

# Advection–Diffusion Modelling of Larval Capelin (*Mallotus villosus*) Dispersion in Conception Bay, Newfoundland

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A numerical model was used to determine the residence time of capelin (*Mallotus villosus*) larvae in Conception Bay, Newfoundland. The larvae were observed in the surface mixed layer of the Bay following release from beaches in June–July in order to examine how they move outside the Bay and what physical factors influence their rate of transport. A diagnostic model of Conception Bay provides a fixed velocity field which drives an advection–diffusion model applied to capelin larval dispersal from the Bay. The model was run for different periods to explore dependence of the residence time on different conditions during the period 1989–90. Model results showed that the residence time depends on the release location of the larvae in the Bay. While the residence time of the larvae does vary, we estimate it to be roughly 30 d for larvae released from the head of the Bay. Residence times are much shorter for larvae near the mouth of the Bay.

Nous avons appliqué un modèle numérique à la détermination du temps de séjour de larves du capelan (*Mallotus villosus*) dans la baie Conception, Terre-Neuve. Nous avons observé les larves dans la zone de mélange superficielle de la baie après les avoir lâchées au bord de plages en juin et juillet pour pouvoir étudier leur déplacement vers l'extérieur de la baie et examiner quels facteurs physiques interviennent dans la vitesse de leur déplacement. Un modèle diagnostique de la baie Conception permet de créer un champ de vitesses déterminées qui alimente un modèle d'advection–diffusion appliqué à la dispersion des larves. Nous avons choisi différentes périodes afin d'explorer la dépendance du temps de séjour avec différentes conditions en 1989–1990. Les résultats montrent que le temps de séjour dépend de l'endroit où se sont faits les lâchers. Il y a effectivement des variations dans le temps de séjour, mais nous estimons qu'il faut une trentaine de jours pour que les larves libérées au fond de la baie la quittent. Les temps de séjour des larves lâchées près de l'embouchure de la baie sont beaucoup plus courts.

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We seek to apply a numerical model to determine the residence time of capelin (*Mallotus villosus*) larvae in Conception Bay, Newfoundland. The use of numerical models integrating physics and biology has proven useful in simulating distributions of fish eggs and in identifying important forcing terms. The models employed and approaches taken vary greatly in complexity. Page and Smith (1989) applied a two-dimensional time-dependent model to investigate dispersion of herring eggs and larvae on Brown's Bank, off Nova Scotia. Helbig et al. (1992) used an Ekman wind model together with a mean current field derived from a barotropic field to simulate cod egg drift on the Newfoundland shelf. Werner et al. (1993) used a tidal model coupled to a diagnostic model to calculate the influence of advection and behaviour on cod larvae on Georges Bank. A much more sophisticated model was applied by Hoffmann et al. (1991) who used a fully nonlinear primitive equation model to determine transport patterns and the residence time in the coastal transition zone off California. A tidally driven model of dispersion of herring larvae was

developed by Bartsch et al. (1989) and applied to the North Sea. Development of more sophisticated models requires an improved understanding of the interactions between the physics and the biology.

Previous studies on capelin in the Northwest Atlantic have reported that dispersal away from spawning sites is an important phase in their life history. In the St. Lawrence estuary, downstream transport of capelin larvae to an area of enhanced productivity in the northwestern Gulf of St. Lawrence is necessary to ensure subsequent growth and survival through juvenile stages (Bailey et al. 1977; Jacquaz et al. 1977; Fortier and Leggett 1983, 1985). Dispersal or retention of capelin larvae will depend upon the water circulation and the swimming behaviour of the larvae. At these early ages, we expect that the most significant biological factor is the vertical position of capelin in the water column, not their ability to swim horizontally. In the St. Lawrence estuary, where transport away from spawning sites is important, capelin larvae were observed predominantly in surface waters (Jacquaz et al. 1977; Fortier and Leggett 1982, 1983).

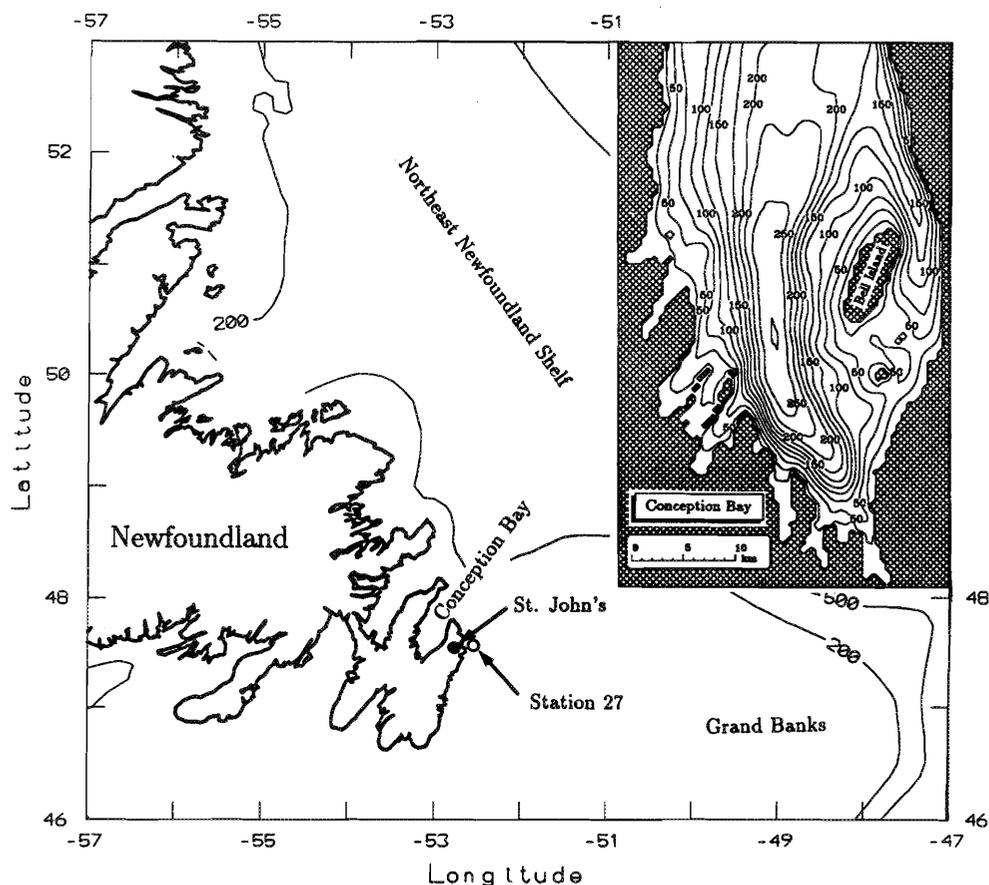


FIG. 1. Bottom topography of the northeast Newfoundland shelf showing the location of Conception Bay. Depth contours are in metres. The model domain at 0.5-km resolution is shown in the panel. The scale in the panel applies to the model domain.

