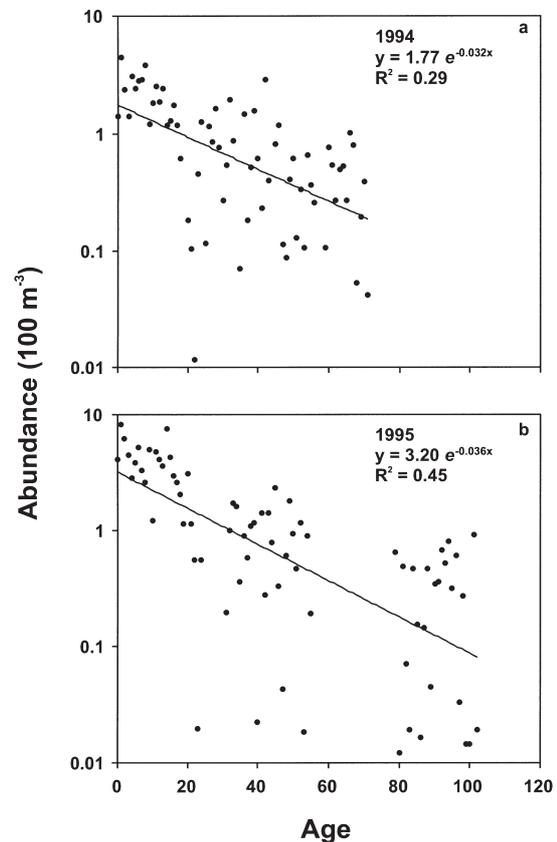
Fig. 4. *Osmerus mordax*. Catch curves and exponential coefficients estimating mortality rates of smelt larvae in St. Lawrence Middle Estuary in (a) 1994, and (b) 1995

Table 1. Proportion of variance explained by relationship between average temperature of water column (T, °C), abundance of zooplankton (Zoo, ind. l^{-1}), abundance of smelt larvae *Osmerus mordax* (A, ind. 100 m^{-3}) and average salinity of water column (AS, psu) from May to July 1994, and from May to August 1995 in St. Lawrence Middle Estuary. T was fitted using linear regression, while $\ln(Zoo)$ and $\ln(A+1)$ were fitted using smoothing spline as illustrated in Fig. 3. n = number of samples used in fitting

| Month | Temperature | | $\ln(Zoo)$ | $\ln(A+1)$ | (n) |
	Equation	R^2	R^2	R^2	
1994					
May	$T = 12.40 - 0.39\,AS$	0.97	0.80	0.82	(18)[a]
Jun	$T = 19.85 - 0.60\,AS$	0.99	0.94	0.69	(12)
Jul	$T = 21.65 - 0.63\,AS$	0.99	0.85	0.95	(12)
1995					
May	$T = 12.93 - 0.40\,AS$	0.99	0.83	0.43	(12)
Jun	$T = 21.71 - 0.63\,AS$	0.99	0.86	0.56	(11)
Aug	$T = 23.95 - 0.63\,AS$	0.99	0.98	0.72	(10)

[a]Only 16 samples of zooplankton in May 1994

growing larvae (Table 2). During the first 20 d and 40 d of life in 1994 and 1995, respectively, >60% of the survivors exhibited a growth rate of ≥0.20 mm d^{-1} or greater, whereas <60% of the population exceeded this value. The difference between the survivors and the population was less important during the Age Intervals 21 to 40 in 1994 and 41 to 50 in 1995, probably because phenotypic selection had operated during a shorter period of time.

Mean back-calculated growth trajectories of larvae caught within the ETM were compared with those collected outside the ETM (Fig. 9). In all cases, larvae collected in the ETM grew significantly faster (RM-MANOVA, p < 0.02) than

(Fig. 7). Cross-correlation analysis with the duration of the feeding window in the ETM during the hatching period showed that low mortality rates of daily cohorts followed periods of maximum duration in the feeding window. Mortality rates lagged by 3 and 5 d after hatching in 1994 and 1995, respectively (Fig. 7).

