

The mechanism of retention of pelagic tomcod, *Microgadus tomcod*, larvae and juveniles in the well-mixed part of the St. Lawrence Estuary

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Synopsis

We tested the hypothesis that the mechanism of retention of tomcod, *Microgadus tomcod*, larvae and juveniles in the well-mixed part of the St. Lawrence Estuary is similar to that of sympatric smelt, *Osmerus mordax*, larvae who actively migrate to the surface during flood tides and to the bottom during ebb tides so as to minimize net downstream displacement. The vertical distribution of tomcod larvae and juveniles was documented during two 98-h sampling series at 2 anchor stations in June and July, 1986. An hourly index of the center of mass of fish in the water column calculated to take into account daytime net avoidance in surface waters suggested that tomcod remained deep in the water column and that their accumulation at the head of the estuary was the result of passive upstream transport by net residual circulation rather than active tidal migrations. For both series, depth of fish was inversely related to density of the water suggesting that the buoyancy of fish influenced their vertical distribution. Tomcod larvae and juveniles were advected by tidal currents. In June, larger larvae were found at low slack water indicating that they were located upstream of smaller larvae. In July, larger juveniles were located downstream of smaller juveniles, the difference in mean length between low and high slack water attaining 20 mm. Ontogenetic buoyancy changes may be responsible for these differences in the vertical distribution of tomcod. Comparisons of the early life-history stages of tomcod and smelt retained in the same area under the same hydrodynamical conditions indicate that more than one mechanism permits retention in a well-mixed estuary and that the observed species-specific patterns of vertical distribution are not simply interpretable as adaptations to retention.

Introduction

Sinclair (1988, p. 109) has recently argued that 'for both estuaries and widely separated oceanic islands, we conclude that certain aspects of life histories (timing of spawning, larval behavior, ontogenetic changes in behavior, duration of larval phase) are 'spatial' adaptations to permit population persistence in a particular geographic space'. Sinclair proposed that the hydrodynamical features of a system may be the principal factor of selection governing behavior of pelagic fish larvae, reflecting

the selective importance of retention. In such a case, behaviors such as vertical migrations or ontogenetic changes in depth distribution may be viewed primarily as adaptations permitting retention in specific hydrodynamic conditions, and several sympatric species of fish larvae occupying the same hydrodynamic regime may be expected to exhibit convergent behavior for the purpose of retention.

The upper section of the St. Lawrence Middle Estuary, located between Ile d'Orléans and Ile-aux-Coudres (Fig. 1), is well mixed at the upstream end and partially stratified at the downstream end

