Spatial Configurations of Young Herring (*Clupea harengus harengus*) larvae in the St. Lawrence Estuary: Importance of Biological and Physical Factors[1,2]

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The phenomenon of larval retention has recently been identified as central to the structuring of herring stocks. It has been shown that retention of larval fish populations in estuaries is dependent on active vertical migration, the capacity for which develops with growth, but the present study shows that mechanisms for spatial structuring of larval herring (*Clupea harengus harengus*) populations act at the earliest (yolk sac and post-yolk sac) stages. The study was carried out on the Isle-Verte stock of the St. Lawrence estuary in 1981 and 1982. Length–frequencies and tide-related abundance fluctuations suggested that larvae are retained in the study area. As a result, larvae remain aggregated throughout the sampling period of approximately 1 mo. Yolk sac larvae were significantly more abundant near the bottom than in the water column, while post-yolk sac larvae were significantly less abundant in the suprabenthic layer than in the water column. Larvae, being negatively buoyant, tend to sink in slack water but are transported upwards by turbulence resulting from tidal flows. The extent of vertical transport of larvae in the water column is greatest for larvae with lesser specific gravities; specific gravity is at a maximum at hatching and decreases to a minimum at yolk sac absorption. We conclude that larval specific gravity, current velocity, and the two-layer residual circulation are the major factors causing retention and aggregation of larvae.

Le phénomène de rétention larvaire a récemment été identifié comme central à la structuration des stocks de hareng. D'après les études publiées, la rétention des larves de poisson dans les estuaires résulte de migrations verticales actives dont la capacité se développe avec la croissance, mais notre étude suggère que des mécanismes de structuration spatiale de populations de larves de hareng (*Clupea harengus harengus*) agissent aux stades les plus jeunes (à sac vitellin et à vitellus nouvellement résorbé). Le stock étudié en 1981 et 1982 est celui de l'Isle-Verte de l'estuaire du Saint-Laurent. Les fréquences de longueur et les fluctuations d'abondance liées à la marée suggèrent que les larves sont retenues dans l'aire d'étude. Conséquemment, les larves sont agrégées durant toute la période d'échantillonnage, approximativement 1 mo. Les larves avec vitellus sont significativement plus abondantes près du fond que dans la colonne d'eau tandis que les larves sans vitellus sont significativement moins abondantes dans la couche suprabenthique que dans la colonne d'eau. Les larves, de flottabilité négative, tendent à s'enforcer durant l'étale et sont transportées vers la surface par l'action turbulente des courants notamment lors du montant. Le transport vertical des larves dans la colonne d'eau est supérieur pour les larves à faible poids spécifique; le poids spécifique est maximal à l'éclosion et diminue jusqu'à un minimum lors de l'absorption du vitellus. Nous concluons que le poids spécifique larvaire, la vélocité du courant et la circulation résiduelle à deux couches sont les facteurs majeurs causant la rétention et l'agrégation des larves.

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The hypothesis has recently been put forward that herring stock structure is linked to areas of larval retention (Iles and Sinclair 1982). In estuaries, two-layer residual circulation has been suggested to provide a physical mechanism for retention of larvae. Various studies (Pearcy 1962; de Wolf 1974; Weinstein et al. 1980; Setzler et al. 1981) have focussed on retention of larvae both in mixed and in stratified estuaries. Graham (1972) demonstrated active vertical migrations leading to retention of larval herring within the Sheepscot estuary of Maine. However, he added that although residual

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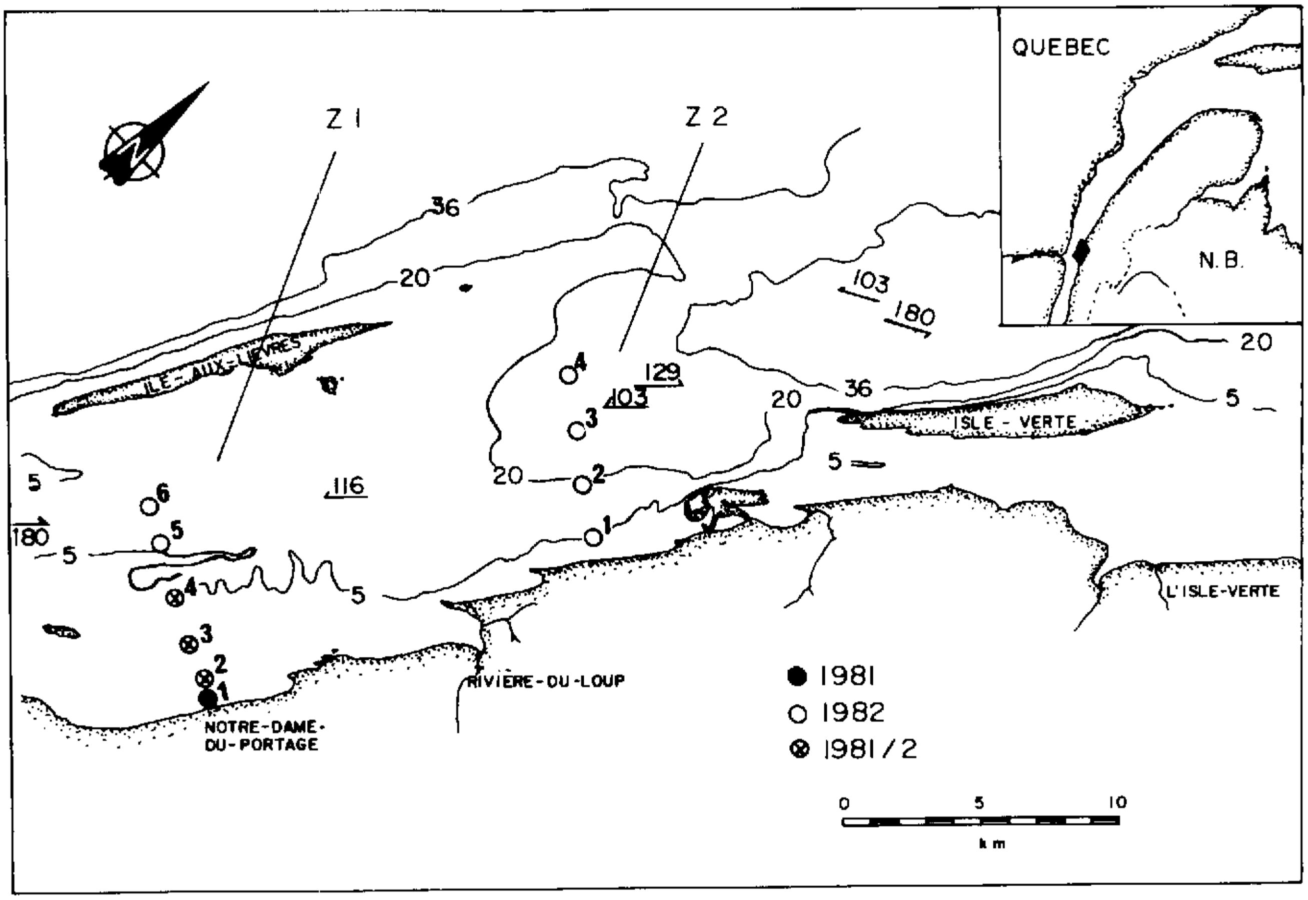

FIG. 1. Study area and sampling stations for the two seasons (1981, 1982). Isobaths (m) and maximum surface currents (cm/s; from marine charts) are indicated.

tidal current affected larval transport, the precise nature of this transport is difficult to determine because of temporal variations in tidal current.

The herring (*Clupea harengus harengus*) stock studied is that of Isle-Verte, characterized by low length-at-age values, possibly a result of slow growth in the first year (Côté et al. 1980). Herring of this stock spawn during the second half of May between Notre-Dame-du-Portage and Isle-Verte (Fig. 1). Several studies have treated distribution, abundance, and transport of larval fishes, in particular herring, in the St. Lawrence estuary. Able (1978) noted that the center of distribution of larval herring moved up-estuary from the presumed spawning ground, over the summer, following spring spawning. Fortier and Leggett (1982) showed that herring larvae were concentrated in the deep layer and carried up-estuary. They proposed that short-term fluctuations in abundance and vertical distribution of larvae should be interpreted in terms of the Fickian representation of transport in partially mixed estuaries (following Fick's law of diffusion of properties along a gradient in a fluid medium).

It has been shown (Graham 1972; Weinstein et al. 1980) that horizontal movements of larvae in estuaries are controlled through vertical migration but that the youngest stages, with very limited swimming capacities, drift passively with currents, as proposed by Fortier and Leggett (1982) for herring larvae < 10 mm. One conclusion might be that larvae disperse after hatching in estuaries until swimming capacities are developed sufficiently to permit vertical migration and, as a result, retention or other spatial structuring of populations. The general objectives of the present paper are to show that the youngest larval stages of herring are strongly retained near the spawning site in a tidally active estuary, and to describe the physical and biological mechanisms that appear to contribute to retention of young larvae.