Growth trajectory

Mean back-calculated growth trajectories of smelt larvae sampled in June of both years were compared with those of larvae caught in July 1994 and August 1995, respectively (Fig. 8). Larvae collected in July 1994 grew significantly faster between Age 0 to 20 d than larvae caught in June 1994 (RM-MANOVA, Wilk's Λ = 0.802, p < 0.0001). Similarly, in 1995, smelt larvae collected in August grew faster during the Age Interval 0 to 30 d than larvae sampled in June (RM-MANOVA, Wilk's Λ = 0.489, p < 0.0001). The observation of faster growth in older individuals was supported by the survival ratios (Table 2). At each age interval, relatively few survivors were observed in the slow-growth classes, while they were more abundant in the fast-growth classes. In most cases the survival ratios increased with increasing growth-rate class, indicating an increasingly greater probability of survival for faster-

Fig. 5. *Osmerus mordax.* Back-calculated hatch-date distributions of smelt larvae collected in St. Lawrence Middle Estuary in (a) May 1994, (b) May 1995, (c) June 1994, (d) June 1995, (e) July 1994, and (f) August 1995. Abundance of larvae (A) and median hatch dates (M) are shown in each panel
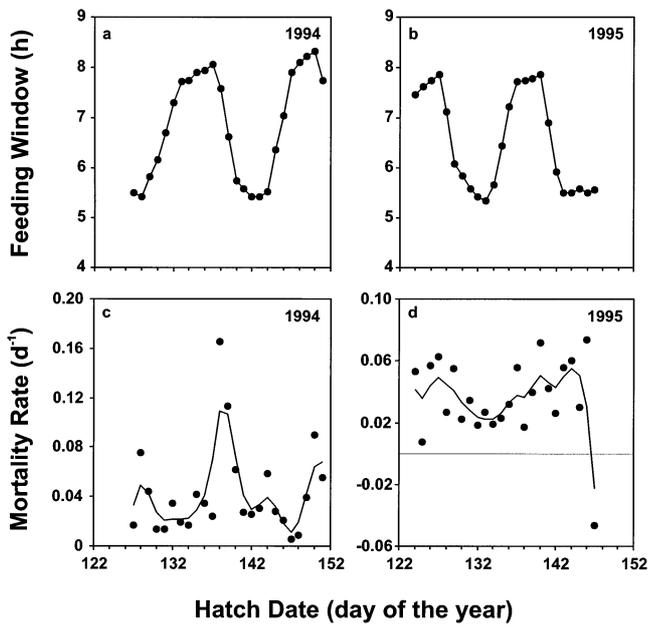
Fig. 6. Time series of duration of feeding window in St. Lawrence ETM during hatching period of smelt larvae *Osmerus mordax* in (a) 1994 and (b) 1995, and time series of daily cohort mortality rate in (c) 1994 and (d) 1995. Feeding windows were not filtered, while daily cohort mortality rates were filtered with smoothing spline fit
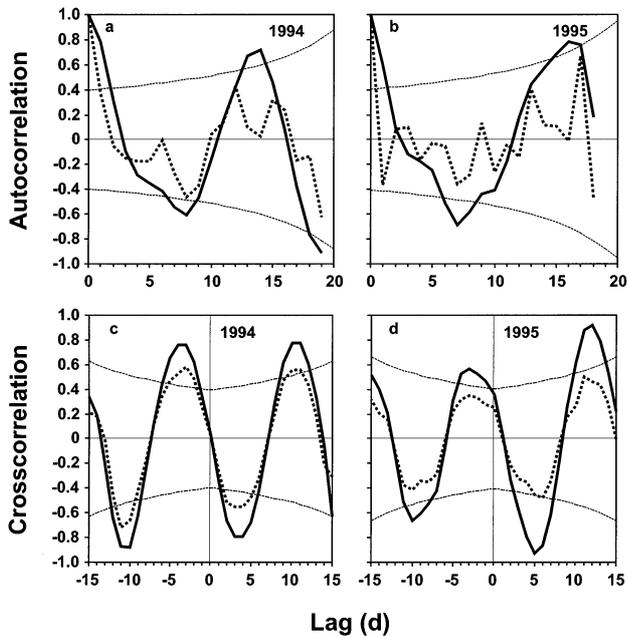
Fig. 7. *Osmerus mordax.* Autocorrelation functions of time series of daily cohort mortality rate of smelt larvae in (a) 1994 and (b) 1995, and cross-correlation functions between former and time series of duration of feeding window in the ETM during hatching period in (c) 1994 and (d) 1995. Autocorrelation and cross-correlation functions were executed on raw data (thick dotted lines) and filtered data (thick continuous lines) of daily cohort mortality rates. Thin dotted lines represent α = 0.05 probability level of correlations
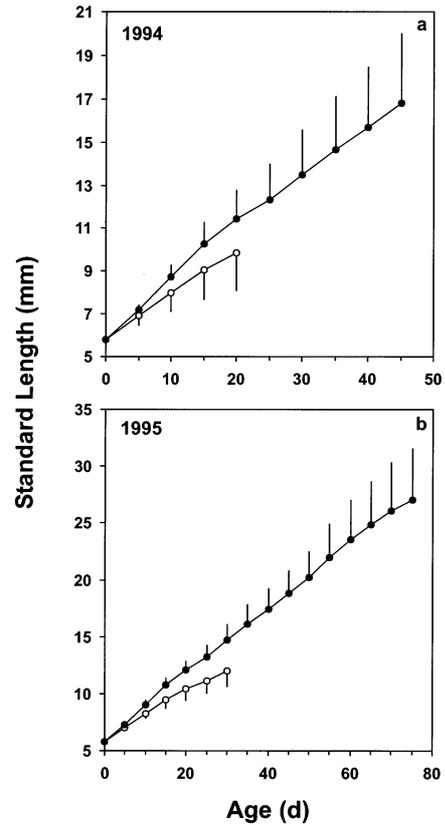
Fig. 8. *Osmerus mordax.* Mean back-calculated growth trajectories of smelt larvae collected in June (○) and July or August (●) of (a) 1994 and (b) 1995. Vertical bars represent the standard deviations