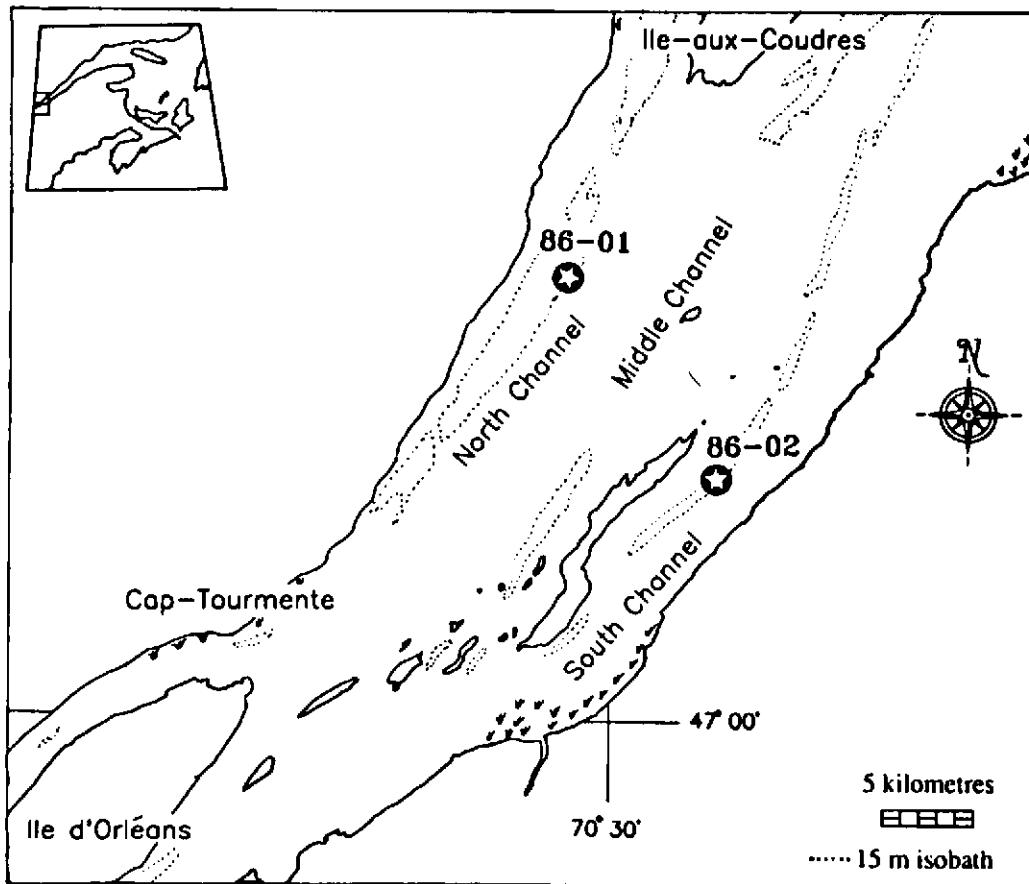


Fig. 1. Location of the stations 86-01 (sampled on June 6 to 10, 1986) and 86-02 (sampled on July 6 to 10, 1986) in the St. Lawrence Middle Estuary.

(Neu 1970, El Sabh 1988). It is classified as highly energetic, tides varying between 3 and 5 m in height and current speed reaching 250 cm s^{-1} , annual mean discharge being $10\,000 \text{ m}^3 \text{ s}^{-1}$ (D'Anglejan & Smith 1973). This part of the estuary is characterized by a permanent turbidity zone, in which the concentration of suspended particulate matter is greater than either upstream or downstream (D'Anglejan & Smith 1973). The pelagic larvae and juveniles of two species of anadromous fishes are retained in this part of the estuary during summer months (Able 1978, Ouellet & Dodson 1985, Dodson et al. 1989). Laprise & Dodson (1989a) have demonstrated that rainbow smelt larvae (*Osmerus mordax*) achieve their retention by active tidal vertical migrations, migrating to the surface during flood tides and to the bottom during ebbs,

so as to minimize their net downstream displacement. Tomcod larvae and juveniles are also retained in the system but the mechanism of retention has not been studied.

The objective of this study was to test the hypothesis that pelagic tomcod larvae and juveniles behave as pelagic smelt larvae to achieve retention in the well-mixed part of the St. Lawrence Estuary. To test this hypothesis, we documented the vertical distribution of tomcod during two 98-h sampling series at 2 anchor stations. If tomcod exhibit a pattern of tidal stream transport similar to smelt larvae, they should be found closer to the surface during flood tides, closer to the bottom during ebbs and at intermediate depths during slack waters (Laprise & Dodson 1989a). In the case that observations do not conform to these predictions, two al-

ternative situations are possible. De Wolf (1973) proposed that negatively buoyant larvae may passively accumulate at the head of turbid well-mixed estuaries by the same physical mechanisms governing the distribution of suspended particulate matter. In such a case, the mean depth of tomcod should be greatest at slack waters and approach the surface during the fastest tidal currents as was observed for suspended particulate matter in this part of the estuary (Laprise & Dodson 1989a). Tomcod could also passively use residual circulation by maintaining their vertical position at depths where the direction of the net water displacement is either null or landward (Weinstein et al. 1980). In this case their mean depth should always be below the depth of null residual current velocity. Either alternative result would indicate that more than one mechanism permits retention of pelagic fish larvae in an intensively flushed system and that the observed species-specific patterns of vertical distribution are not simply interpretable as adaptations to retention.

Materials and methods

The sampling procedure, described in detail by Laprise & Dodson (1989a), consisted of two 98-h sampling series conducted at a fixed anchor station in June (6 to 10) and July (6 to 10), 1986, in the Northern and Southern channels of the St. Lawrence Middle Estuary (Fig. 1). For each series, the 21-m water column was sampled hourly. At each hour, biological and physical data were recorded for 3 depth layers (0 to 7 m, 8 to 14 m and 15 to 21 m). Conductivity, temperature, current speed and direction, and turbidity were measured in the middle of each depth stratum. Fish larvae and juveniles were sampled using a Tucker trawl (1.09 × 1.19 m), equipped with an opening-closing device and a 0.5 m standard plankton net (0.51 mm mesh). A General Oceanic Flowmeter was fitted at the mouth of the gear to measure the filtration rate. The gear was towed obliquely against the current at a speed of 2 to 3 knots. The simultaneous use of a depth recorder, fixed on the net frame, and of an onboard echo-sounder allowed sampling to within 1 m from the bottom in the deepest depth stratum.