Study Area

The study area is located in the south channel of the St. Lawrence estuary, between Notre-Dame-du-Portage and Isle-Verte (Fig. 1). The 20-m isobath divides this area into two zones. The first (Z1) is shallow and vertically mixed, while the second (Z2), representing the south channel, is stratified. Two-layer estuarine circulation is a feature of the south channel (d'Anglejan and Ingram 1976); thus, a residual up-estuary bottom current is present here. Surface currents are strong in this area (Fig. 1) and mean minimum and maximum currents at mean depth are approximately 35–67 cm/s (Table 1). Near the south shore of the St. Lawrence estuary, mean current at mid-depths is approximately 20 cm/s down-estuary, in compensation for the mean up-estuary drift in the north channel (Ingram 1979). Maximum tidal fluctuations are approximately 5 m.

Materials and Methods

Field Sampling

Sampling was conducted along a lateral transect of four stations in zone Z1 in 1981 and in zone Z2 in 1982 (Fig. 1). In

TABLE 1. Mean currents (component *u* (range)) at mean depths (4 m in zone Z1, 14 m in zone Z2) for various tidal amplitudes in the study area.

Area	Date	Mean currents at mean depths (cm/s)		Tidal amplitude (m)
		Ebb	Flow	
Z1	18 June 1981	62 (34–89)	48 (5–81)	3.52
Z1	24 June 1981	58 (8–83)	40 (3–57)	2.87
Z1	2 July 1981	51 (1–82)	58 (26–78)	4.42
Z1	17 June 1982	42 (6–70)	35 (10–55)	3.12
Z1	25 June 1982	56 (2–90)	43 (10–65)	4.17
Z2	11 July 1982	51 (2–120)	62 (38–87)	3.11
Z2	21 July 1982	61 (18–120)	67 (23–96)	4.46
Z2	31 July 1982	37 (14–65)	43 (10–83)	2.36

zone Z1 in 1982, two stations (Nos. 5 and 6, Fig. 1) were added to the transect and the inshore station (No. 1) was dropped. Time series sampling (1-h intervals) was conducted over 13-h tidal cycles at one station in each zone (station 4 in Z1, station 3 in Z2). In 1981, two time series were conducted at neap tides and two at spring tides. A fifth was carried out on 28 June 1981 at station 5 in zone Z1. In 1982, three time series were conducted in each zone. Times of sampling in zone Z1 in 1982 were based on the hatching patterns observed in 1981 and were independent of tidal stage.

On the transects, when depth permitted, an oblique tow was made with a conical plankton net (mouth diameter 0.5 m, mesh 0.333 m) fitted with a General Oceanics flowmeter. Horizontal tows were made at shallow (<2 m) depths. Tows were of 10 min duration at approximately 1.1 m/s (2 knots). Secchi depths were taken following each tow.

On time series stations, an oblique tow and a bottom tow were made hourly for 13 h. In zone Z1 in 1981 and in zone Z2 in 1982, bottom tows were made with a plankton net and in zone Z1 in 1982 with a suprabenthic sled weighing 22 kg and measuring 0.5 m in length, width, and height. The sled was designed to sample at 0.5 m from the bottom. Bottom tows made with the plankton net sampled at approximately 1–2 m from the bottom. Sled samples are hereafter referred to as suprabenthic tows, while bottom plankton net samples are referred to as near-bottom tows. Tows referred to as "bottom tows" are either suprabenthic sled tows or bottom plankton net tows. The suprabenthic sled's plankton net was shorter but otherwise identical to that used for plankton tows. In addition to plankton tows, Secchi disc measurements and hourly current observations at depth were made. Speed and direction of currents were measured five times during 5 min with an Endeco type 1014 current meter. Observations were made at 2 and 4 m at station 4, zone Z1 and at 7, 14, and 21 m at station 3, zone Z2.

Two drogue experiments were carried out. The drogue, constructed of three 1-m-diameter plywood discs fixed perpendicular to each other with a depressor for negative buoyancy, was maintained at 5-m depth and was marked by a lighted buoy. Both experiments began at station 4, zone Z1 (Fig. 1). The first 18 June 1982) lasted 5 h during the ebbing tide. Hourly oblique and suprabenthic sled tows were made near the drogue. In addition, 5-m temperature, Secchi depth, bottom depth, and position were recorded. The second experiment (16–17 July 1982) lasted 32 h. Observations were similar but at 2-h intervals, and the plankton net rather than suprabenthic sled was used for bottom tows.

Laboratory Observations

Herring larvae were counted from fractions containing a minimum of 200 larvae or from whole samples. Presence/absence of yolk sac was recorded. Total lengths were measured to 0.05 mm, on a subsample of 50 larvae in 1981 and 25 larvae in 1982, or the whole sample if numbers were low.

Analytical Methods

The larval abundance index for transects was defined as

$$\frac{\sum_{i=1}^{n} x_i w_i}{n}$$

where x_i = larvae/10 m^2 surface area, w_i = (distance between midpoints of adjacent stations)/(total distance over all stations on the transect), and n = number of stations. The index serves as a weighted average of larval abundance over stations on the transect.

Analysis of time series data from fixed stations was directed at evaluating spatial heterogeneity of larval distributions. Sampling hourly is considered adequate for describing contagious distributions of larvae in tidal current regimes (de Wolf 1974).

The spatial scale of aggregation was estimated to identify the center of the larval concentration in the retention zone. Abundance values (number per 10 m^2) were calculated using the equation described by Smith and Richardson (1977). The patch of herring larvae is presented as though sampling was carried out instantaneously along longitudinal and lateral axes at the end of the ebbing tide. To do this, a part of the time series data (abundance values during either ebb or flood tide) was converted to a longitudinal spatial axis by displacing successive abundance values downstream by distances calculated according to current values measured during the time series. For abundance values measured during ebb tides, the first sample (beginning of ebb) represents the most downstream value. For abundance values measured during flood tides, the last sample (end of flood) represents the most downstream value. To permit incorporation of data from the lateral transects, the abundance values at station 4 in zone Z1 or at station 3 in zone Z2 were interpolated among the time series values on the longitudinal axis. The remaining abundance values from the lateral transect were positioned using tidal displacements relative to the reference station. To detect the center of the larval patch using this procedure, one must obtain a maximum abundance value for both the longitudinal and lateral axes.

The patchiness index used in this study (Lloyd 1967) is derived from an estimate by moments; values of larvae per 100 m^3 replaced the quadrat data usually used to calculate this index. The index measures the intensity but not the spatial scale of patchiness (Hewitt 1981). Since it is independent of mean number per 100 m^3, the index can be used to compare results from periods of different overall abundances. The index was calculated for three data series: oblique tows from temporal series (n = 13), bottom tows from temporal series (n = 13), and all oblique tows including those on the lateral transect (n = 17 for Z1 in 1981 and Z2 in 1982, n = 18 for Z1 in 1982). It should be noted that standard error of the patchiness index cannot be adequately estimated (Lloyd 1967). Thus, statistical comparison of patchiness index values is not possible.