those collected downstream of the ETM (Table 3). These results are consistent with the lower growth rates reported in previous years for smelt larvae sampled downstream of Île-aux-Coudres in the St. Lawrence Middle Estuary (Table 4).

DISCUSSION

Survival related to hatch date

Survival of smelt larvae of *Osmerus mordax* was clearly related to feeding windows, i.e. the coincidence of daylight and flooding tide experienced by first-feeding larvae (3 to 5 d after hatching). Larvae hatched during days preceding a period of longer feeding windows in the ETM survived better than those hatched prior to shorter feeding windows. Therefore, starvation of first-feeding larvae appears to be an important cause of mortality for larval smelt in the St. Lawrence Middle Estuary.

Cross-correlations between daily cohort mortality rate and the duration of the feeding window revealed a

Table 2. *Osmerus mordax*. Relative frequencies of back-calculated growth rate classes and resulting survival ratios (*SR*) of survivor smelt larvae (*S*) and population smelt larvae (*P*) collected in 1994 and 1995 in St. Lawrence Middle Estuary. *SR* = 0: growth class only represented in population (*P*); *SR* = ∞: growth class only present in survivors; *SR* = –, undetermined: growth class not represented in either population or survivors. Numbers of fish (n) used in frequency distribution of population and of survivors are shown for each growth interval. See 'Materials and methods' for further details