Biological samples were preserved in 4% buffered formalin (Markle 1984). In the laboratory, tomcod were sorted and measured to the nearest 0.5 mm (total length). Physical and biological data were analysed by time-series analyses according to Legendre & Legendre (1984). Univariate statistics were made according to Scherrer (1984).

Results

Hydrodynamics

Sampling was performed during spring-tide conditions. Tides were characterized by an asymmetry in amplitude, duration and current speed between flood and ebb phases for a given tide, and between tides for a given day. At station 86-01, located in the Northern Channel which is the preferred route for flooding tides, the flood tides were longer than ebbing tides and the net longitudinal displacement of water masses was landward throughout the water column (Fig. 2). At station 86-02, located in the Southern Channel which is the preferred route for ebbing tides, ebbs were always longer than floods. There was thus a net outflowing current in the major part of the water column and a landward compensatory current near the bottom.

There was significant cross-channel movement of water masses at both stations and the direction of the movement was predictable by the Coriolis force, except for surface waters in June (Fig. 2). The southern movement of surface water at station 86-01 was most probably due to constant northeasterly winds during the sampling period (Laprise & Dodson 1989a).

Both stations were well-mixed most of the time, the station in June becoming slightly stratified at the turn of the tide. In June, salinity varied with the tide from 6.10 to 15.46 g kg⁻¹ and in July, from 0.03 to 6.67 g kg⁻¹. Both stations were characterized by highly turbid waters, values ranging from 8 to 68 NTU (Nephelometric Turbidity Unit) in June and 8 to 140 NTU in July. The concentration of suspended particulate matter during the series varied with the tide due to the longitudinal advection of the turbidity zone. Turbidity was greatest in the

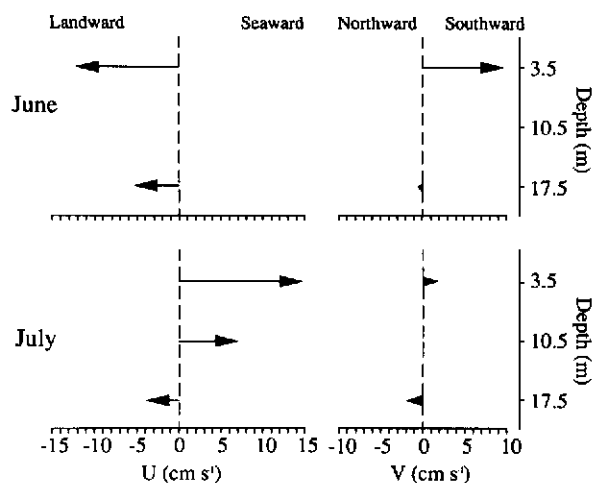


Fig. 2. Vector diagrams illustrating the net residual current speed in June (station 86-01) and July (station 86-02) 1986 for the surface (3.5 m), middle (10.5 m) and bottom layers (17.5 m) in the longitudinal (U) and transversal (V) axis of the St. Lawrence Middle Estuary. Data were averaged over 77.4 h (6 tidal cycles) except for the bottom layer in July, which is averaged over 24.8 h. There were no data for the depth of 10.5 m in June.

bottom layer where there was an increase in concentration every flood and ebb related to the resuspension of bottom sediments by tidal currents.

Abundance, length and net avoidance

Average densities of tomcod were $421 \pm 444 \cdot 1000 \text{ m}^{-3}$ in June and $50 \pm 61 \cdot 1000 \text{ m}^{-3}$ in July. The mean length of tomcod captured during the night in the 3 depth layers was $24.4 \pm 0.4 \text{ mm}$ in June and $49.1 \pm 7.7 \text{ mm}$ in July. The length frequency distributions of tomcod are illustrated in Figure 3. Based on these observations, the average growth rate of young-of-the-year tomcod between June and July was 0.82 mm d^{-1} . Although no data exist on the development of *Microgadus tomcod* after 12.5 mm (Booth 1967), Dunn & Matarese (1984) observed that transformation from larval to juvenile period occurs at about 28–46 mm for *Microgadus proximus*. As the early development of both species of *Microgadus* is very similar, it indicates that tomcod sampled in June were composed mainly of larvae whereas tomcod sampled in July were composed predominantly of juveniles.