All tow data (number per 10 m^2 or number per 100 m^3) were

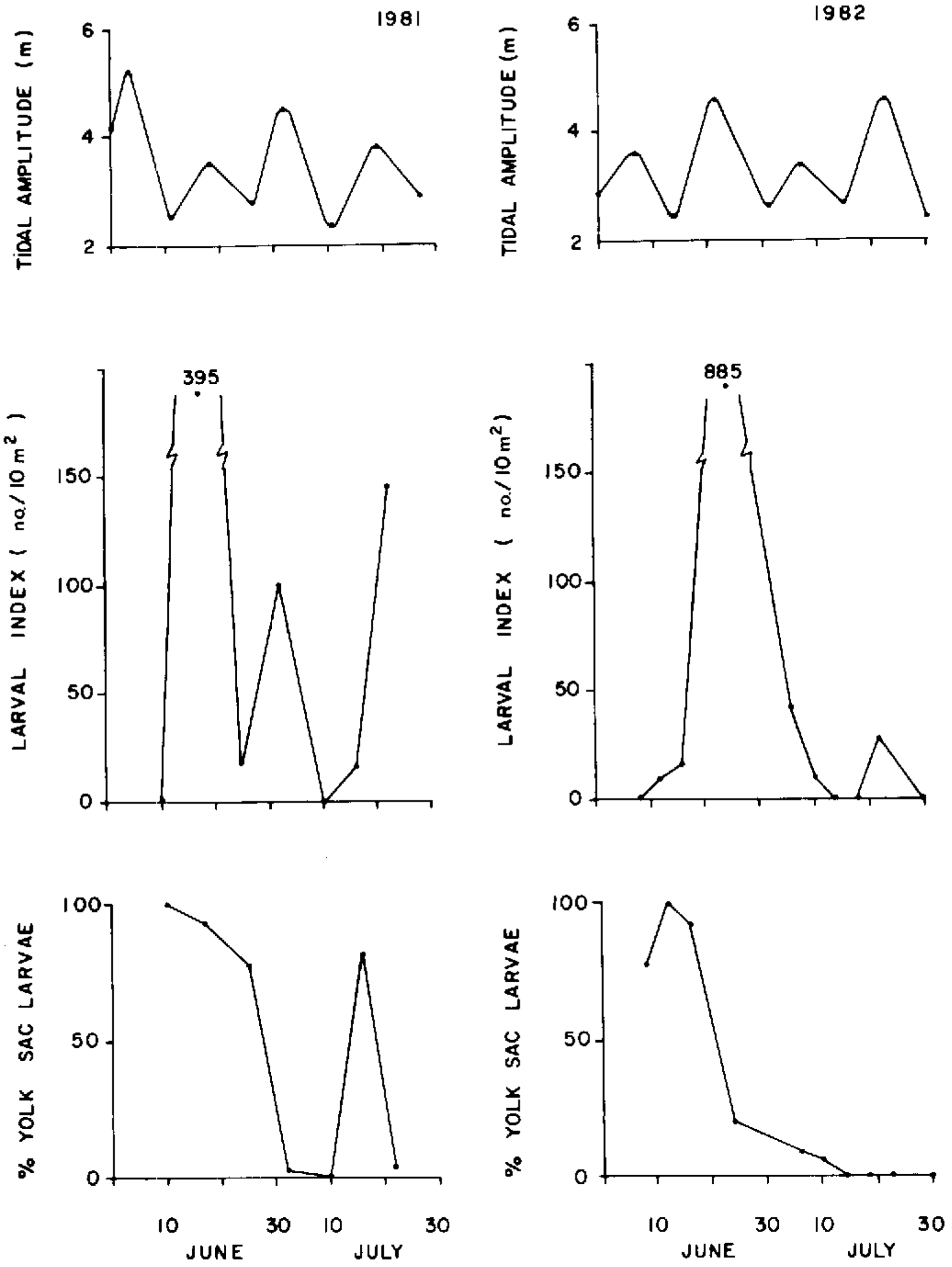

FIG. 2. Fluctuations in tidal amplitude, larval abundance index, and percent yolk sac larvae in zone Z1 for the two sampling seasons (1981, 1982).

transformed by $\log_{10}(x + 1)$, and normality of distributions was verified by the Kolmogorov–Smirnov test prior to carrying out t-tests and calculating Pearson correlation coefficients. Ratios of log-transformed abundance values (oblique tow/bottom tow) were used to reduce masking of the vertical component by the longitudinal component when transformed abundance values alone are used. Changes in these ratios with time indicate vertical transport; for example, an increase in the ratio over time indicates upward transport of larvae with time. The role of currents in vertical transport was investigated by correlating current speeds and the ratios of larval densities. Significant positive correlations indicate the transport of larvae from the bottom upwards through the water column with increasing current speed.

Results

Retention

Tide-related abundance fluctuations and length–frequency observations indicate that young herring larvae return with spring tides to the study sites. We observed a relationship between the larval abundance index and tidal amplitude (Fig. 2). For 1981 data, the Pearson correlation coefficient was $r = 0.79$ ($p < 0.05$). Thus, 63% of the variability (r^2) in the larval index was explained by tide. Length–frequencies indicate production of two cohorts, of which the first was still present on 22 July (Fig. 3). Thus, larval growth occurred in zone Z1. The peak in larval abundance index observed 1 July did not result from appearance of a new cohort, since only 2% of larvae had

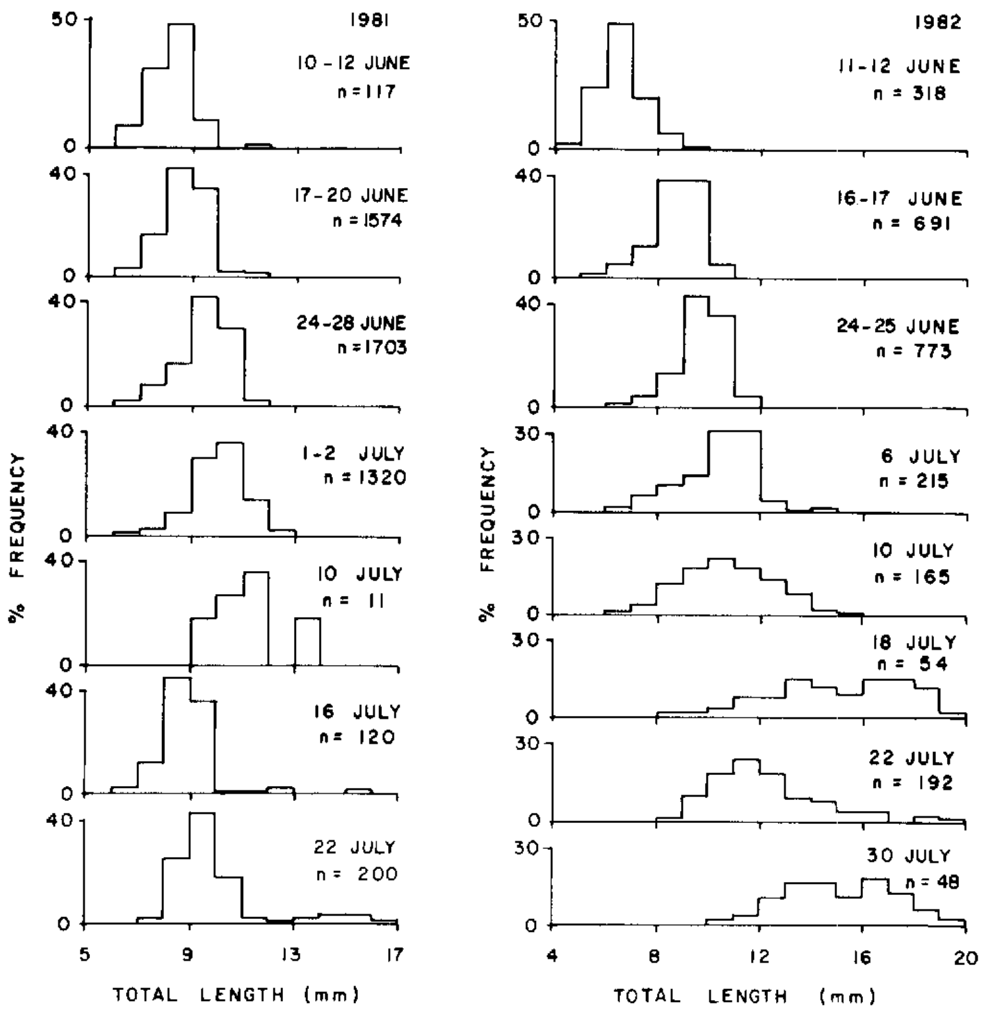

FIG. 3. Larval length–frequencies in zone Z1 for the two sampling seasons (1981, 1982).

yolk sacs (Fig. 2). This peak thus suggests transport of larvae into zone Z1 during spring tides.

In 1982, an abundance peak on 24 June during spring tides was 75% made up of post-yolk sac larvae (Fig. 2). This peak does not appear to result from hatching events as was observed on 18 June 1981. Hatching coincided with spring tide in 1981 but not in 1982. The larval index in 1982 was not significantly correlated with tidal stage ($r = 0.52$, $n = 10$). However, a mean larval index value for the first three cruises was used in calculations, reducing variability due to hatching between 8 and 16 June. Increase in abundance due to hatching could mask the effect of tide in transporting larvae. This mean value is associated with the first period of neap tides. The correlation coefficient became $r = 0.72$ ($p < 0.05$) so that just over 50% of the variability is explained by tide. Length–frequencies (Fig. 3) do not indicate production of a second cohort of larvae in mid-July as was observed in 1981, but these data show that length composition in the area sampled is related to the tide. During spring tides occurring on 10 and 22 July, larvae were smaller than for neap tides occurring on 18 and 30 July.

Return transport of larvae into the area sampled was greater in 1981 (larval index 1 July/larval index 18 June = 0.25) than in 1982 (larval index 6 July/larval index 24 June = 0.05) (Fig. 2). The difference may be due in part to greater tidal amplitudes on 1 July 1981 than on 6 July 1982.

Tide-related abundance fluctuations similar to those observed in zone Z1 were also observed in zone Z2. On 10, 23, and 30 July 1982, tidal amplitudes were 3.11, 4.46, and 2.36 m, respectively, and larval abundance index values were 29, 559, and 27 larvae/10 m^2, respectively. These values were generally an order of magnitude higher than those observed in zone Z1 during the same period. The highest abundance value observed during spring tides on 23 July in zone Z2 was at station 2, whose bottom depth was 20 m. This depth corresponds to the depth of zero residual current in this area (Bio-Conseil 1982).

The results indicate that larvae are retained in the study area despite strong tidal currents. During both years, results demonstrate return transport of larvae into zone Z1 during spring tides. Annual differences in return transport to Z1 were observed. Tide-related variations in length composition for zone Z1 were observed in July 1982. Larval retention appears to be more important in zone Z2, where up-estuary bottom drift occurs, than in zone Z1.