Fortier et al. (1992) concluded that the influence of hydrography on the larvae depends upon the number of larvae produced and their foraging competence. They applied ecological arguments (Pianka 1970) to suggest that large numbers of small offspring with limited foraging skills depend on export for reproduction; but large larvae, produced in fewer numbers, can colonize less productive regions. Fitting this model, capelin were found to produce large numbers of relatively small larvae, and transport was important.

Capelin that spawn along the northeast coast of Newfoundland are released from beach sediments into nearshore waters in association with large-scale meteorological forcing (Frank and Leggett 1981; Leggett et al. 1984). These postemergent larvae are dispersed quickly from the nearshore environment, under the influence of wind-forced surface currents (Taggart and Leggett 1987). In contrast with these beach-spawning capelin, larvae from capelin that spawn offshore on the Southeast Shoal of the Grand Bank of Newfoundland are retained there after their release from bottom sediments (Frank and Carscadden 1989). On the Southeast Shoal, where retention within the spawning area is important, capelin larvae >8 mm migrated below the surface waters at night, remaining above the pycnocline by day (Frank and Carscadden 1989). It was concluded that diel migration coupled with the circulation was responsible for the retention of capelin larvae in these waters.

Our approach is to apply a relatively simple physical model to test the sensitivity of larval dispersal to oceanographic conditions in different months. We use a fixed

velocity field derived from a diagnostic model of the Bay (deYoung et al. 1993a) as input to an advection-diffusion model. For our model to be valid, we must assume that the capelin larvae are distributed in the surface mixed layer. Our data suggest that this is a reasonable first assumption for capelin larvae in Conception Bay. The model and analysis presented here have the advantage of simplicity, both in development and application. The model design is such that additional complexity, both physical and biological, can be added easily. Ultimately, we intend to apply a time-dependent model to this problem, one in which the velocity field evolves with time and the larvae can migrate vertically.

The primary aim of this work is to estimate the dispersion time of capelin larvae from Conception Bay. Our approach is to focus on the influence of the circulation in the surface mixed layer, here considered as vertically homogeneous. First, we present data to describe the vertical distribution of the capelin larvae in the Conception Bay, then develop the model, and follow this with a presentation of the model results from Conception Bay.

### Study Area

Our study area, Conception Bay, is located on the northeast coast of Newfoundland (Fig. 1). The Bay is approximately 70 km long and 32 km across at the mouth, with a maximum depth in the center of about 300 m. There is a sill about 150 m deep at the mouth of the Bay. The bottom topography of the Bay, shown at 0.5-km resolution in the

inset of Fig. 1, reveals a deep basin with an irregular coastline and a group of small islands on the eastern side of the Bay. Capelin spawning takes place primarily on beaches on the western shore of the Bay (Templeman 1948; B.S. Nakashima and C.T. Taggart, unpublished data). The spawning takes place in June–July, with larval release from the beaches throughout July–August and into September (Frank and Leggett 1981). As mentioned in the introduction, there have been some limited measurements of the vertical distribution (Taggart and Leggett 1987), but only in the nearshore zone and for very young larvae.

### Vertical Distribution of Larvae

Sampling to determine the vertical distribution of capelin larvae was carried out in August and September 1988 and September 1989 in Conception Bay. Vertically discrete samples were collected using a 0.25-m<sup>2</sup> opening and closing sampling system, similar in design to the BIONESS (Sameoto et al. 1977), monitoring sampled depth, water volume filtered, CTD, and other net parameters in real time. The net mesh was 0.333 mm. Different depth strata were sampled depending upon the water depth, with no samples taken at depths greater than 100 m. Samples were collected at seven or eight stations (during each cruise) within Conception Bay, mostly towards the head of the Bay and in the vicinity of the three islands. Up to nine nets per tow were used, sampling from 5 to 100 m depth. Water volumes filtered varied with depth interval, but a minimum of 70–80 m<sup>3</sup> was filtered for each sample. In 1988, all sampling was done in daylight whereas in 1989, samples were collected during both daylight and darkness. All samples were preserved in 5% formalin-buffered seawater. Capelin larvae were removed from the sample, counted, and measured to the nearest millimetre. Center of mass calculations were estimated from  $D = \sum_{i=1}^n (p_i d_i)$  where  $D$  is the center of mass (metres),  $p_i$  is the proportion of capelin sampled in the  $i$ th depth stratum, and  $d_i$  is the depth of the  $i$ th stratum. All statistical analyses were done using SAS (1988).

The vertical distribution of capelin larvae was sampled in Conception Bay during the period of peak release in the summer of 1988 and immediately following peak release in both 1988 and 1989. Capelin larvae caught in August 1988 ranged in size from 4 to 15 mm in length and averaged 7.2 mm. In September 1988, capelin larvae ranged from 4 to 26 mm and averaged 11.8 mm whereas in September 1989, larvae ranged in size from 5 to 29 mm and averaged 13.7 mm. The average depth of the center of mass for these three months was 14.0, 30.0, and 25.0 m, respectively.

Examination of capelin by size class (millimetres) demonstrated a monotonic increase in depth as capelin increased in size. In August 1988 the smallest capelin (4–5 mm) were centered at 8 m depth whereas larger larvae (17 mm) were centered at 26 m depth. In September the smallest capelin were centered from 14 to 18 m depth whereas, the larger capelin (19–21 mm) were centered from 30 to 44 m depth. Larger capelin larvae were distributed, on average, deeper for all three periods sampled. Whereas larger, older larvae were found at greater depths, most of the larvae were found in the top 40 m of the water column.

Comparisons of the depth distribution of capelin larvae with the vertical water structure demonstrated that capelin occurred primarily in the surface mixed layer during each

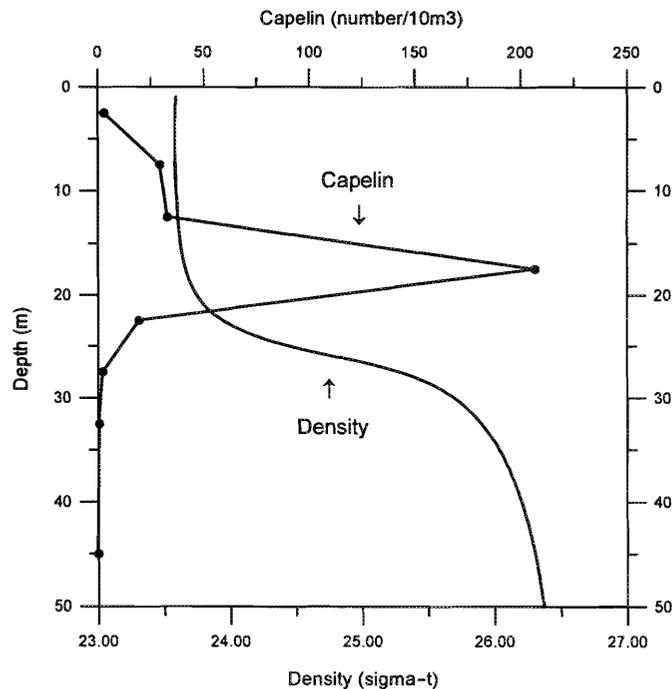


FIG. 2. Concentrations of capelin larvae during the daytime in August 1988 near the head of Conception Bay. Also shown is the  $\sigma_t$  (density) profile for the same time.

cruise. This was particularly true for August 1988 when capelin concentrations were approximately one order of magnitude greater than in September and larval sizes were smaller. Individual plots of capelin concentrations with density profiles demonstrated peak concentrations that were mostly at or above the pycnocline (Fig. 2 shows a representative plot).