In order to evaluate daytime net avoidance, we compared the abundance and length of tomcod captured during the day and night in the three depth layers. However, because of the asymmetry of the tides and the relationship between fish length and tidal state (see below), daytime-nighttime comparisons were made only during the 'ebbing-low slack water' phase of the tidal cycle occurring during the 6-h period of darkness and in the middle of the daytime period. There were significantly fewer fish during the day in the surface layer than at night for both cruises while there were no significant differences in abundance in deeper layers (Fig. 4). The mean length of tomcod, calculated from samples obtained during the periods defined for the daytime-nighttime abundance comparisons, was significantly smaller in the surface layer during the day in June. In July, there was no significant difference even though mean length appeared smaller during the day than at night in surface waters (Table 1). The small daytime sample could account for this result. No significant daytime-nighttime differences in length were detected in the middle and bottom layers.

These results suggest that tomcod avoided the sampler in the surface layer during the day but were unable to do so during the night. Diel vertical migrations cannot explain the observed patterns as the decrease of surface-layer densities during the day was not related to an increase in deeper-layer densities. The absence of avoidance in the middle and deep layers (8–21 m) was most probably due to the high turbidity levels observed at these stations, the secchi disc disappearing between 0.2 and 0.5 m from the surface.

Vertical distribution

Vertical distribution was documented by studying changes in the center of mass of tomcod (mean depth, Fortier & Leggett 1982) calculated from time series of densities for each hour. Due to the avoidance behavior observed in the surface layer, it is impossible to know the real value of the mean depth of tomcod during daytime periods, and, for the same reasons, we cannot calculate an index of

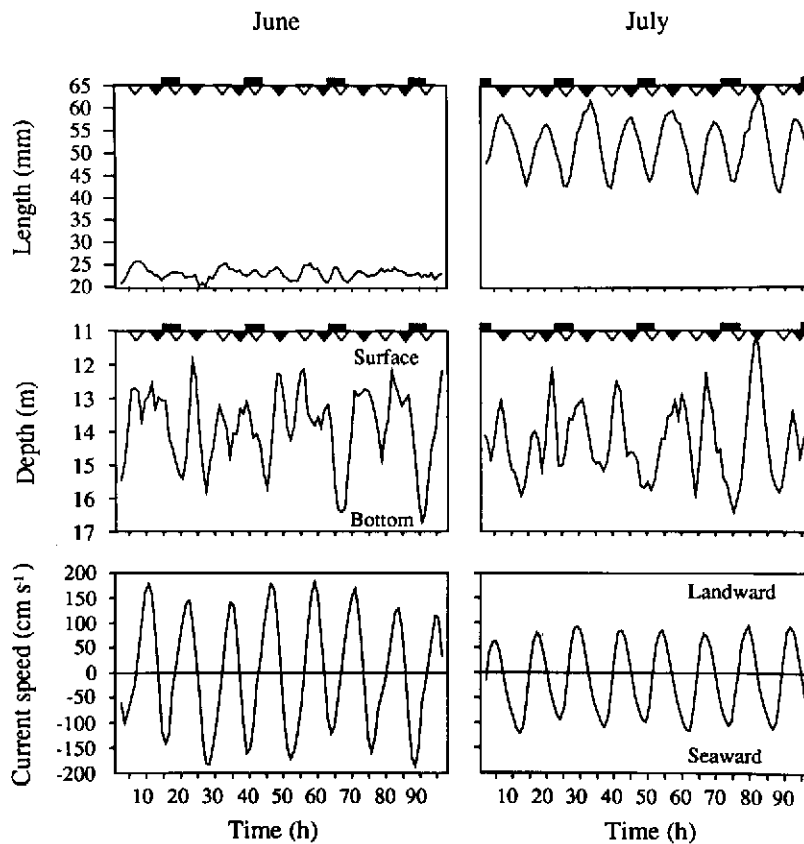


Fig. 5. Time series of mean body length and mean vertical position (depth) of tomcod and longitudinal current speed (U) at stations 86-01 (June 1986) and 86-02 (July 1986), St. Lawrence Middle Estuary. Polynomial long-term trends were removed from the original data and residues were filtered by an order 3 unweighted moving average. Dark triangles = high slack waters; open triangles = low slack waters; dark bars = night periods.

initial predictions of tidal stream transport were unsupported.