Aggregation

Aggregation of larvae is linked to the phenomenon of retention. Considerable temporal variation of larval abundance in near-bottom water was noted during tidal cycle sampling on 18 June 1981 (Fig. 4). This variation can be interpreted as spatial variability, since different parcels of a moving water mass are sampled over time at the fixed station. The yolk sac stage

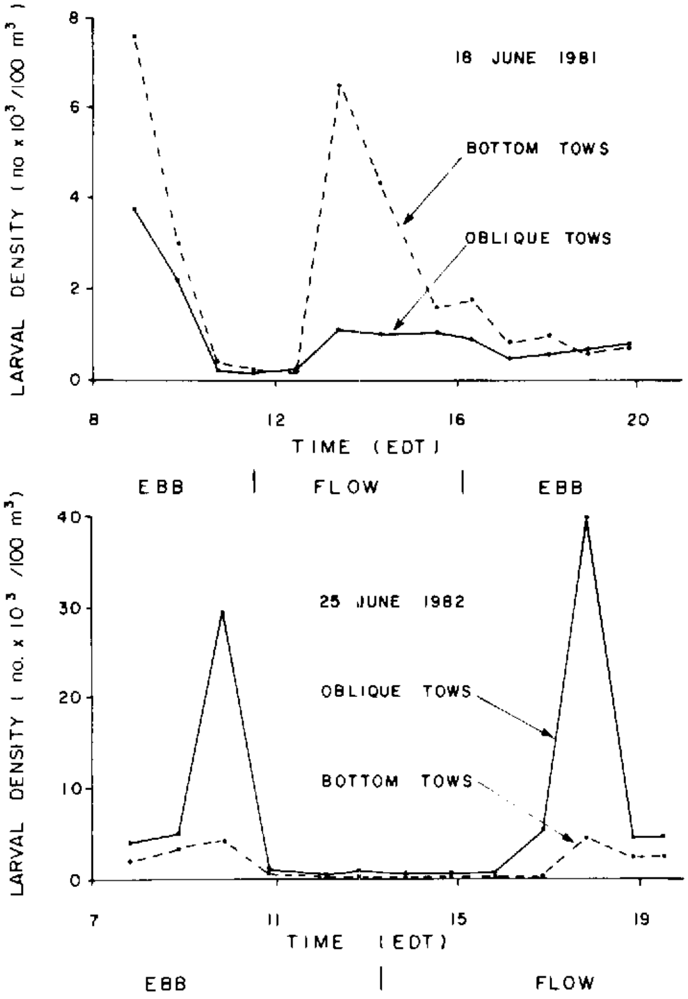

FIG. 4. Larval densities in oblique and bottom tows for two tidal cycles (18 June 1981, 25 June 1982). Bottom tows were made with plankton net in 1981 and suprabenthic sled in 1982.

accounted for 99% of larvae. At first sight, this spatial heterogeneity might appear to result from a discrete hatching event. However, similar heterogeneity was observed on 25 June 1982 for larvae from oblique tows. At this time, only 26% of larvae had yolk sacs. Thus, heterogeneity probably did not result from discrete hatching events but from retention of larvae in a discrete patch and oscillatory transport of the patch with tidal currents.

Data from the two time series conducted during spring tides in 1982 were used to describe the spatial scale of aggregation and to determine the position of the center of the patch of larval herring (Fig. 5). In 1981, the return of larvae to zone Z1 was not sufficient to obtain a maximum abundance value for the longitudinal axis. For 1982, we estimate a down-estuary displacement of the center of the patch equal to 0.2 km/tidal cycle. This rate is 22 times inferior to the rate of displacement of the water mass as estimated by drogue experiments.

In 1981, the patchiness index for 1–2 July was similar to that for 17–18 June, the peak of yolk sac larval abundance (Table 2). Both dates were characterized by spring tides. In 1982, the patchiness index was positively correlated with tidal amplitude (zones Z1 and Z2; $r = 0.93$, $p < 0.05$).

Higher values of the patchiness index were obtained near bottom (plankton net tows) than in the water column during spring tides (tidal amplitude > 3.47 m, Table 2). Patchiness index values increased with increasing tidal amplitude, but the increase was greater in the water column as shown by indices from oblique tows than in the suprabenthic layer as shown by bottom tow indices.

Higher values of the patchiness index were obtained for yolk sac larvae than for post-yolk sac larvae in three of four cases (Table 3). Comparison of the index for total larvae with that of the dominant stage reveals that yolk sac larvae (17–18 June 1981, 16–17 June 1982) were more highly aggregated than total larvae and post-yolk sac larvae (1–2 July 1981, 24–25 June 1982) less aggregated. These values were not independent but support the previous observation that yolk sac larvae are more aggregated than post-yolk sac larvae.

The results suggest that larvae are aggregated by the retention process, apparently related to the deep up-estuary drift that concentrates larvae at the channel entrance. The patchiness index remained high throughout the period mid-June to end of July in both years.

Vertical Distribution

The observed retention and aggregation of herring larvae may be a result of an interaction between their vertical distribution and the currents prevailing at different depths. In 1981, yolk sac larvae were significantly more abundant near the bottom than in the water column (Table 4). The difference was more significant during the peak of yolk sac larval abundance observed on 18 June. Post-yolk sac larvae, however, were as abundant in bottom tows as in oblique tows (Table 4). The value of t for the 2 July sampling series, when post-yolk sac larvae comprised 99% of the sampled larvae, is inferior to that calculated for the whole season (Table 4). Use of the suprabenthic sled in 1982 revealed further differences in the vertical distribution of yolk sac and post-yolk sac larvae. For the entire season, fewer post-yolk sac larvae were observed in the suprabenthic layer than in the water column (Table 4) whereas yolk sac larvae were equally abundant in the suprabenthic layer and in the water column. The same distribution was observed on 25 June during the peak of abundance.

To summarize, the greatest concentrations of yolk sac larvae appear near the bottom with lower concentrations observed in the water column and in the suprabenthic layer. Post-yolk sac larvae appear equally abundant in the water column and near bottom, but less abundant in the suprabenthic layer than in the water column.

Vertical Transport of Larvae

Turbulence created by tidal currents acts to produce vertical transport of herring larvae in the water column. During the flood tide, 83% of the correlations between magnitude of current and the ratios of larval densities between oblique and bottom tows are positive, although only three are significant (Table 5). Since increasing values of the ratio oblique to bottom tow abundance suggest the occurrence of upward transport, positive correlations suggest that degree of transport and current speed are related. No clear tendency exists during the ebbing tide.

The vertical transport of yolk sac and post-yolk sac larvae is different, and many of the nonsignificant correlations are due to the interaction between developmental stage and sampling gear. In 1982, when the suprabenthic sled was used, correlations for yolk sac larvae were significant, suggesting the association between current strength and upward transport (Table 5). As