The deeper fall distributions of capelin were related to a deeper surface mixed layer, which was 20–25 m deep in September but only 15–20 m deep in August 1988. This observation suggests that a deeper distribution of capelin may be related to a deeper surface mixed layer. To determine if there was a direct relationship between capelin depth distribution and the surface mixed layer depth, we compared the capelin center of mass distribution (all sizes) with mixed layer depth (MLD) for 13 tows stratified across the three cruises. For these tows the MLD ranged from 13 to 33 m. The comparison was not significant ( $r = 0.11$ ,  $P = 0.7193$ ,  $n = 13$ ), demonstrating that there was no simple relationship between the mean vertical distribution of capelin larvae and the thickness of the surface mixed layer depth.

The concentration of larvae in the surface layer is a crucial result for the numerical model that we wish to apply. The average center of mass for the August and September periods ranges from 14 to 30 m depth. Although there is some evidence of vertical migration, and an increase in size with depth, for purposes of this analysis, we shall ignore vertical gradients of larvae in the surface waters.

### Physical Models

#### Diagnostic Model

The approach in the physical modelling is to solve an advection–diffusion model using as input a fixed velocity field derived from a diagnostic model (deYoung et al. 1993a).

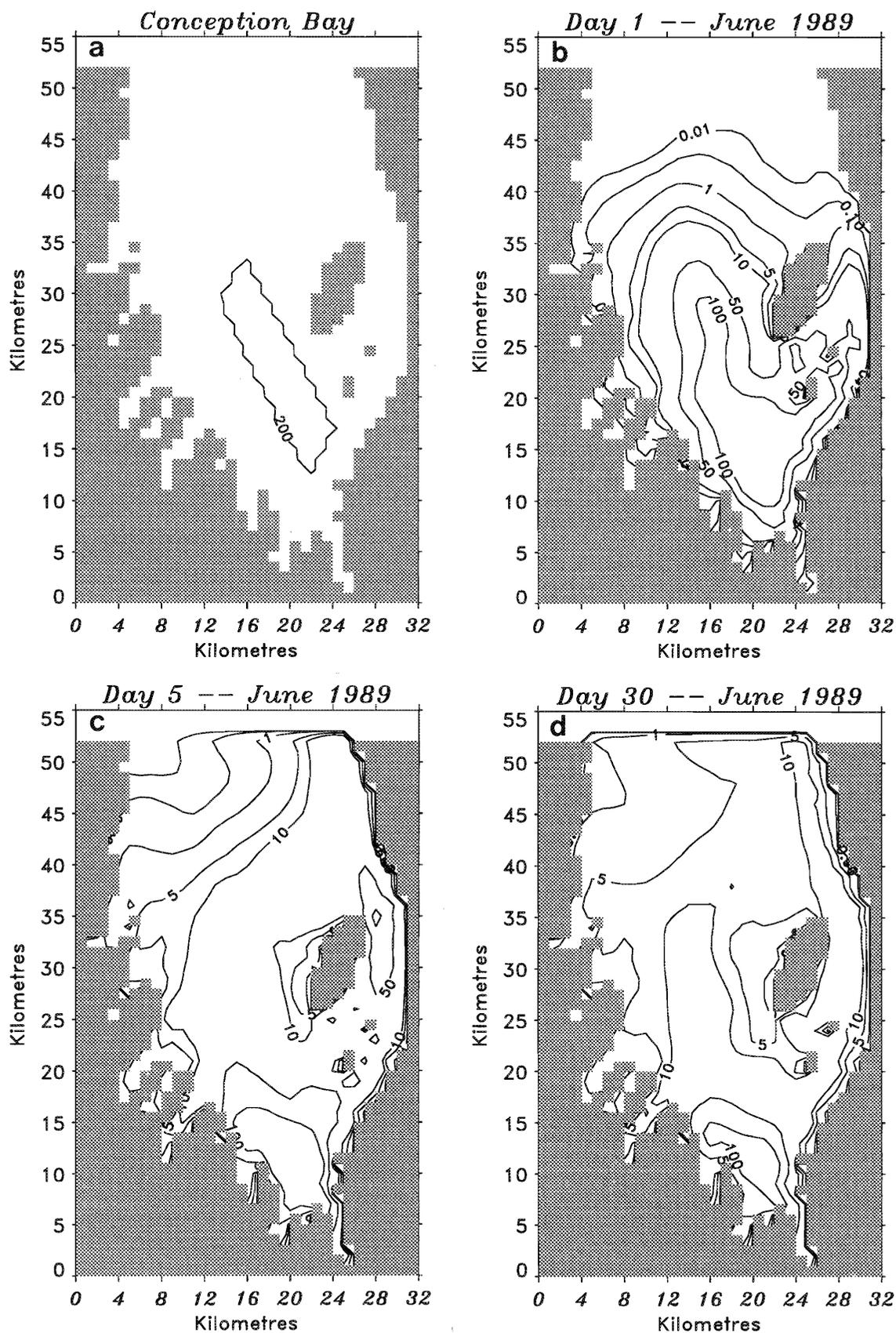


FIG. 3. Vertically integrated larval concentration (in arbitrary units of numbers per cubic metre) for the June 1989 run at (a) 0 d, (b) 1 d, (c) 5 d, and (d) 30 d.