Growth rate class (mm d^{-1})	Days 1–10 Rel. Freq. P	S	SR	Days 11–20 Rel. Freq. P	S	SR	Days 21–30 Rel. Freq. P	S	SR	Days 31–40 Rel. Freq. P	S	SR	Days 41–50 Rel. Freq. P	S	SR
1994															
0.00–0.05	0.0	0.0	–	7.3	0.0	0	13.3	0.0	0	0.0	1.3	∞			
0.05–0.10	5.7	0.0	0	34.1	0.0	0	17.8	3.8	0.2	14.3	3.8	0.3			
0.10–0.15	48.6	0.0	0	24.4	12.8	0.5	24.4	33.3	1.4	51.4	26.9	0.5			
0.15–0.20	40.0	14.1	0.4	12.2	17.9	1.5	22.2	23.1	1.0	25.7	21.8	0.8			
0.20–0.25	5.7	24.4	4.3	12.2	20.5	1.7	13.3	17.9	1.3	0.0	24.4	∞			
0.25–0.30	0.0	37.2	∞	9.8	26.9	2.8	2.2	10.3	4.6	5.7	9.0	1.6			
0.30–0.35	0.0	23.1	∞	0.0	17.9	∞	4.4	1.3	0.3	2.9	6.4	2.2			
0.35–0.40	0.0	1.3	∞	0.0	2.6	∞	0.0	9.0	∞	0.0	5.1	∞			
0.40+	0.0	0.0	–	0.0	1.3	∞	2.2	1.3	0.6	0.0	1.3	∞			
(n)	(35)	(78)		(41)	(78)		(45)	(78)		(35)	(78)				
1995															
0.00–0.05	0.0	0.0	–	0.0	0.0	–	0.0	0.0	–	0.0	0.0	–	0.0	0.0	–
0.05–0.10	4.8	0.0	0	8.2	0.0	0	17.8	1.3	0.1	22.2	1.3	0.1	15.4	2.6	0.2
0.10–0.15	31.0	0.0	0	24.5	0.0	0	46.7	11.5	0.2	50.0	7.7	0.2	30.8	5.1	0.2
0.15–0.20	28.6	2.6	0.1	32.7	10.3	0.3	28.9	23.1	0.8	24.1	24.4	1.0	7.7	21.8	2.8
0.20–0.25	21.4	20.5	1.0	30.6	15.5	0.5	6.7	15.4	2.3	3.7	23.1	6.2	15.4	26.9	1.8
0.25–0.30	11.9	43.6	3.7	4.1	47.4	11.6	0.0	21.8	∞	0.0	24.4	∞	15.4	20.5	1.3
0.30–0.35	0.0	25.6	∞	0.0	26.9	∞	0.0	26.9	∞	0.0	14.1	∞	15.4	10.3	0.7
0.35–0.40	2.4	7.7	3.2	0.0	0.0	–	0.0	0.0	–	0.0	3.8	∞	0.0	6.4	∞
0.40+	0.0	0.0	–	0.0	0.0	–	0.0	0.0	–	0.0	1.3	∞	0.0	6.4	∞
(n)	(42)	(78)		(49)	(78)		(45)	(78)		(54)	(78)		(13)	(78)	

lag of 3 d in 1994 and of 5 d in 1995. This difference may be related to river discharge in the spawning region at the time of hatch, which determines the duration of drift from hatching to first-feeding in the ETM. Recent work has demonstrated that the larval population exploiting the pelagic zone of the St. Lawrence Middle Estuary hatches in the freshwater portion of the river, in the area of Neuville (Quebec, Canada) ca 100 km upstream of the ETM (F. Lecomte & J.J.D. unpubl. data). It was also observed that larvae drifted to the ETM immediately after hatching (F. Lecomte & J.J.D. unpubl. data). The mean daily river discharge in May was 14 210 m^3 s^{-1} (SD = 495) in 1994, and 10 661 m^3 s^{-1} (SD = 555) in 1995 (M. Mingelbier, Faune et Parcs, Québec City, Canada, pers. comm.). These values represented roughly the limits of the range of river discharge observed in the St. Lawrence at that time of the year (M. Mingelbier pers. comm.). Although the exact location of the spawning ground and the behaviour of smelt larvae during downstream drift are unknown, it is plausible that the difference of 2 d in the lag time was caused by the difference of 4000 m^3 s^{-1} in discharge between the 2 yr.