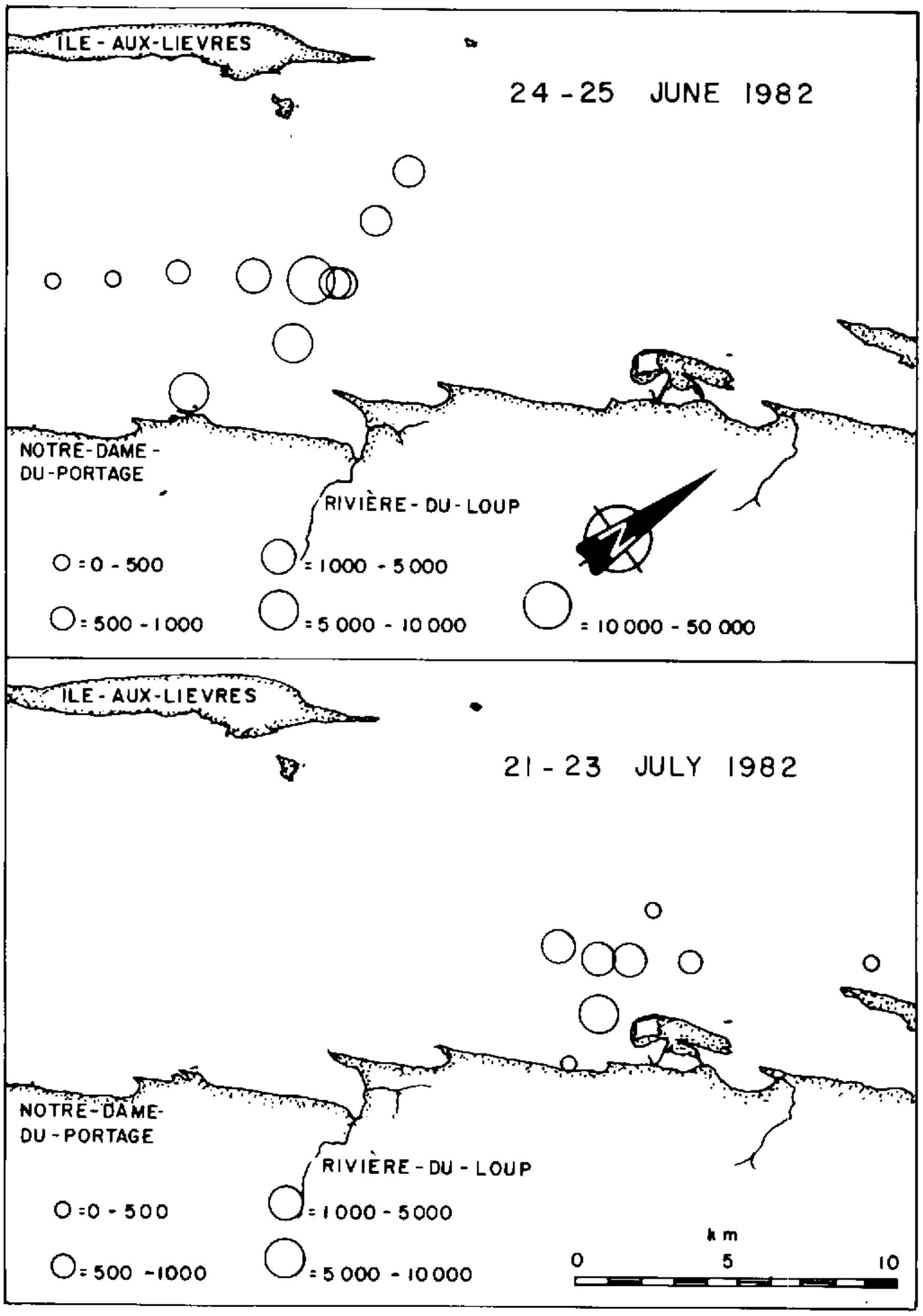

FIG. 5. Spatial scale of larval aggregation for two cruises (24–25 June in zone Z1, 21–23 July in zone Z2) in 1982. Larval densities (no./10 m^2) are indicated by the circles.

post-yolk sac larvae are rare in the suprabenthic layer relative to the water column (Table 4), no significant correlation would be expected between tidal current velocity and the ratio of larvae in oblique tows to suprabenthic tows, and none are observed (Table 5, 1982). In 1981, however, the use of horizontal tows with plankton nets close to the bottom revealed vertical transport of post-yolk sac larvae during flood tides, becoming significant on 28 June when the proportion of post-yolk sac larvae in the sampled population had increased. The failure of horizontal tows close to the bottom in 1981 to reveal vertical transport of yolk sac larvae suggests that although they are transported out of the suprabenthic layer by tidal currents, they nevertheless remain close to the bottom and are not dispersed throughout the water column.

As the vertical transport of post-yolk sac larvae throughout the water column appears more extensive than that of yolk sac larvae, the horizontal dispersion during any one tidal cycle of post-yolk sac larvae should be greater than that of yolk sac larvae. The sampling series of 24 June 1981 supports this hypothesis (Table 5; Fig. 6). A significant vertical transport of post-yolk sac larvae was observed during the ebbing tide (Table 5). At the end of the ebb, few larvae were present, as the patch

Table 2. Patchiness index of larvae (SE in parentheses) for various tidal amplitudes at Notre-Dame-du-Portage (Z1) and Rivière-du-Loup (Z2) (n = number of samples).

Area	Date	Patchiness index: Oblique tows, temporal series (n = 13)	Patchiness index: Bottom tows, temporal series (n = 13)	Patchiness index: Oblique tows series and transect (n = 17 or 18)	Tidal amplitude (m)
Z1	17–18 June 1981	2.01 (0.53)	2.29 (0.70)	1.84 (0.42)	3.47
Z1	1–2 July 1981	1.89 (0.45)	2.04 (0.54)	2.24 (0.59)	4.45
Z1	16–17 June 1982	1.38 (0.17)	1.59 (0.28)[a]	1.76 (0.32)	2.92
Z1	24–25 June 1982	3.99 (1.97)	2.06 (0.55)[a]	3.01 (1.25)	4.00
Z2	10–11 July 1982	2.76 (1.03)	1.95 (0.50)	2.86 (1.09)	3.20
Z2	21–23 July 1982	2.86 (1.09)	6.15 (3.84)	3.52 (1.59)	4.49
Z2	30–31 July 1982	2.04 (0.55)	2.04 (0.55)	1.63 (0.27)	2.31

[a] With suprabenthic sled.

Table 3. Comparative patchiness index of yolk sac larvae and post-yolk sac larvae for various tidal amplitudes at Notre-Dame-du-Portage (Z1) (n = number of samples).

Date	Patchiness index: Yok sac larvae	Patchiness index: Post-yolk sac larvae	Patchiness index: Total larvae	% of yolk sac larvae	n	Tidal amplitude (m)
17–18 June 1981	1.96	2.81	1.84	93	17	3.52
1–2 July 1981	7.13	2.23	2.24	2	17	4.47
16–17 June 1982	1.79	1.74	1.76	92	18	3.12
24–25 June 1982	4.21	2.83	3.01	25	18	3.82

Table 4. Results of t-tests of larval densities (no./100 m^3) between oblique and bottom tows at Notre-Dame-du-Portage (Z1) (n = number of samples, p = probability level, NS, not significant).

Date	Stage of larval development	Mean (SE) of log-transformed densities for oblique tows	Mean (SE) of log-transformed densities for bottom tows	t-value	p	n
Season of 1981	Yolk sac	1.3857 (0.141)	1.5126 (0.152)[a]	2.25	<0.05	51
	Post-yolk sac	1.5634 (0.131)	1.4628 (0.133)[a]	1.54	NS	51
18 June 1981	Yolk sac	2.7392 (0.126)	3.0453 (0.154)[a]	4.55	<0.01	13
	Post-yolk sac	1.5432 (0.196)	1.1015 (0.170)[a]	2.46	<0.05	13
2 July 1981	Yolk sac	0.6147 (0.172)	0.4941 (0.105)[a]	0.68	NS	13
	Post-yolk sac	2.5939 (0.237)	2.5309 (0.233)[a]	0.95	NS	13
Season of 1982	Yolk sac	2.2041 (0.138)	2.1971 (0.134)[b]	0.10	NS	42
	Post-yolk sac	1.9020 (0.183)	1.4293 (0.164)[b]	7.25	<0.01	42
25 June 1982	Yolk sac	2.5884 (0.224)	2.3803 (0.178)[b]	2.17	NS	13
	Post-yolk sac	3.3050 (0.188)	2.5796 (0.221)[b]	6.54	<0.01	13

[a] Bottom plankton net.
[b] Suprabenthic sled.

was located downstream of the station (Fig. 6). During the ensuing flood tide, yolk sac larvae were once again detected in abundance whereas very few post-yolk sac larvae were observed to return within the sampling area (Fig. 6). This supports the deduction that greater horizontal dispersion is experienced by post-yolk sac larvae than yolk sac larvae.

The above observations may be less than conclusive, since correlations are often nonsignificant, but the relationship between upward transport and flood tide current speed is confirmed by examination of information on suspended particulate matter. The Secchi disc readings are inversely related to the quantity of suspended particulate matter. The significant negative correlations observed between Secchi disc readings and larval abundance in the water column and near bottom during the flooding tide (Table 6) support the hypothesis that larvae are vertically transported as is suspended particulate matter and that this occurs principally during flooding tide.

The correlations reported in Table 6 may also have resulted from a decrease in net avoidance by larvae during periods of greater turbidity. If these results are an artifact of net avoidance,

TABLE 5. Pearson correlation coefficients between currents (cm/s; component u at mean depth) and ratio (oblique tow/bottom tow) of larval densities (no./100 m^3) at Notre-Dame-du-Portage (Z1). $*p < 0.05$; $**p < 0.01$.

Date	Stage of larval development	Tidal stage	
		Ebb	Flow
18 June 1981[a]	Yolk sac	0.71	−0.28
	Post-yolk sac	−0.35	0.32
24 June 1981[a]	Yolk sac	−0.21	0.02
	Post-yolk sac	0.76*	0.54
28 June 1981[a]	Yolk sac	−0.09	0.50
	Post-yolk sac	−0.47	0.83*
2 July 1981[a]	Yolk sac	−0.60	0.67
	Post-yolk sac	0.45	−0.70
17 June 1982[b]	Yolk sac	−0.30	0.81*
	Post-yolk sac	0.37	0.16
25 June 1982[b]	Yolk sac	0.45	0.94**
	Post-yolk sac	−0.10	0.05

[a] Bottom plankton net for bottom tows.

[b] Suprabenthic sled for bottom tows.

the mean length of larvae should also be negatively correlated with Secchi disc readings. For five of the six significant negative correlations obtained between abundance and turbidity, no significant increase in length of larvae was observed. Thus, we conclude that the relationship between larval abundance and suspended particulate matter is due to a common physical mechanism of vertical transport and is not an artifact of net avoidance.