Tidal variations of length

In order to evaluate the effect of tidal water-mass displacements on our sampling, we calculated the mean length of tomcod in the water column for each hour by averaging middle and bottom data. Length did not vary with depth for a given hour (Kolmogorov-Smirnov test, $p < 0.05$).

The hourly series of average length of tomcod observed in June and July presented regular cyclic fluctuations (Fig. 5) of 12.4 and 24.8 h periods (Fig. 6) which are correlated with the longitudinal vector

of tidal current (Fig. 7). In June, larger tomcod appeared during low slack water and smaller tomcod during high slack water. In contrast, larger tomcod were associated with high slack water in July, and smaller tomcod with low slack water. The 24.8-h period is associated with the diurnal asymmetry of the tide.

Discussion

Our results indicate that the mechanism of retention of tomcod in the well-mixed part of the St. Lawrence Estuary does not conform to the model of tidal vertical migrations as defined for smelt in the same region (Laprise & Dodson 1989a). No

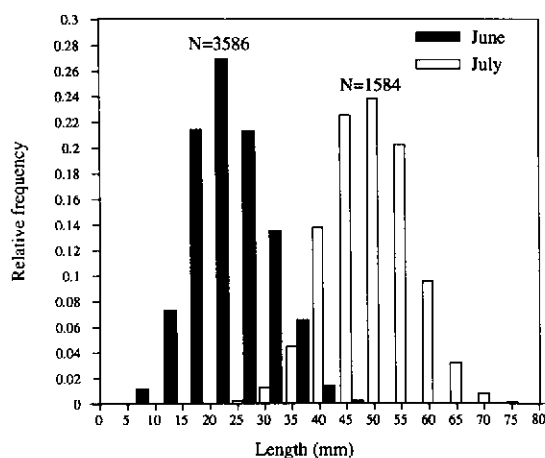


Fig. 3. Relative length frequency distribution of tomcod in June (station 86-01) and July (station 86-02) 1986, St. Lawrence Middle Estuary.

dispersion around the center of mass. However, we calculated an index of center of mass using only middle and bottom-layer data which were not affected by the net avoidance behavior observed in the surface layer. The resultant values are considered to be reliable indicators of the relative hourly vertical position of tomcod. Vertical migrations of tomcod between the bottom and the surface layers would necessarily be detected by hourly variations in abundance in the middle and bottom layers.

The index of center of mass of tomcod larvae and juveniles was on average 14.07 ± 1.24 m from the surface in June, and 14.26 ± 1.24 m in July (Fig. 5)

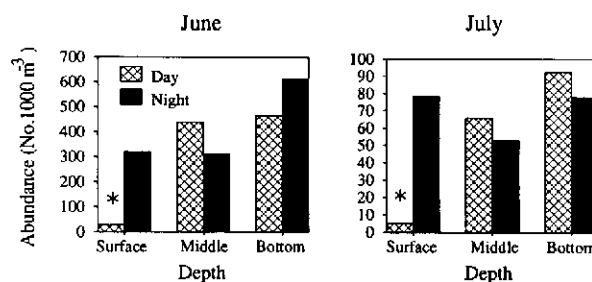


Fig. 4. Mean tomcod densities in the surface (0 to 7 m), middle (8 to 14 m) and bottom (15 to 21 m) layers during daytime and nighttime periods in June (station 86-01) and July (station 86-02) 1986, St. Lawrence Middle Estuary. Stars indicate significant differences between daytime and nighttime abundances (Wilcoxon-Mann and Whitney test, $p < 0.05$).

and was not significantly different between the two months (two-tailed test, $Z_{\text{obs}} = 1.07$, $p = 0.05$).

Autocorrelation functions conducted on the series of the index of center of mass (Fig. 5) revealed significant cycles of 12.4 and 24.8 h periods at both stations (Fig. 6). Crosscorrelation analysis with the longitudinal vector of tidal current (Fig. 7) showed that the center of mass approached the surface at high slack water, was deeper in the water column at low slack water, and was at intermediate depths at the maximum of the flooding and the ebbing currents. The 24.8-h periods were related to the asymmetry of the tidal cycle; during the highest low slack water, fish were found closer to the surface than during the lower low slack water. As such, our

Table 1. Average daytime-nighttime length of tomcod at stations 86-01 (June 1986) and 86-02 (July 1986) in three depth strata (0 to 7 m, 8 to 14 m, 15 to 21 m), St. Lawrence Middle Estuary. Sample sizes are in brackets. (* significantly different according to a Kolmogorov-Smirnov test: $p < 0.05$).