The importance of physical factors such as water temperature and river discharge have been reported
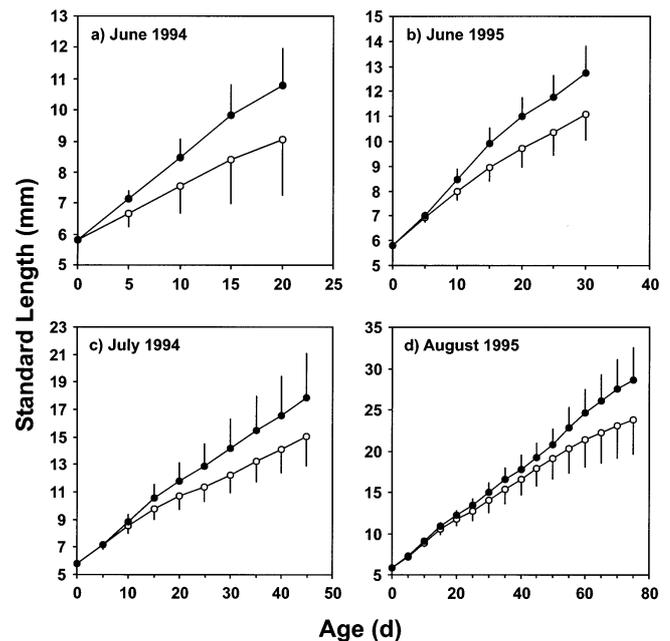
Fig. 9. *Osmerus mordax*. Mean back-calculated growth trajectories of smelt larvae collected within ETM (●) and downstream of ETM (○) in (a) June 1994, (b) June 1995, (c) July 1994, and (d) August 1995. Vertical bars represent standard deviations

Table 3. *Osmerus mordax.* Comparisons of individual growth trajectories for larvae caught within estuarine turbidity maximum (ETM) and downstream of ETM. Repeated-measures multivariate of analysis was executed on natural log-transformed standard lengths. Mean growth trajectories are shown in Fig. 9

Month	Age interval tested	No. of larvae within ETM	No. of larvae downstream of ETM	Wilk's Λ	p
Jun 1994	0–20	50	57	0.666	< 0.0001
Jul 1994	0–45	60	34	0.710	0.0005
Jun 1995	0–30	60	52	0.521	< 0.0001
Aug 1995	0–75	53	25	0.660	0.0197

to affect survival of larval fish in estuarine environments (Crecco & Savoy 1985, Rutherford & Houde 1995). In the present study, the observation of a higher mortality caused by poorer feeding conditions for first-feeding larvae is consistent with the concept of the critical period (Hjort 1914, May 1974). This hypothesis states that a lack of food during the transition from endogenous to exogenous feeding causes catastrophic mortality. For larval smelt in the St. Lawrence ETM, the abundance of food was not lacking but rather the accessibility to food was limiting. Furthermore, variations in the duration of the feeding window followed a regular cycle of 15 d associated with tides. Thus, the larval smelt population would experience recurrently the entire range of feeding conditions during their hatching period, which lasted 26 and 27 d in 1994 and 1995, respectively.

Survival related to growth trajectory and estuarine retention

The present study demonstrated the existence of a strong link between fast growth and survival of rainbow smelt during the larval stage throughout the St.