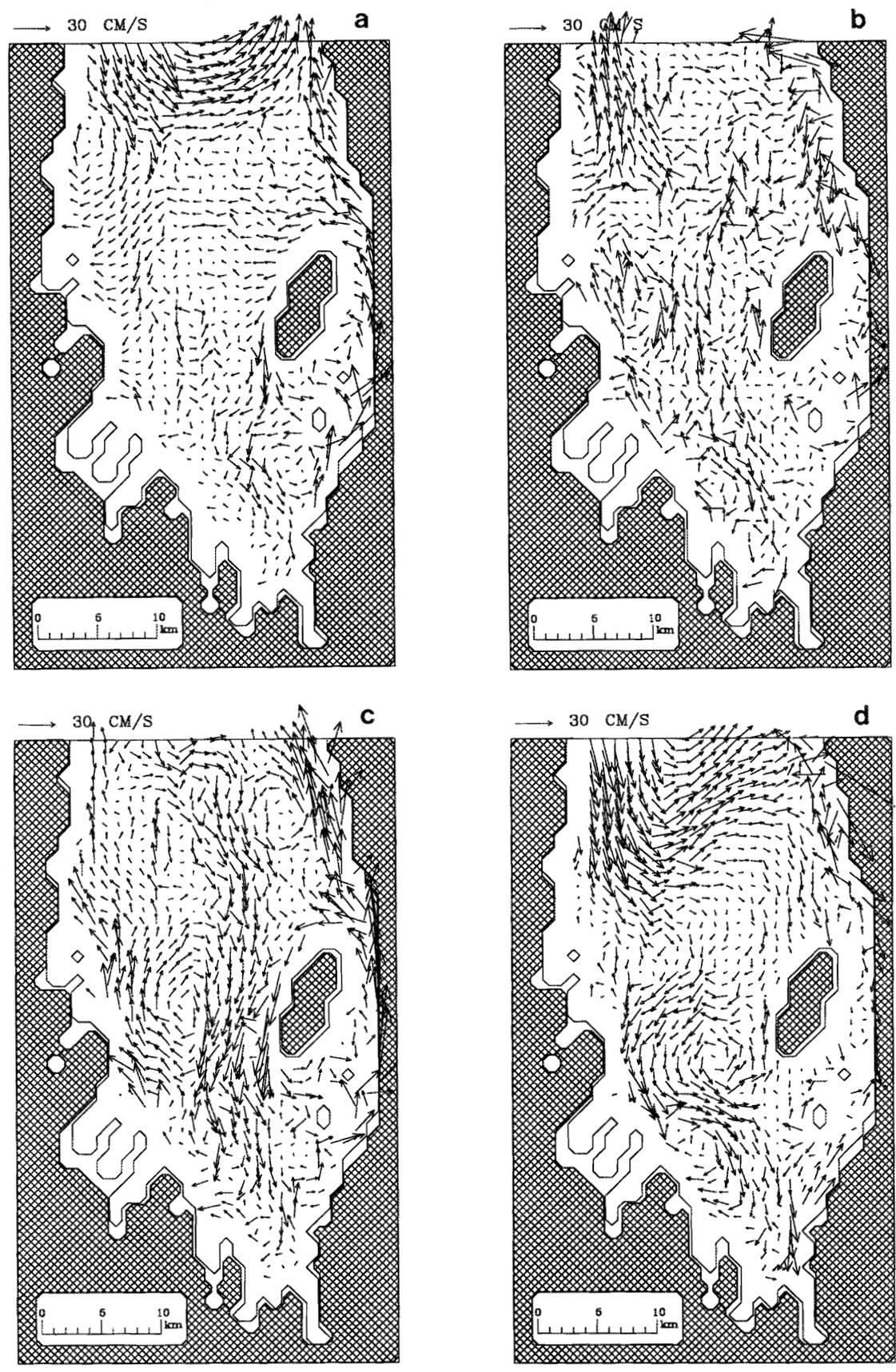


FIG. 4. Current velocity fields at 10 m depth for (a) June 1989, (b) September 1989, (c) October 1989, and (d) June 1990, Conception Bay. The horizontal resolution is 1 km and the scale of the vector arrows is indicated at the top of each panel.

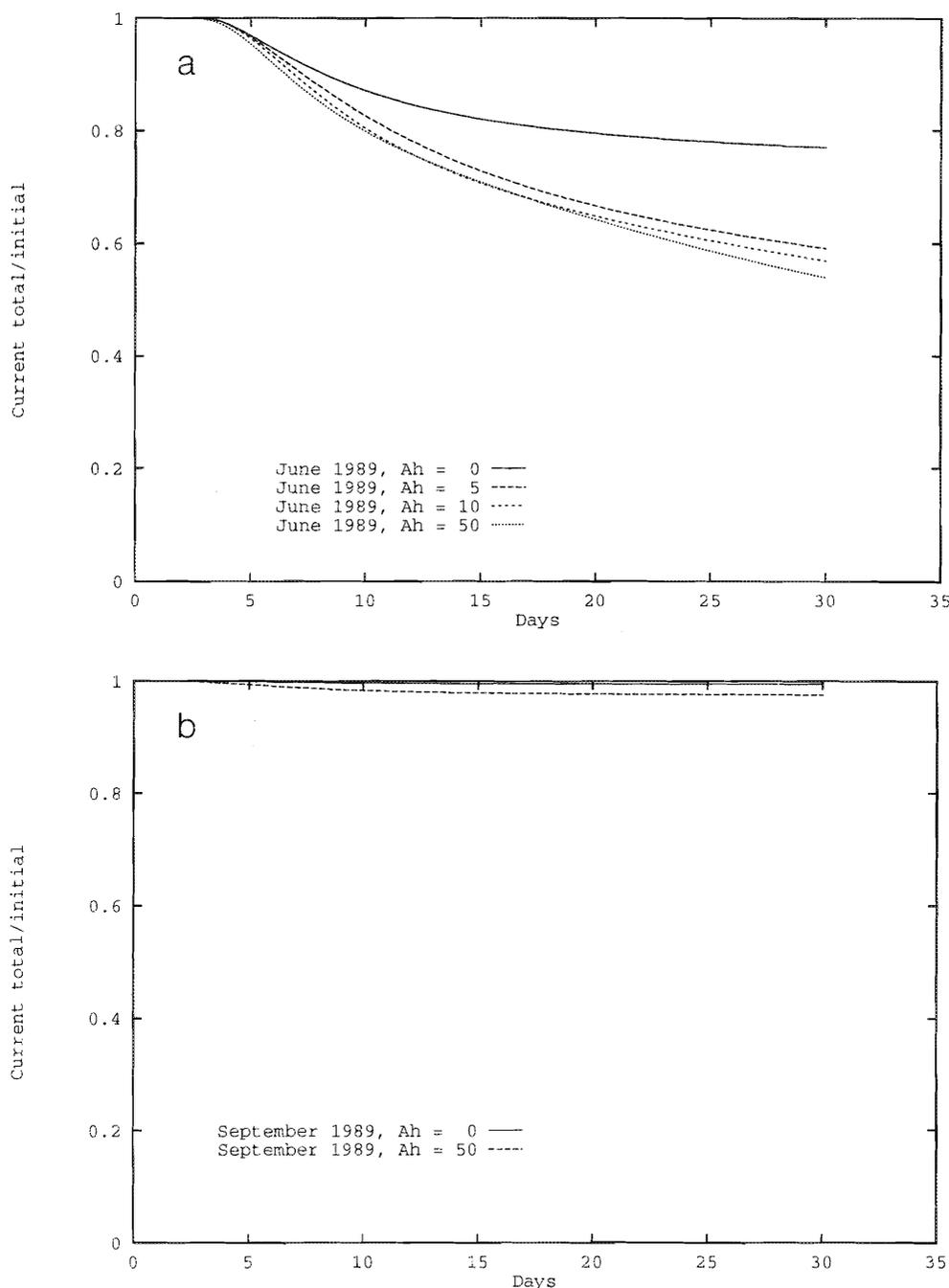


FIG. 5. Plots of the ratio of current total larval concentration relative to the initial concentration for (a) June 1989, (b) September 1989, (c) October 1989, and (d) June 1990, Conception Bay. In all cases the solid line shows runs for which  $A_h = 0$ . For the June 1989 case, three different runs are shown with  $A_h$  ranging from 5 to 50  $\text{m}^2/\text{s}$ . The broken line in Fig. 5b–5d is for runs with  $A_h = 50$   $\text{m}^2/\text{s}$ . (Fig. 5 continued next page)