To summarize, in the absence of turbulence generated by tidal currents, herring larvae are found deeper in the water column. Upward vertical transport of larvae is associated with higher values of tidal current speed, principally during flood tides, similar to suspended particulate matter. Post-yolk sac larvae are vertically transported to a greater extent than yolk sac larvae and thus experience greater horizontal dispersion.

Drogue Experiments

The drogue experiment of 18 June 1982 covered the region between sampling zone Z1 and the entrance to the south channel (Fig. 7a). Significant differences were observed between densities of yolk sac larvae from oblique and suprabenthic tows only during slack water at the end of the experiment (Fig. 8a). However, the increase of yolk sac larvae in the suprabenthic layer was not reflected by a decrease of yolk sac larvae in the water column. This suggests that yolk sac larvae accumulate on the bottom at the entrance of the south channel.

The second drogue experiment resulted in a downstream displacement sufficient to reach areas deeper than 20 m in the south channel (Fig. 7b). A patch of larvae is indicated by three successive peaks of abundance during the first 22 h of the experiment (Fig. 8b). For these peaks, the proportion of larvae on the bottom relative to those sampled throughout the water column increased with time, indicating that larvae were sinking and accumulating close to the bottom as the south channel was approached. Thus, the patch of larvae was drifting at a slower rate than the drogue situated at a depth of 5 m. During the last tidal cycle, the patch of larvae is absent, as the drogue had drifted farther downstream than the patch. The net movement of the drogue was approximately 8 km/d. In less than 4 d, the drogue would have drifted out of the coastal zone whereas the larvae had already been retained in the zone for approximately 1 mo.

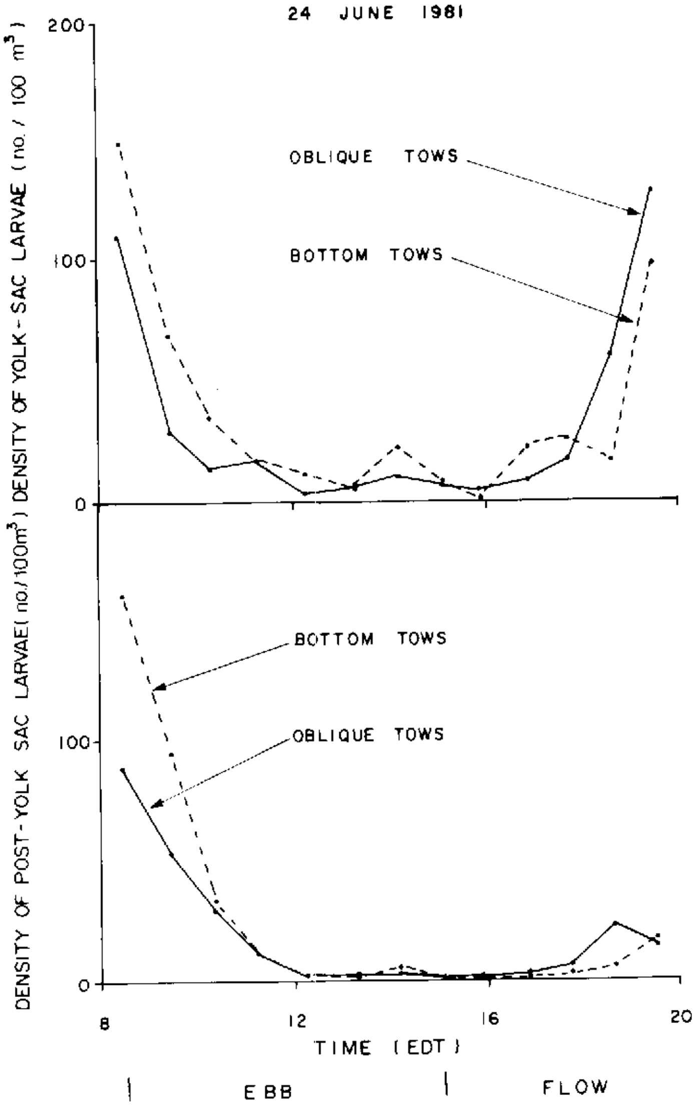

FIG. 6. Densities for yolk sac and post-yolk sac larvae in oblique and bottom tows on one tidal cycle, 24 June 1981.

TABLE 6. Pearson correlation coefficients between larval densities (no./100 m^3) and Secchi disc readings (m) at Rivière-du-Loup (Z2). $*p < 0.05$; $**p < 0.01$.

Date	Tow type	Tidal stage	
		Ebb	Flow
11 July 1982	Oblique	0.25	−0.85*
	Bottom	−0.19	−0.86*
21 July 1982	Oblique	−0.46	−0.74*
	Bottom	−0.55	−0.70
31 July 1982	Oblique	−0.78*	−0.97**
	Bottom	−0.55	−0.83*

To summarize, data from the first drogue experiment sug-

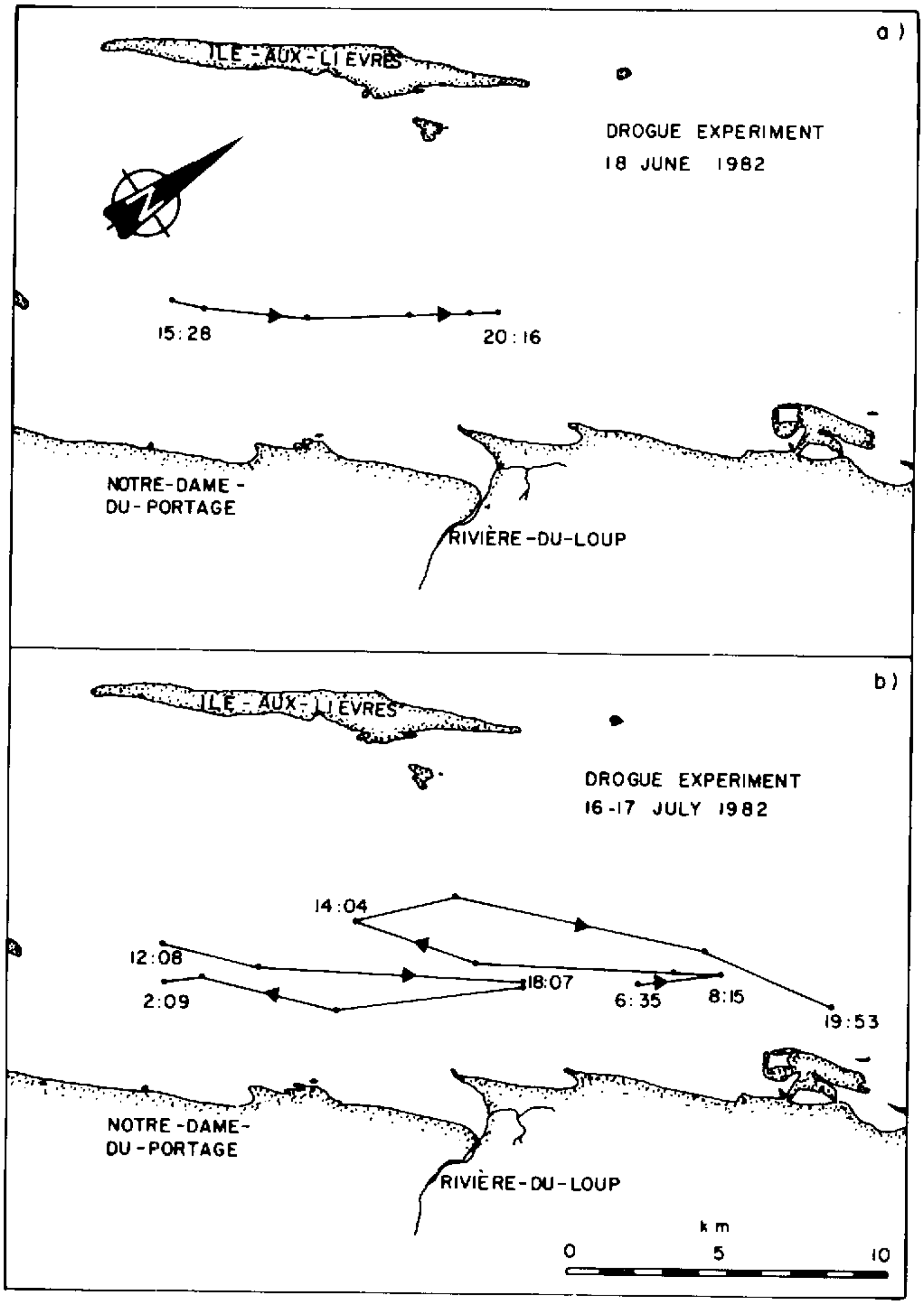

FIG. 7. (a) Drogue trajectory (5-m depth), 18 June 1982. (b) Drogue trajectory (5-m depth), 16–17 July 1982. Discontinuity due to temporary loss of drogue for 4 h.

gested the accumulation of yolk sac larvae on the bottom at the entrance to the south channel. The experiment was of too short a duration to detect any significant changes in the vertical distribution of yolk sac larvae during their transport. The second drift experiment clearly demonstrates the increasing depth distribution of post-yolk sac larvae during their displacement from the coastal zone towards the south channel.