Lawrence Estuary in 1994 and 1995. This study also corroborated the high densities of larval smelt observed within the St. Lawrence ETM in comparison to concentrations observed downstream (Laprise & Dodson 1989b). Furthermore, smelt larvae within the ETM were larger and grew faster than larvae downstream. Therefore, according to the survival-ratio analysis, larvae within the ETM have substantially higher survival probabilities compared to those downstream of the ETM. Moreover, most of the growth rates of smelt larvae reported downstream of the ETM are below the value of 0.20 mm d^{-1} determined in the survival-ratio analysis (Table 4). However, growth rates reported by Able (1978) were above this value, at 0.24 mm d^{-1}. Two elements may explain this discrepancy. First, in the presence of a link between growth and survival, the simple calculation of growth rate by the difference in mean observed length during a time interval tends to overestimate growth rate. In the present study, mean growth rate estimated from observed lengths were overestimated by 32 to 65 % compared to rates estimated from back-calculated lengths. Second, Able (1978) collected many samples at the downstream boundary of the ETM, which may have influenced the estimation of growth rate.

The ETM represents a favourable environment for larval smelt. First, predation, which is considered as the major cause of mortality for larval fish (Bailey & Houde 1989), appears to be of little importance. Analysis of the stomach contents of adult smelt and tomcod, which constitute the major part of the fish community in this part of the estuary, revealed little or no predation on larvae (R. Laprise & J.J.D. unpubl. data). Second, turbid waters have been shown to reduce ener-

Table 4. *Osmerus mordax.* Reported mean growth rates of larvae estimated within ETM and downstream of ETM (DWN) during June and July

Year	Zone	Mean growth rate (mm d^{-1}) estimated from:		Source
		Observed lengths	Back-calculated lengths	
1974	DWN	0.24	–	Able (1978)
1975	DWN	0.24	–	Able (1978)
1979	DWN	0.13	–	Fortier & Leggett (1982)
1980	ETM	0.25	–	Simoneau (1986)
1986	ETM	0.33	–	Laprise & Dodson (1989a)
1994	ETM	0.33	0.25	This study
1994	DWN	0.26	0.16	This study
1995	ETM	0.35	0.26	This study
1995	DWN	0.28	0.17	This study

getic costs associated with stress or activity (Sirois & Dodson 2000). Third, the quantity of food (zooplankton) is very abundant, averaging 81 and 141 ind. l^{-1} in 1994 and 1995, respectively. On the other hand, downstream of the ETM, predators are present (Courtois et al. 1982, Dodson et al. 1989), low-turbidity levels result in higher energetic cost, and there is roughly 10 times less zooplankton prey than in the ETM. Thus, both growth rates and environmental conditions downstream of the ETM decrease survival probability.

Growth rates of smelt larvae may be considered as an index of energetic competence. High growth rates indicate an important surplus in the energy budget. In order to achieve this surplus, smelt larvae need to actively migrate to the surface layer of the water column to feed (Laprise & Dodson 1989a, Sirois & Dodson 2000). Active vertical migrations also allow smelt larvae to achieve retention within the ETM. On the other hand, larvae exhibiting lower growth rates have acquired less energy (lower feeding rate) and thus may be less capable of migrating vertically. Thus, these larvae are expected to be transported out of the ETM. We suggest that larvae collected downstream of the ETM are those that disperse and are lost from the retention zone. Examination of the growth history of smelt larvae collected in August 1995 (Fig. 9) indicated that larvae up to 30 d of age captured within and downstream of the ETM exhibited similar growth trajectories, but after this age, growth rate decreased in larvae captured downstream of the ETM. This suggests that the latter larvae exploited the ETM during a major part of their early life but were expulsed and experienced poorer growth conditions during the latter part of the summer.