The velocity field is three-dimensional and is calculated from a specified density field and surface wind stress with current meter data used to constrain the boundary condition at the mouth of the Bay. The diagnostic model provides a steady-state solution to the density and wind-forced circulation. The model includes vertical mixing and bottom friction. The horizontal resolution is 1 km. In the vertical, there are 20 equally spaced sigma levels (where  $\sigma = z/H$ , see Gill (1982) for a discussion of sigma coordinates). The vertical resolution varies from 1 to 2 m in shallow water to ~15 m in the center of the Bay where the water depth is 300 m. This approach

permits good vertical resolution in shallow water and, while giving up some resolution in deep water, is relatively efficient numerically. The density data used as input to the model were collected using either a Neil Brown MKIIB or a Seabird SBE25 CTD. Approximately 35–40 stations were occupied in the Bay during each survey, with a horizontal spacing of roughly 7–8 km (deYoung et al. 1993a). The vertical resolution of the processed data is 1 m. The time needed to survey the Bay is roughly 2 d; thus, tidal aliasing is unimportant, since tidal constituent velocities are weak, less than 1–2 cm/s (deYoung et al. 1993a).

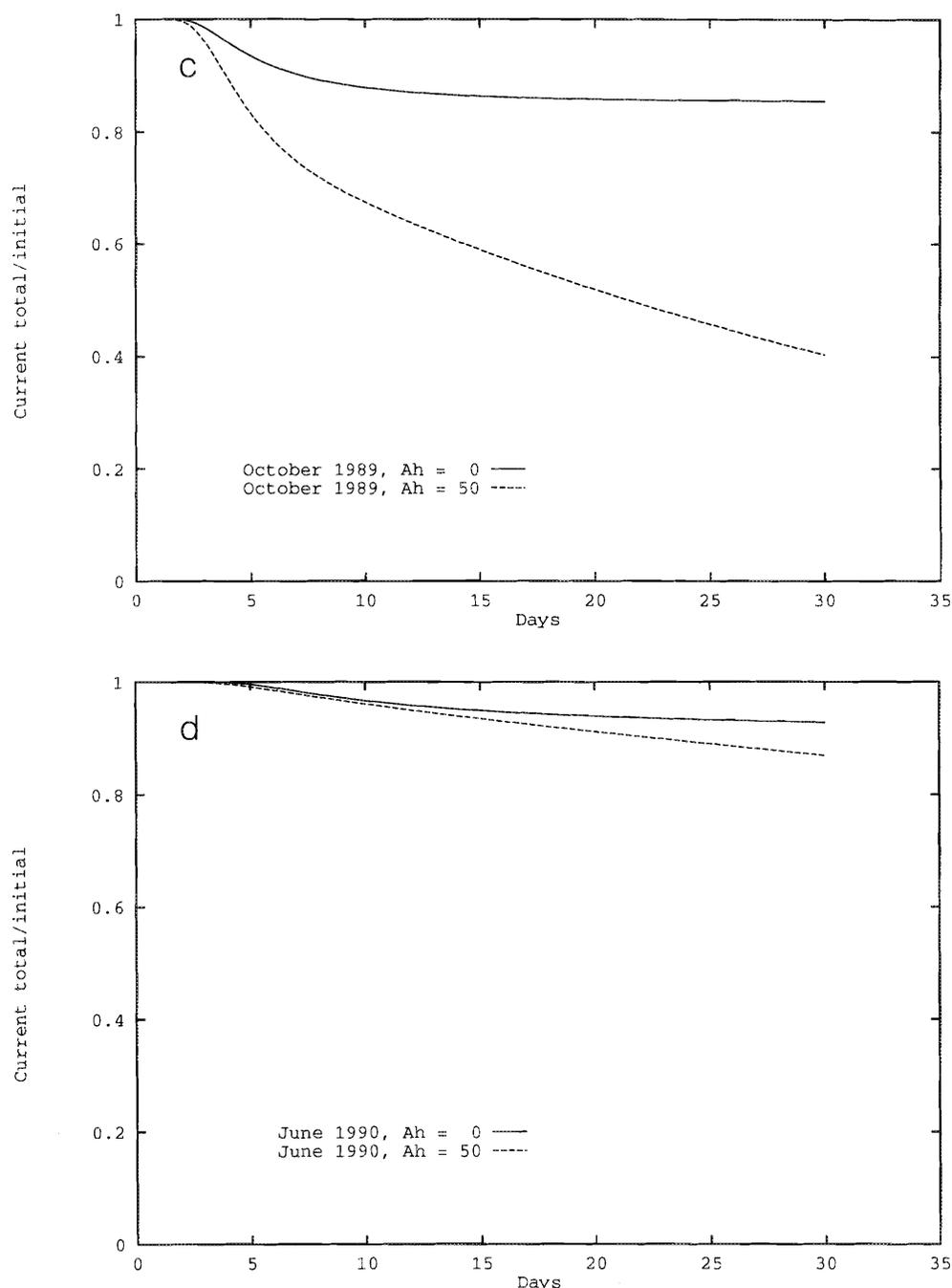


FIG. 5. (Concluded)

The wind stress used to force the model at the surface is obtained from winds measured at St. John's airport with wind stress computed following Large and Pond (1981). This wind stress has been used successfully in a reduced-gravity model of the thermocline response in the Bay (deYoung et al. 1993b). Furthermore, a comparison with stress calculated from a short time series of winds measured at the head of the Bay showed good agreement. Thus, St. John's wind data appear to be representative of winds over Conception Bay.

Four current meters were deployed on moorings across the mouth, at approximately 100–150 m depth separated by roughly 5–7 km. Data from these instruments were used to constrain the boundary condition on the barotropic flow at the mouth of the Bay. Current and wind data were averaged over a 2-d period to match the time required to collect the data.

One problem common to all numerical models is the need for verification. The diagnostic model presented here was verified by deYoung et al. (1993a), through comparison with current meter and surface radar (CODAR) data. They were able to show good agreement between modelled patterns of the circulation and those determined from radar measurements of surface currents (CODAR). We believe that the model does represent the primary features of the surface circulation.