Depth layer	Length (mm)			
	June		July	
	Day	Night	Day	Night
Surface	$22.5 \pm 0.4^*$ (337)	24.7 ± 0.4 (1334)	47.4 ± 7.3 (62)	49.0 ± 8.0 (416)
Middle	24.4 ± 0.4 (1202)	24.5 ± 0.4 (1164)	48.2 ± 8.2 (502)	49.1 ± 7.1 (496)
Bottom	24.3 ± 0.4 (1164)	24.0 ± 0.4 (1088)	49.0 ± 8.0 (606)	49.2 ± 8.0 (672)

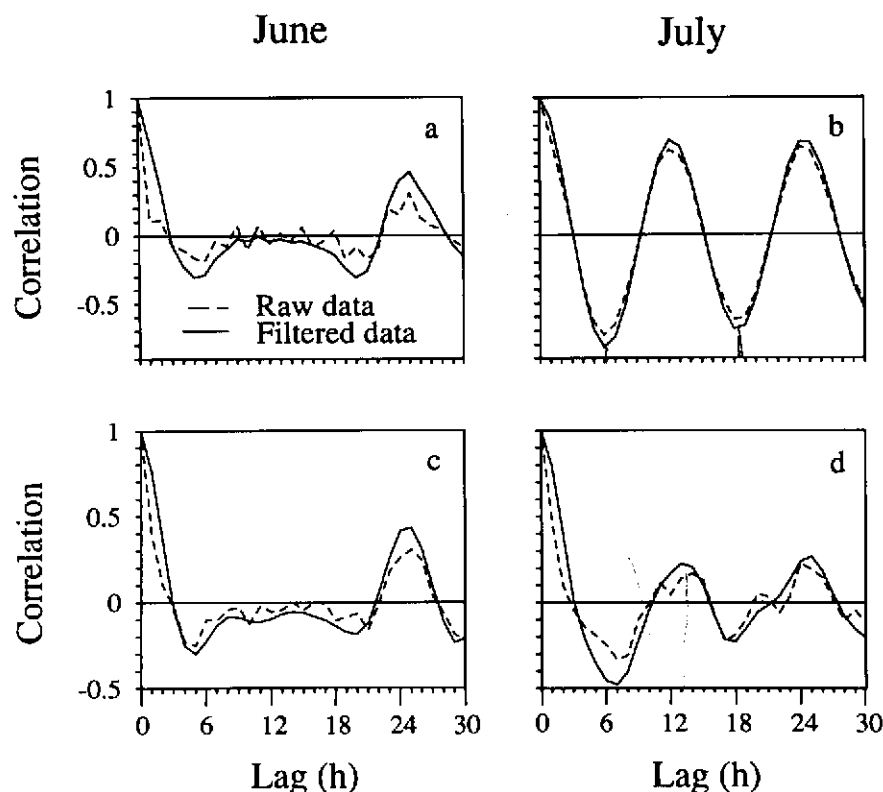


Fig. 6. Autocorrelation functions of the time series of the mean length (a and b) and vertical position (c and d) of tomcod at stations 86-01 (June 1986) and 86-02 (July 1986), St. Lawrence Middle Estuary. Raw data = residues of the polynomial regression; filtered data = residues of the polynomial regression smoothed by an order 3 unweighted moving average.

pattern of vertical migrations allowing selective use of the tidal currents was detected. Tomcod larvae and juveniles were at intermediate depths during both floods and ebbs. The hypothesis of De Wolf (1973), suggesting that fish larvae could be retained in well-mixed estuaries by the same mechanisms as suspended particulate matter (SPM) cannot explain the retention of tomcod. In such a case, we would have observed a similar pattern of vertical position of tomcod and SPM. The concentration of SPM in the bottom layer increased every flood and ebb due to resuspension of bottom sediments by tidal currents. During slack waters, these negatively buoyant particles sank towards the bottom. There is no evidence in the index of vertical position that tomcod could have been 'resuspended' by the floods and the ebbs as bottom sediments. In addition, we did not observe an increase in the depth of center of mass during slack waters. On the

contrary, tomcod were found nearer the surface during high slack waters.