Discussion

The greatest concentrations of yolk sac larvae were found near the bottom in the present study. Several authors (Tibbo et al. 1963; Schnack and Hempel 1971; Caddy and Iles 1973; Colton and Green 1975) have either observed or proposed that yolk sac herring larvae are associated with the bottom. Graham and Chenoweth (1973), on the other hand, found no relationship between the relative abundance of yolk sac larvae and depth. However, their sampling program involved oblique tows at the surface, at 20 m, and at 30 m whereas maximum depth in the study area was 48 m. Saville (1971) suggested that standard plankton nets do not representatively sample the entire water column. In the present study, the use of the suprabenthic sled

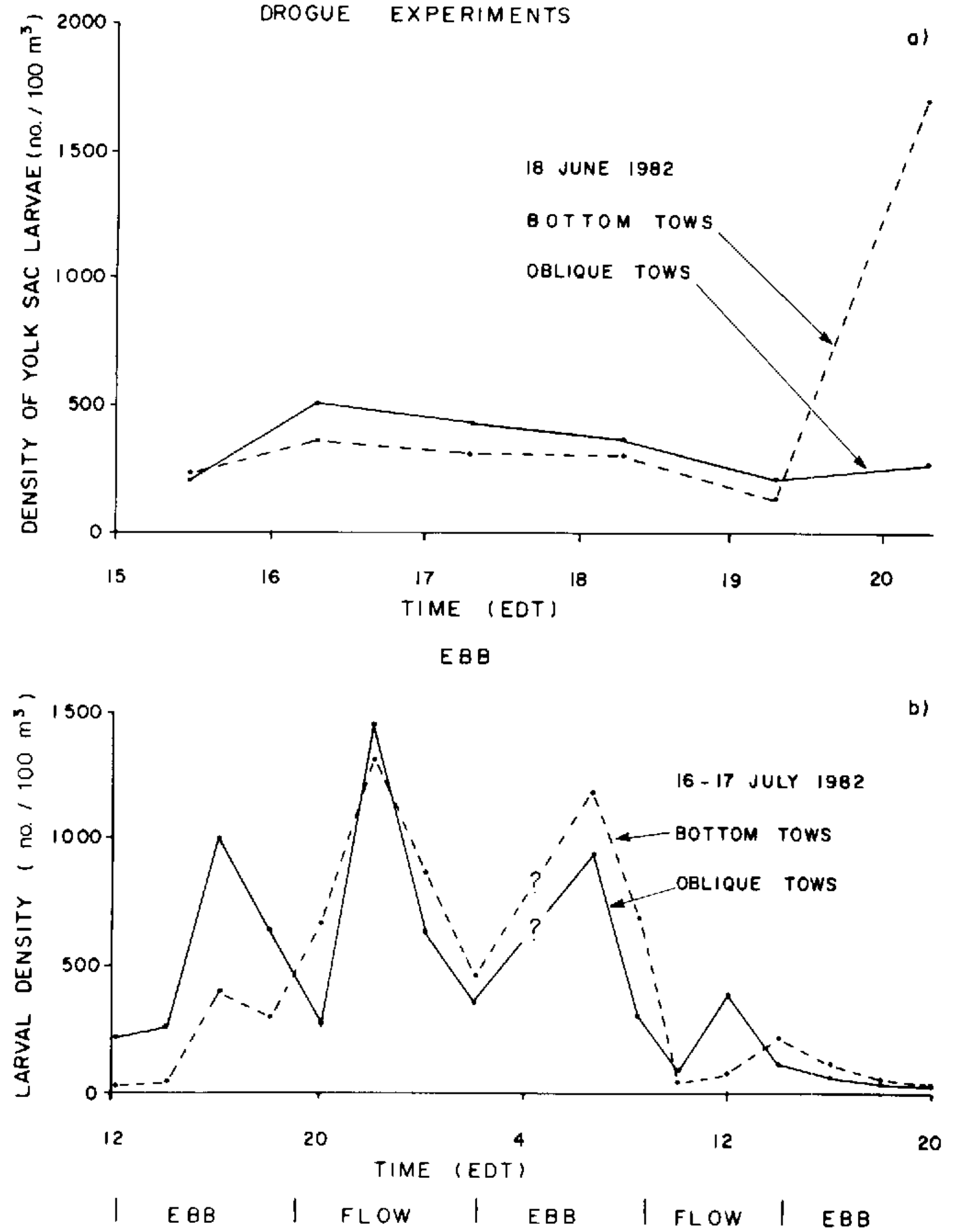

FIG. 8. (a) Densities of yolk sac larvae in oblique and suprabenthic sled tows for drogue experiment, 18 June 1982. (b) Densities of larvae in oblique and bottom plankton net tows for drogue experiment, 16–17 July 1982. Question marks are for period of temporary loss of drogue.

demonstrated the importance of sampling the suprabenthic layer to detect variations in the distribution of yolk sac larvae near the bottom.

While several factors might contribute to this vertical distribution pattern, we believe that negative buoyancy is particularly important. Rosenthal and Hempel (1970) determined that the sinking rate of yolk sac larvae varies between 0.2 and 0.5 cm/s; the larger the yolk sac, the greater the sinking rate. Larvae sink during periods of inactivity that range from 60% of the time for 1-d-old larvae to 34% of the time for immediate post-yolk sac larvae (Rosenthal and Hempel 1970). Therefore, sinking rate varies from 10.8 to 2.9 m/h from the beginning to the end of the yolk sac period. Thus, in the context of the present study such vertical displacements during periods of slack water are significant relative to depths of 7–25 m found in the study area.

The apparent relationship between upward vertical transport and current speed is similar to that shown by de Wolf (1974), who observed a sinking rate of cypris larvae (*Balanus crenatus*) comparable with that of yolk sac herring larvae. In the laboratory, de Wolf (1974) observed upward vertical transport of cypris larvae at current speeds of 35–67.5 cm/s. The range of mean current speeds at mean depths during flooding tides in the study area (35–67 cm/s, Table 1) is comparable with the range noted by de Wolf (1974).

While earlier studies have shown that the yolk sac plays an important role as a regulator of specific gravity, our results suggest that this function of the yolk sac contributes to spatial structuring of larval populations. Sinking rate diminishes as water content of the yolk sac increases accompanying the absorption of yolk (Blaxter and Ehrlich 1974). Water and lipid diminish sinking rate whereas proteins and sugars augment sinking rate. For herring larvae, lipid content is only 1–3% of the total weight of the yolk (Blaxter and Hempel 1966). Although lipid globules are found in other larvae, herring do not possess them. These observations suggest that yolk sac composition may have evolved in response to a "need" for negative buoyancy.

Our observations, in combination with earlier laboratory studies (Rosenthal and Hempel 1970; Blaxter and Ehrlich 1974), suggest that immediate post-yolk sac larvae are more subject to transport out of the retention area than younger and older larvae. Blaxter and Ehrlich (1974) demonstrated that immediate post-yolk sac larvae have a minimal sinking rate. Sinking rate increases from 0.2 to 1.4 cm/s for larvae measuring from 12 to 25 mm (Blaxter and Ehrlich 1974). Our length–frequency observations in zone Z1 in July 1982 (Fig. 3) suggest that the center of distribution of immediate post-yolk sac larvae (lengths approximately 10 mm) is farther down-estuary than that of larger larvae. Both small and large larvae were taken at spring tides (10 and 22 July 1982, mean lengths 10.7 ± 1.6 and 12.3 ± 1.9 mm, respectively), but only large larvae were taken at neap tides (18 and 30 July, mean lengths 15.0 ± 2.3 and 15.2 ± 2.0 mm, respectively). Thus, since return transport to Z1 is greater on spring tides than on neap tides, immediate post-yolk sac larvae must on average be distributed farther down-estuary than larger larvae. Thus, the pattern of dispersion is related to sinking rate. At minimal values of sinking rate, dispersal is greatest; this characterizes immediate post-yolk sac larvae. The observed developmental differences in vertical distribution and vertical transport are summarized in Fig. 9.

It seems unlikely that active migration is as important a contributor to retention of young larvae as negative buoyancy. Active migration requires that a certain stage of development be attained. Seliverstov (1974) observed the onset of circadian vertical migrations in herring larvae at mean lengths of 13 mm. Moreover, the relationship between the vertical transport of herring larvae and turbidity in the south channel supports the hypothesis that herring larvae are passively transported. Pearcy (1962) was the first to invoke specific gravity as a passive factor to explain why several organisms classified as planktonic are not entirely at the mercy of currents.

The aggregation of larvae remains intense in our study area during the summer months. A coefficient of dispersion (c) between 0.1 and 0.2 is frequent for planktonic population (Cassie 1959), and a patchiness index (c + 1, Lloyd 1967) of 1.1–1.2 was considered plausible for herring larvae. Values for patchiness index in the present study ranged from 1.63 to 3.52.