#### Advection-Diffusion Model

The advection-diffusion equation is solved in sigma coordinates, just as for the velocity field in the diagnostic model. A conservative differencing scheme is used which is a mixture of centered and forward differencing (James 1986) and allows the coefficient of horizontal diffusion to be very

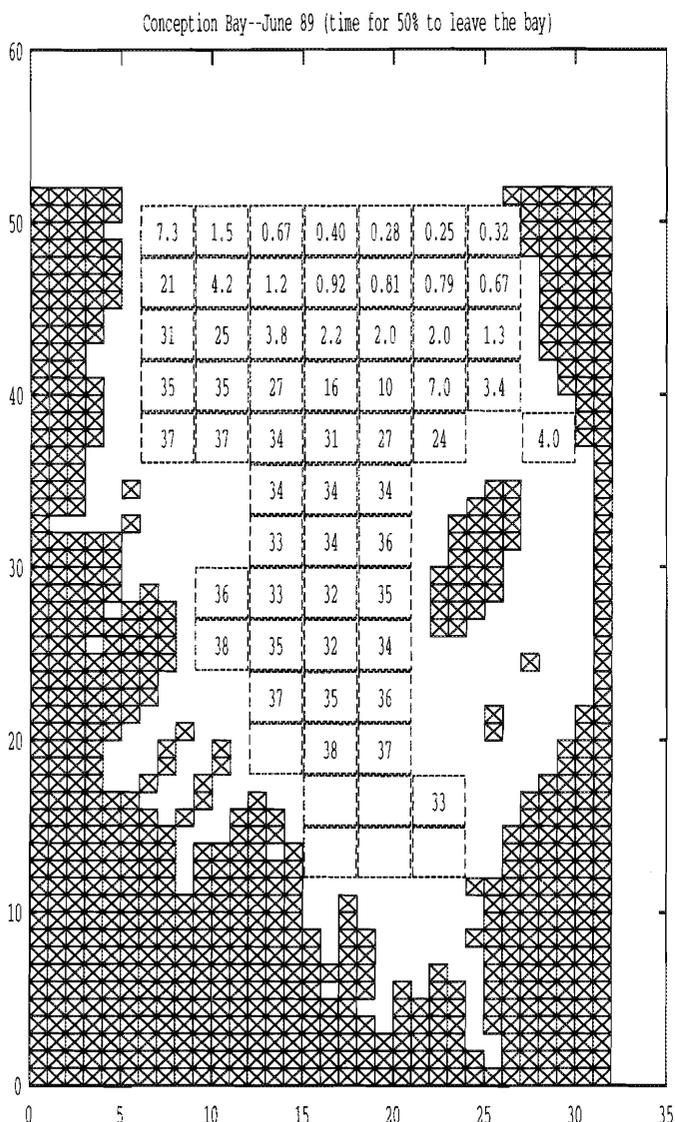


FIG. 6. Time in days to 50% loss for  $3 \times 3$  km patches in Conception Bay. The June 1989 velocity (Fig. 4a) is used for these runs with  $A_h = 50 \text{ m}^2/\text{s}$ .

small. In sigma coordinates the advection-diffusion equation that must be solved is

$$\frac{\partial(bH)}{\partial t} + \frac{\partial(ubH)}{\partial x} + \frac{\partial(vbH)}{\partial y} + \frac{\partial(\Omega bH)}{\partial \sigma}$$

$$= \frac{\partial}{\partial x} \left( A_h H \frac{\partial b}{\partial x} \right) + \frac{\partial}{\partial y} \left( A_h H \frac{\partial b}{\partial y} \right) + \frac{1}{H} \frac{\partial}{\partial \sigma} \left( K_v \frac{\partial b}{\partial \sigma} \right)$$

where  $H$  is the total water depth,  $A_h$  is the lateral diffusivity,  $K_v$  is the vertical diffusivity,  $b$  is the larval concentration,  $u$  and  $v$  are the components of horizontal velocity, and  $\Omega$  is the vertical velocity in sigma coordinates given by

$$\Omega = \frac{1}{H} \left( w - \sigma \left( u \frac{\partial H}{\partial x} + v \frac{\partial H}{\partial y} \right) \right)$$

where  $w$  is the usual vertical velocity measured vertically upwards.

In spite of the high vertical and horizontal resolution, we are able to run the model with fairly long time steps, roughly

20 min, by using an implicit time stepping routine. In some model runs, a time step of 10 min was needed to ensure numerical stability. This shorter time step was probably necessary because of the differencing scheme used, which mixes forward and centered differencing.

The larvae are placed in a uniform patch located from the surface down to a depth of 40 m. The location of the patch is chosen to simulate the location of larvae released from the beaches on the western side of the Bay (Templeman 1948). The model is initialised with a patch located near the head of the Bay (Fig. 3a). The placement of the larvae in the surface layer is based upon the results of the biological observations presented in the previous section. Although a simplification, it does seem a reasonable one given that the center of the mass of the larvae is in the top 30 m of the water. The patch size is  $4 \times 10$  km. The concentration of the larvae is in arbitrary units, since we are only interested in the changes in the patch structure and relative concentration for these model runs. One difficulty with the model is that the larvae are purely passive in that they can be carried into the lower layer by the vertical velocity. The larvae have no buoyancy that would keep them in the near surface, as is indeed observed (Fig. 2). To overcome this, we have added a weak velocity of 2 mm/s for depths below 40 m. This artificial vertical velocity effectively keeps the larvae in the surface waters of the Bay. Without this velocity, the larvae are quickly distributed nearly homogeneously in the vertical plane.

There is only one boundary through which the larvae can leave the Bay, i.e., across the mouth. Larvae can only leave the Bay; there is no transport of larvae into the Bay at the open boundary. Larvae that have left the Bay cannot return to the model.

## Model Results

Five different model runs are presented in this section using data from April, June, September, and October 1989 and June 1990. These runs span the period from the spring to the fall of 1989 with one data set from 1990. The spring runs are used to test sensitivity of the model results. A  $4 \times 10$  km patch of larvae was located at the head of the Bay, in the top 40 m of the water (Fig. 3a). The same starting patch configuration is used in all the model runs to be presented here. We shall also look at results of some tests to determine the spatial dependence of residence time.

The distribution patterns of the larvae at different periods (Fig. 3) show that within a few days the larvae disperse to cover the Bay. In this model run,  $A_h = 50 \text{ m}^2/\text{s}$ , a value that is representative of coastal waters (Csanady 1982). Later, we shall investigate the sensitivity to the choice of  $A_h$ . Larvae begin to leave the Bay within 3 d of starting the model run. Outflow occurs in the northeast corner of the circulation field and the resulting outflow of larvae can be seen in Fig. 3c and 3d. In addition, there are several closed circulation cells in the velocity field, for instance near the head of the Bay (Fig. 4a), which might be expected to trap larvae. The results of the dispersion model can be confirmed by looking at the velocity field used as the input (Fig. 4a). Velocity fields for other months (Fig. 4b-4d) show similar features to those observed in the June run, although they differ in detail.