Analyses of mean length of tomcod indicated cyclic fluctuations correlated with the tidal cycle. Larger tomcod larvae were associated with low slack waters in June while larger tomcod juveniles were associated with high slack waters in July. Several factors may create tidal variations of length when sampling fish larvae at a fixed anchor station in a tidally-influenced estuary. The longitudinal movements of water masses may cause fluctuations due to the horizontal pattern of fish distribution in the estuary or by influencing fish catchability. In the first case, fish larvae and juveniles are unable to resist the movement of water masses. For example, in the St. Lawrence Middle Estuary, the longitudinal component of tidal current speed attains at least 100 cm s^{-1} (Fig. 5). Assuming that pelagic fish in the water column are able to assess the speed of

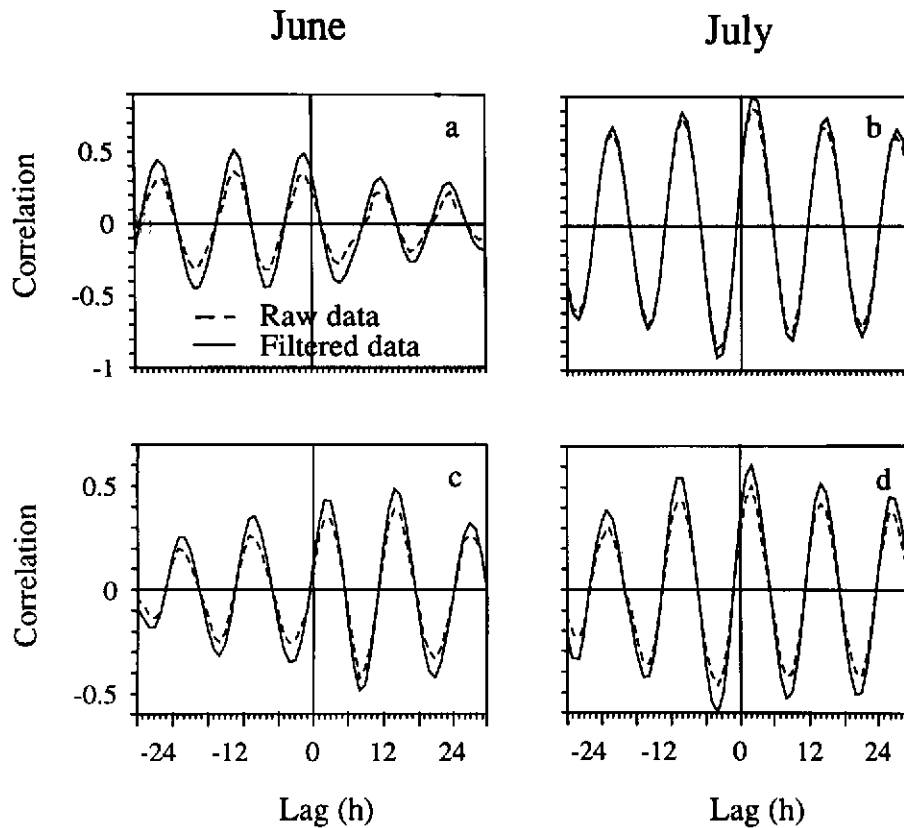


Fig. 7. Crosscorrelation functions between the time series of the mean length (a and b) and vertical position (c and d) of tomcod at stations 86-01 (June 1986) and 86-02 (July 1986), St. Lawrence Middle Estuary, and the longitudinal tidal current speed (U). Raw data = residues of the polynomial regression; filtered data = residues of the polynomial regression smoothed by an order 3 unweighted moving average.

water masses without visual or tactile contact with the bottom, a fish measuring 5 cm (mean length of tomcod in July) must swim against the current at a speed of 201 s^{-1} (body lengths per second) and sustain that speed for at least one hour to maintain horizontal position in the estuary. This seems most unlikely as the maximum prolonged swimming speed recorded for a non scombroid-fish of 5 cm is 81 s^{-1} (40 cm s^{-1} , Blake 1983). We conclude that tomcod larvae and juveniles are unable to maintain a fixed horizontal position in the estuary and are advected by water masses. As such, tidal fluctuations of length reflect their longitudinal distribution. In the St. Lawrence Middle Estuary, the landward or seaward displacements of water masses were on average 13 km, varying between 9 and 26 km depending on the part of the tidal cycle. In

the case of tidal variations caused by fluctuating catchability, the variations of current speed would be the major factor affecting catchability by changing the net efficiency (Fortier & Leggett 1983). Therefore, length of fish should be positively correlated with current speed if catchability was influenced by tidal variation. As the cyclic fluctuations of average length are not associated with the current speed, they indicate that they were caused by the longitudinal advection of tomcod rather than catchability. These results suggest that larger tomcod were located upstream of smaller tomcod in June and downstream of smaller tomcod in July. These results were confirmed by a survey of the horizontal distribution of tomcod in June and July 1987 (Laprise & Dodson 1989b).