Size-selective or growth-dependent mortality is frequently interpreted in terms of predation through the 'bigger is better' hypothesis (Miller et al. 1988), or the 'stage-duration' hypothesis (Anderson 1988, Cushing 1990), respectively. In the present study, predation seemed to be of little importance in the ETM, thus the significance of larval body size is different. Absolute larval size is probably less important than growth rate which reflects energetic competence. For example, a smelt larva hatched on 16 May 1995 and collected on 5 June at a length of 12 mm in the St. Lawrence Estuary exhibited a high growth rate (>0.30 mm d^{-1}), is energetically competent, and thus has a high probability of survival ($SR = \infty$). However, a larva hatched on the same date and sampled on 5 July at a length of 12 mm exhibited low growth rate (<0.15 mm d^{-1}), is energetically less competent, and has a low probability of survival ($SR = 0.2$). Therefore, survival is probably largely explained by growth rate and its attendant impact on the ability of larvae to remain within the ETM.

Growth-dependent survival and the role of parasites

Sirois & Dodson (2000) suggested that parasitism may have an important impact on survival of smelt larvae. Parasitised larvae (38% of the total) collected at the end of July 1996 in the St. Lawrence ETM were significantly smaller than non-parasitised larval smelt (Sirois & Dodson 2000). Furthermore, the presence of parasites in the gut reduced the ingestion rate of smelt larvae by 50% (Sirois & Dodson 2000). Heath & Nicoll (1991) reported a similar influence of parasites on the feeding incidence of larval herring (*Clupea harengus*) from the North Sea. Parasites in the gut may affect ingestion by consuming a proportion of the digestive tract content (Heath & Nicoll 1991); by affecting condition (Yamashita 1979) and behaviour (Rosenthal 1967) resulting in reduced foraging activity; or by occupying food space in the gut (Sirois & Dodson 2000).

The reduction of ingestion rate affects growth rate and may contribute to diminishing the probability of survival by increasing dispersion out of the ETM. To illustrate this, we calculated individual growth rates of the smelt larvae captured in the St. Lawrence ETM in 1996 (Sirois & Dodson 2000) using the length at capture, length at hatching (5.81 mm), and a median hatch date (16 May). This analysis revealed that 69% of the parasitised larvae exhibited growth rates below 0.20 mm d^{-1}, while the proportion was 41% for non-parasitised larvae. According to the survival-ratio analysis, these results supported the hypothesis that parasitism has an important impact on survival of smelt larvae by reducing growth rate.

Regulator of year-class strength: critical period or dispersion?

We suggest that larval rainbow smelt in the St. Lawrence Estuary experience 2 major causes of mortality: (1) early starvation during the transition of larvae from endogenous to exogenous feeding, and (2) dispersion during the larval stage related to energy accumulation that is insufficient for larvae to actively migrate in the water column and achieve estuarine retention. Poor growth rates may be linked to parasitic infection. A question is: 'How do these 2 mechanisms interact and determine year-class strength?'

It is unlikely that mortality due to early starvation is a major cause of interannual variability in year-class strength as suggested by the critical-period hypothesis (Hjort 1914). The hatching period of smelt larvae covers almost 2 cycles of variability in the duration of the feeding window. Hence, larvae will experience recurrently good, medium and bad first-feeding conditions

each year. River discharge during the hatching period surely mediates larval drift to the nursery area. However, it seemed to have little influence on interannual variability in early mortality in this study. The instantaneous mortality rate estimated in 1995 was not significantly different than that estimated in 1994, despite a 25% lower mean river discharge in 1995. It is possible, however, that if hatching were to be more concentrated in time, possibly related to extreme environmental conditions, year-class strength could be more affected by the feeding window. This, however, is speculative. On the other hand, all factors reducing growth rate of smelt larvae are important in the determination of year-class strength. We propose that slow growth reflects poor larval condition and insufficient energetic surplus to achieve estuarine retention, resulting in transportation out of the ETM where the probability of survival is low. In particular, parasitism may act as a major regulator of interannual variability in year-class strength in smelt, as has been suggested for animal populations in general (May 1983, Minchella & Scott 1991).

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