One important question concerns the influence of horizontal diffusion. The problem of horizontal mixing in the

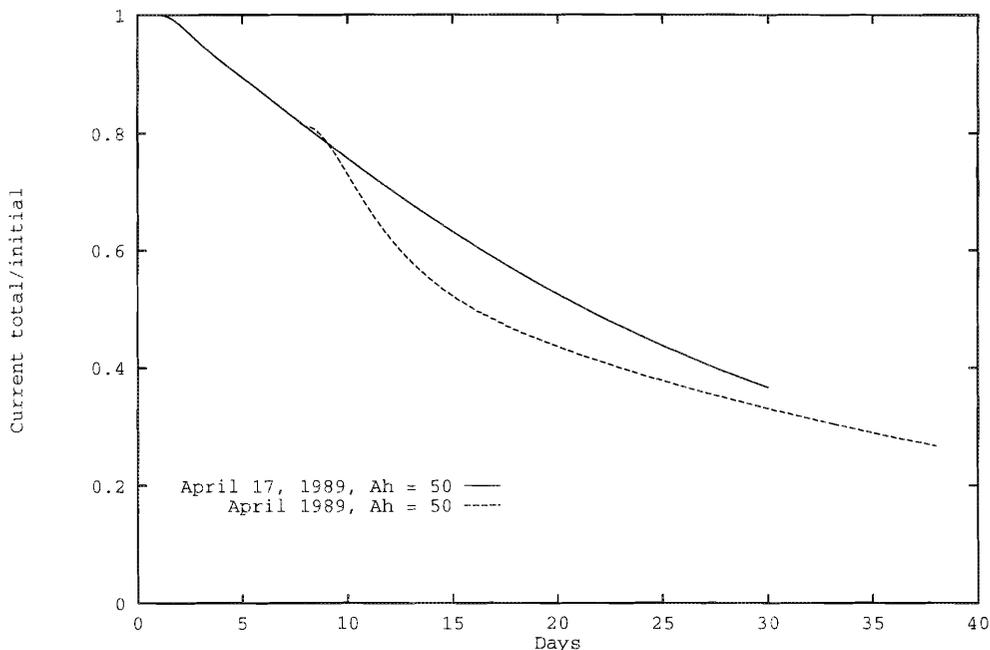


FIG. 7. Ratio of current total larval concentration relative to the initial concentration for April 1989, Conception Bay. Two different runs are shown, both using  $A_h = 50 \text{ m}^2/\text{s}$ ; one is for the April 17 velocity field alone (solid line) and the other (broken line) uses the April 25 velocity field after day 8.

ocean is a difficult one, and there are relatively few direct measurements of horizontal diffusivity (Csanady 1982). We have run the model for June 1989 with different values of  $A_h$  to investigate sensitivity to horizontal diffusion (Fig. 5a). The solid line shows the ratio of current larval concentration in the Bay to the total concentration for  $A_h = 0 \text{ m}^2/\text{s}$ . After 30 d, about 20% of the initial concentration has left the Bay. As the other lines show, adding horizontal diffusion greatly increases the rate of loss, although it appears that there is little sensitivity to the magnitude of  $A_h$ . Adding any amount of horizontal diffusion has nearly the same effect. After 30 d, about 40–50% of the initial mass has left the Bay. As we might expect, the greatest loss occurs for the largest value of  $A_h$ , although it is less than 10% greater than the loss obtained when  $A_h$  is 10 times smaller. Given this weak dependence upon  $A_h$ , we shall assume  $A_h = 50 \text{ m}^2/\text{s}$ , a value reasonable for coastal waters (Csanady 1982).

We have run the advection–diffusion model for all the velocity fields shown in Fig. 4; June, September, and October 1989 and June 1990. Plots of the residual concentration in the Bay show that there is some variability in residence time (Fig. 5). The percentage loss after 30 d is 45% for June 1989, 5% for September, 60% for October, and 15% for June 1990. If we take the residence time to be the point at which 50% of the initial mass has left the Bay, then residence time ranges from 22 d to well beyond 30 d. From these plots, one would conclude that the residence time is not less than 22 d and that it may be much longer.

One question raised by these plots concerns the spatial dependence of the residence time, since plots of the circulation (Fig. 4) suggest that there should be some spatial variability in the residence time. To answer this question, we ran the June 1989 case, with  $A_h = 50 \text{ m}^2/\text{s}$ , for many different  $3 \times 3 \text{ km}$  patches (Fig. 6). The residence times varied from less than a day to just less than 40 d. The shortest residence times were near the mouth of the Bay where the

larvae have comparatively little distance to travel before leaving the Bay. In general, larvae released near the head of the Bay take the longest to leave the Bay.

One further concern is the sensitivity to the velocity field. The only data collected close together in time are for April 17 and April 25, 1989. We carried out one run using just the April 17 velocity field and one run where the April 25 field was used after day 8 in the model. The results (Fig. 7) show that the change in velocity field does cause a small increase in the rate of loss. Clearly the proper test of this effect awaits the implementation of a time-dependent model.

In summary, we have shown that residence time for larvae near the head of Conception Bay lies between 20 and 40 d. Larvae released near the mouth of the Bay may have much shorter residence times, as little as a few days. The data presented from different months and years show similar features.

## Discussion and Conclusions

The model results showed that the larvae can disperse throughout the Bay quickly. In most runs the patch spread throughout the Bay in just a few days. From the model results, we conclude that the residence time for larvae released near the head of Conception Bay is from 20 to 40 d; thus, most of the larvae are resident in the Bay during the critical period for growth (Bakun et al. 1982). No consistent seasonal pattern was found with the limited set of data used.

We tested the influence of horizontal diffusion by running the model with varying values of  $A_h$  from 0 to  $50 \text{ m}^2/\text{s}$ . We found that adding even a small amount of horizontal diffusion can have a large effect when coupled with the circulation field. On its own, a lateral diversity of  $50 \text{ m}^2/\text{s}$  can only move the patch roughly 5 km over 6 d, but coupled with the circulation field, it can easily double the rate of

loss from the Bay. Thus the coupling between diffusion and advection is important, not diffusion alone, hence the weak dependence on the magnitude of  $A_h$ .

Our results are roughly consistent with times we might expect based upon simple scale analysis of the system. For example, if we take the length scale as 70 km, the length of the Bay, and consider a mean speed of 5 cm/s (roughly the standard deviation of observed currents in the Bay (unpublished data)), then considering the system to be one-dimensional, the residence time would be 16 d. This estimate is clearly strongly dependent upon the value we choose for the speed, and because there is no particularly strong mean circulation in the Bay and the tides are weak, it is difficult to choose and defend a single estimate of the mean along-bay velocity (deYoung et al. 1993a). The value chosen is, however, a reasonable one and does permit some comparison with the effective mean along-bay speed as derived from the numerical model.

Taggart and Leggett (1987) demonstrated that recently released capelin larvae are dispersed quickly (on the order of hours) from the nearshore region of the Bay. Given that these capelin are 3–4 mm long and growth rates are on the order of 0.20–0.25 mm/d (Jacquaz et al. 1977), the larvae leaving Conception Bay after 20–30 d would be 7.5–14.3 mm long. The mean size of larvae in August and September ranged from 7.2 to 13.7 mm, in good agreement with these predictions.