The tidal variations in the vertical distribution of

tomcod are characteristic of a static horizontal gradient in vertical distribution. Results on the center of mass indicate, for both months, that tomcod were found closer to the surface during high slack waters, and nearer to the bottom during low slack waters. As our results showed that cyclic fluctuations of length were associated with the tidal advection at a fixed anchor station of the longitudinal distribution of tomcod, it indicates that the cycles observed in the vertical distribution were also related to longitudinal tidal advection. The tidal advection of a static longitudinal pattern of vertical distribution where tomcod located downstream are closer to the surface than tomcod located upstream creates the same pattern of temporal variations in the center of mass as those observed in June and July. Thus, it appears that movements of water masses at a fixed anchor station were responsible for the cyclic fluctuations observed in the vertical position and length of tomcod. It also indicates that the vertical position and the length of tomcod are associated with their longitudinal position in the estuary.

In June, when the residual flow was landward for the whole water column, it is obvious that retention was assured at any depth. But in July, where the residual flow was seaward for the major part of the water column, staying in deeper layers was the only way for a fish not migrating vertically to be retained in the upper part of the estuary. We propose that tomcod maintain their vertical position at depths where the direction and the net water displacement is either null or landward as proposed by Weinstein et al. (1980). As such, tomcod accumulate passively at the head of the estuary by drifting with the deep landward residual circulation.

We may only speculate about the factors responsible for the longitudinal differences in the vertical position and length of tomcod. These differences may be related to water density and fish buoyancy. A relatively constant buoyancy of fish associated with the strong longitudinal density gradients in the estuary would create the static horizontal distribution observed in the vertical position of tomcod in both months, with fish located downstream in denser water being closer to the surface than fish located upstream in less dense water. However, differences in the index of center of mass

between months and among lengths for the same month suggest that buoyancy is not constant but varies with fish length. In July, tomcod juveniles measuring a mean length of 49 mm exhibited the same index of center of mass as tomcod larvae measuring a mean of 24 mm in June despite major differences in salinity. Salinities at mid-depth (10.5 m) were on average 10.18 g kg⁻¹ and 2.3 g kg⁻¹ with associated water densities of 7.73 and 0.63 in June and July, respectively. Therefore, tomcod juveniles in July were apparently more buoyant than larvae in June and located higher in the water column for a given salinity. Such length related buoyancy differences may also account for the strong longitudinal gradient in mean length observed in July, the length of juveniles captured at high tide exceeding that of juveniles captured at low tide by as much as 20 mm. Larger, more buoyant juveniles occupying shallower depths than smaller juveniles may be displaced downstream due to the vertical pattern of residual current speed and direction. In June, the longitudinal length difference was much less evident and opposite to that observed in July. Larvae captured at low tide measured only 3 mm greater than those captured at high tide. Developmentally controlled changes in buoyancy have been recorded or implied during the transition from yolk sac to post-yolk sac larvae (Blaxter & Ehrlich 1974, Henri et al. 1985, Frank & Carscadden 1989), but we know of no data that support the mechanisms we have proposed to explain the longitudinal distribution of tomcod larvae and juveniles. Although quite speculative, we propose that ontogenetic buoyancy changes may be of major importance in controlling the vertical position of the early life history stages of fishes living in tidally energetic systems where active sustained swimming cannot be hypothesized to control longitudinal position.

In the upper part of the St. Lawrence Middle Estuary, we observed two species of fish larvae retained in the same area under the influence of the same hydrodynamical conditions. The results of this paper do not support the hypothesis that retention is the major factor of selection of the behavior of fish larvae, the differences in the vertical distribution of the two species not being related to the hydrodynamical particularities of their retention

zone. It indicates that, even in an intensively flushed area, at least two solutions to the problem of retention are possible and suggests that other factors must be considered. Elsewhere (Laprise & Dodson 1989b), we have proposed that the ontogenetic changes in vertical distribution of smelt and tomcod may be related to a mechanism serving to partition the retention zone so as to minimize competitive interactions between the two species.

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