The following description is presented as a model to explain and illustrate the dynamics of the Isle-Verte retention zone. The 20-m isobath appears to be, on average, the up-estuary limit of the retention zone (Fig. 10). As such, it may also represent a preferred zone of egg deposition. During spring tides, the greatest concentrations of herring larvae are found at the entrance to the south channel. Larvae are also found up-estuary in zone Z1. Vertical transport during flood tides appears responsible for this up-estuary transport, the extent of which varies according to the magnitude of tidal speed and the developmental stage of larvae. Horizontal dispersion is less for larvae with greater specific gravities.

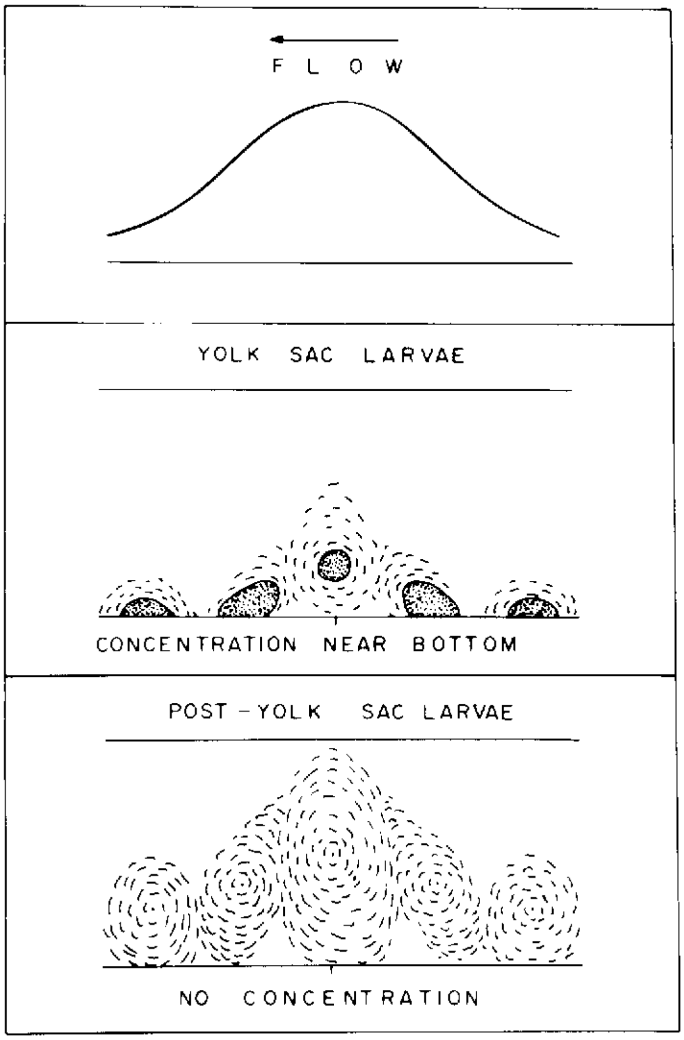

FIG. 9. Schematic illustration representing the differential vertical transport of yolk sac and immediate post-yolk sac larvae. Differences in vertical distribution reflect vertical transport of larvae that varies according to developmental stage with yolk sac larvae associated principally with the bottom.

Following the maximum of spring tides, larval patches are observed to have experienced net downstream transport. Larvae sink progressively as zone Z2 is approached, their net displacement over one tidal cycle becoming nil once a depth of 20 m is attained. Larvae found at depths greater than 20 m are transported up-estuary by the deep residual current characteristic of zone Z2. This residual current, however, cannot be responsible for the up-estuary transport of larval patches into the relatively shallow and vertically mixed zone Z1. The specific gravity of the larvae should be great enough to minimize down-estuary transport during ebbing tides. Deep currents experienced at the beginning of the flooding tide vertically transport larvae that are subsequently displaced up-estuary. As such, these larval patches return to zone Z1 after having lost a proportion of their numbers to dispersion out of the coastal retention zone and to natural mortality.

Thus, although yolk sac larvae are probably not characterized by strong directed swimming powers, they are not strictly comparable with passive components of the estuarine environment as proposed by Fortier and Leggett (1982). Rather, the presence of a negatively buoyant yolk sac, whose effect decreases with larval development, combines with the inter-

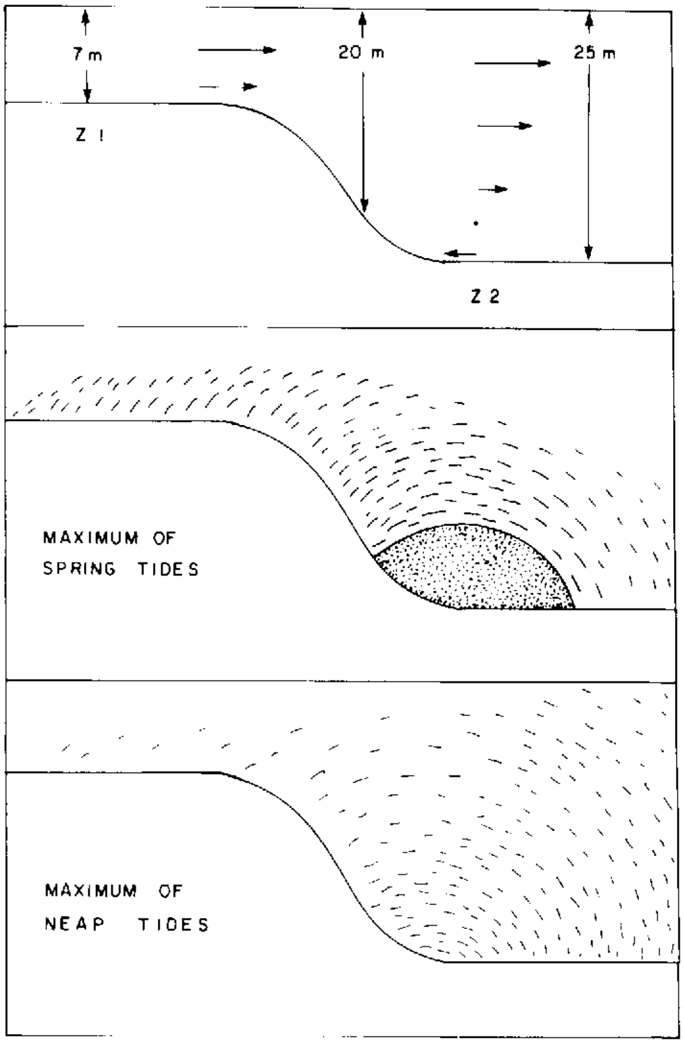

FIG. 10. Schematic illustration representing the model explaining the dynamics of the Isle-Verte retention zone. The 20-m isobath appears to be, on average, the up-estuary limit of the retention zone. During spring tides, the greatest concentrations of herring larvae are found at the entrance to the south channel. Larvae are also found up-estuary in zone Z1. Vertical transport during flood tides appears responsible for this up-estuary transport, the extent of which varies according to the magnitude of tidal speed and the development stage of larvae. The arrows indicate the direction of residual currents.

section of the level of no net motion with the bottom to contribute to strong spatial structuring of larval populations rather than to random dispersal of yolk sac larvae. Our results suggest that the degree of retention is least for immediate post-yolk sac larvae; increased dispersal at this stage may be the result of minimal specific gravity of these larvae and the fact that swimming capabilities are relatively little developed at this stage.

The present study has raised several hypotheses that merit study in the future. Annual differences in the fluctuations of the larval index may be due to an interaction between temperature and tidal stage that acts to modulate the dispersion of larvae in the study area. Temperature influences the date of spawning (Messieh and Moore 1979) and the duration of egg incubation (Blaxter 1956) and therefore influences the date of hatching. The extent of larval retention or dispersion will depend on tidal stage during hatching, particularly if hatching occurs in a short period of time. Laboratory experiments demonstrate that the majority of herring larvae hatch within a period of 3 or 4 d (Blaxter and Hempel 1963). Tibbo et al. (1963) observed patches of newly hatched larvae indicative of waves of hatching separated by 3 or 4 d and correlated with waves of spawning. Observations of the schools of Isle-Verte herring spawners (Bio-Conseil 1982) suggest that peaks of yolk sac larval abundance observed in 1981 and 1982 were associated with individual peaks of spawning. Therefore, we hypothesize that the degree of retention or dispersion of each year-class of Isle-Verte herring larvae depends on the tidal state occurring during rapid mass hatching. As the exact location of egg beds in our study region is unknown, no bottom temperatures were measured and we are unable to develop this hypothesis further.

Increased dispersion at the beginning of exogenous feeding may be considered as having survival advantage by increasing the probability of encounter with food patches. However, increased dispersion leading to premature transport out of the coastal zone may reduce the probability of survival, as food may be less available in deepwater areas than in shallow coastal zones (Pearcy 1962). The optimal equilibrium between dispersion and aggregaton leading to maximum survival must be the subject of future study.

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