Our observations support the use of a model that confines the larvae to the top 40 m of the water column. The 40 m depth was chosen to include the peak densities of larvae observed in the Bay and also was based upon the mean summer density field (Petrie et al. 1991). However, this simplification overlooks known variability in the pycnocline depth and capelin vertical structure. At long time scales (weeks, months), we expect seasonal heating to be important (Petrie et al. 1991) whereas at shorter time scales (days) the effects of wind forcing must be considered (deYoung et al. 1993b). A fully baroclinic three-dimensional model is needed to account for such effects (Greatbatch and Goulding 1992).

Peak larval densities were a function of size with smaller, younger larvae being more numerous at shallower depths. The largest larvae captured were concentrated at, or below, the thermocline (25 m), at a depth where the influence of the surface wind stress might be reduced. Thus, older larvae might exhibit longer residence times, being in a water mass with a weaker circulation. In this regard, our predictions of dispersion are most applicable to the smallest, youngest capelin larvae.

Another factor to consider is the possible influence of diurnal vertical migration. The vertical migration observed by Frank and Carscadden (1989) occurred in shallow water (60 m) with a mixed-layer depth of 20 m. Clearly the importance of vertical movement will be greatest where the mixed layer depth is smallest. Here, where the mixed-layer depth in late summer is roughly 40 m, vertical migration may be less important. More sophisticated models are needed, together with new biological data, to determine the influence of vertical migration.

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## References

- BAILEY, R.J.F., K. ABLE, AND W.C. LEGGETT. 1977. Seasonal and vertical distribution and growth of juvenile and adult capelin (*Mallotus villosus*) in the St. Lawrence estuary and western Gulf of St. Lawrence. *J. Fish. Res. Board Can.* 34: 2030–2040.
- BAKUN, A., J. BEYER, D. PAULY, J.G. POPE, AND D.G. SHARP. 1982. Ocean sciences in relation to living resources. *Can. J. Fish. Aquat. Sci.* 39: 1059–1070.
- BARTSCH, J., K. BRANDER, M. HEATH, P. MUNK, K. RICHARDSON, AND E. SVENDSEN. 1989. Modelling the advection of herring larvae in the North Sea. *Nature (Lond.)* 340: 632–636.
- CSANADY, C.T. 1982. *Circulation in the Coastal Ocean*. Reidel, Amsterdam, The Netherlands. 274 p.
- DEYOUNG, B., R.J. GREATBATCH, AND K.B. FORWARD. 1993a. A diagnostic circulation model with application to Conception Bay, Newfoundland. *J. Phys. Oceanogr.* 23: 2617–2635.
- DEYOUNG, B., T. OTTERSON, AND R.J. GREATBATCH. 1993b. The local and non-local response of Conception Bay to wind forcing. *J. Phys. Oceanogr.* 23: 2636–2651.
- FORTIER, L., AND W.C. LEGGETT. 1982. Fickian transport and the dispersal of fish larvae in estuaries. *Can. J. Fish. Aquat. Sci.* 39: 1150–1163.
- FORTIER, L., AND W.C. LEGGETT. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. *Can. J. Fish. Aquat. Sci.* 40: 1543–1555.
- FORTIER, L., AND W.C. LEGGETT. 1985. A drift study of larval fish survival. *Mar. Ecol. Prog. Ser.* 25: 245–257.
- FORTIER, L., M.E. LEVASSEUR, R. DROLET, AND J.C. THERRIAULT. 1992. Export production and the distribution of fish larvae and their prey in a coastal jet frontal region. *Mar. Ecol. Prog. Ser.* 85: 203–218.
- FRANK, K.T., AND J.E. CARSCADDEN. 1989. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic. *J. Cons. int. Explor. Mer* 45: 146–164.
- FRANK, K.T., AND W.C. LEGGETT. 1981. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 38: 215–223.
- GILL, A.E. 1982. *Atmosphere–ocean dynamics*. Academic Press, New York, N.Y. 662 p.
- GREATBATCH, R.J., AND A. GOULDING. 1992. A long-time scale, density-stratified shelf circulation model. *Continental Shelf Res.* 12: 115–141.
- HELBIG, J., G. MERTZ, AND P. PEPIN. 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. *Fish. Oceanogr.* 1: 32–38.
- HOFFMANN, E.E., K.S. HEDSTRÖM, J.R. MOISAN, D.B. HAIDVOGEL, AND D.L. MACKAS. 1991. Use of simulated drifter tracks to investigate general transport patterns and residence times in the coastal transition zone. *J. Geophys. Res.* 96: 15,041–15,052.
- JACQUAZ, B., K.W. ABLE, AND W.C. LEGGETT. 1977. Seasonal distribution, abundance and growth of larval capelin (*Mallotus villosus*) in the St. Lawrence estuary and northwestern Gulf of St. Lawrence. *J. Fish. Res. Board Can.* 34: 2015–2029.
- JAMES, I.D. 1986. A front-resolving sigma coordinate sea model with a simple hybrid advection scheme. *Appl. Math. Model.* 10: 87–92.
- LARGE, W.G., AND S. POND. 1981. Open ocean momentum flux measurements in moderate to strong winds. *J. Phys. Oceanogr.* 11: 324–336.
- LEGGETT, W.C., K.T. FRANK, AND J.E. CARSCADDEN. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 41: 1193–1201.
- PAGE, F., AND P.C. SMITH. 1989. Particle drift in the surface layer off southwest Nova Scotia: description and evaluation of a model. *Can. J. Fish. Aquat. Sci.* 46(Suppl. 1): 21–43.
- PETRIE, B., J.W. LODER, S. AKENHEAD, AND J. LAZIER. 1991. Temperature and salinity variability on the eastern Newfoundland Shelf. *Atmosphere–Ocean* 29: 14–36.
- PIANKA, E.R. 1970. On  $r$ - and  $K$ -selection. *Am. Nat.* 104: 592–597.
- SAMEOTO, D.D., L.O. JAROSZYNSKI, AND W.B. FRASER. 1977. A multiple opening and closing sampler based on the MOCNESS and NIO nets. *J. Fish. Res. Board Can.* 34: 1230–1235.
- SAS. 1988. *SAS/STAT user's guide*, release 6.03 edition. SAS Institute Inc., Cary, N.C. 1028 p.

TAGGART, C.T., AND W.C. LEGGETT. 1987. Wind-forced hydrodynamics and their interaction with larval fish and plankton abundance: a time-series analysis of physical-biological data. *Can. J. Fish. Aquat. Sci.* 44: 438-451.

TEMPLEMAN, W. 1948. The life history of the capelin (*Mallotus villosus* O.F. Müller) in Newfoundland waters. *Bull. Nfld. Gov. Lab.* 17: 1-151.

WERNER, F.E., F.H. PAGE, D.R. LYNCH, J.W. LODER, R.G. LOUGH, R.I. PERRY, D.A. GREENBERG, AND M.M. SINCLAIR. 1993. Influence of the mean advection and simple behaviour on the distribution of cod and haddock early life stages on Georges Bank. *Fish. Oceanogr.* 2: 43-64.

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