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Physical Oceanographic Features and Processes Relevant to *Illex illecebrosus* Spawning in the Western North Atlantic and Subsequent Larval Distribution

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Abstract

On the assumption that the larvae of short-finned squid, *Illex illecebrosus*, are neutrally buoyant and drift passively with the currents, a shear dispersion model is used to predict the subsequent distribution of larvae from a point source located at or near the northern edge of the Gulf Stream at Cape Hatteras. The results indicate that under idealized conditions the patch would rapidly elongate into a long thin "ribbon" approaching a length of about 3,000 km in a 30-day period. On the further assumption that spawning occurs on bottom where temperatures exceed 13° C, the most likely spawning area for larvae found in the Slope Water/Gulf Stream frontal zone, in the January-March period, is the continental shelf south of Chesapeake Bay and possibly south of Cape Hatteras.

Introduction

The laboratory work of O'Dor *et al.* (1982) indicated that the eggs of short-finned squid, *I. illecebrosus*, do not develop at temperatures below 13° C. The only eggs, in which normal development was observed, were spawned at 13° C and developed at an average temperature of 14° C to produce normal hatchings after 11 days. Boletzky *et al.* (1973) reported that eggs of *Illex coindetii* develop normally at 15° C but fail to develop at 10° C. O'Dor *et al.* (1982) reported that the egg mass from *I. illecebrosus* was deposited on the bottom of the tank, and they stated that, under oceanic conditions, free-floating eggs would be unlikely to hatch successfully.

The Scientific Council of NAFO through its Standing Committee on Fishery Science identified five hypotheses concerning where *I. illecebrosus* may spawn in the western North Atlantic and how the juveniles return to the continental shelves off the Canadian coast (NAFO, 1981). This paper addresses principally one of these hypotheses on the assumption that *I. illecebrosus* spawns only on bottom in areas where the temperature exceeds 13° C. A dispersion model is developed to predict an idealized larval distribution over a period of 1-2 months after spawning.

Seasonal Thermal Structure and Bottom Temperature

The waters on the continental shelf between Cape Hatteras and the Grand Bank undergo a pronounced seasonal cycle of heating and cooling. This cycle, which is most pronounced at the surface and becomes progressively diminished in amplitude with depth, is confined usually to the upper 100-200 m of the water column. There is generally a phase lag with depth in the timing of seasonal maximum temperatures.

Daily temperature profiles have been taken at a number of lightship sites on the continental shelf from Cape Hatteras to the Gulf of Maine for many years. Data from seven of these sites (Fig. 1) have been examined for the 1956-60 period. Data for 1 year (1957) from the Portland, Chesapeake and Diamond Lightships are

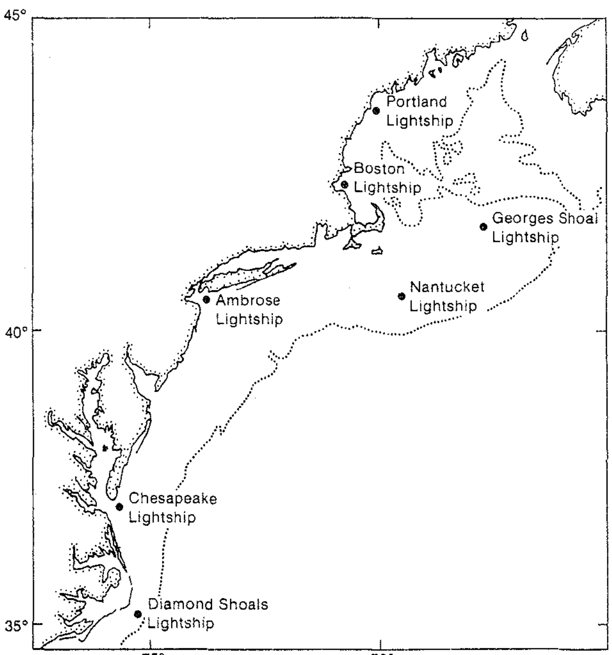

Fig. 1. Lightship locations where water temperature observations have been made daily for a number of years.

used to illustrate the general nature of the seasonal cycle (Fig. 2). The times when bottom temperature increased to 13° C and later declined below 13° C were noted for the seven sites over the 5-year period (Table 1). The measurements were taken over a range of depths (17–55 m) on the shelf, and care must therefore be taken in inferring the overall representativeness of the measurements in a detailed sense. Also, the data

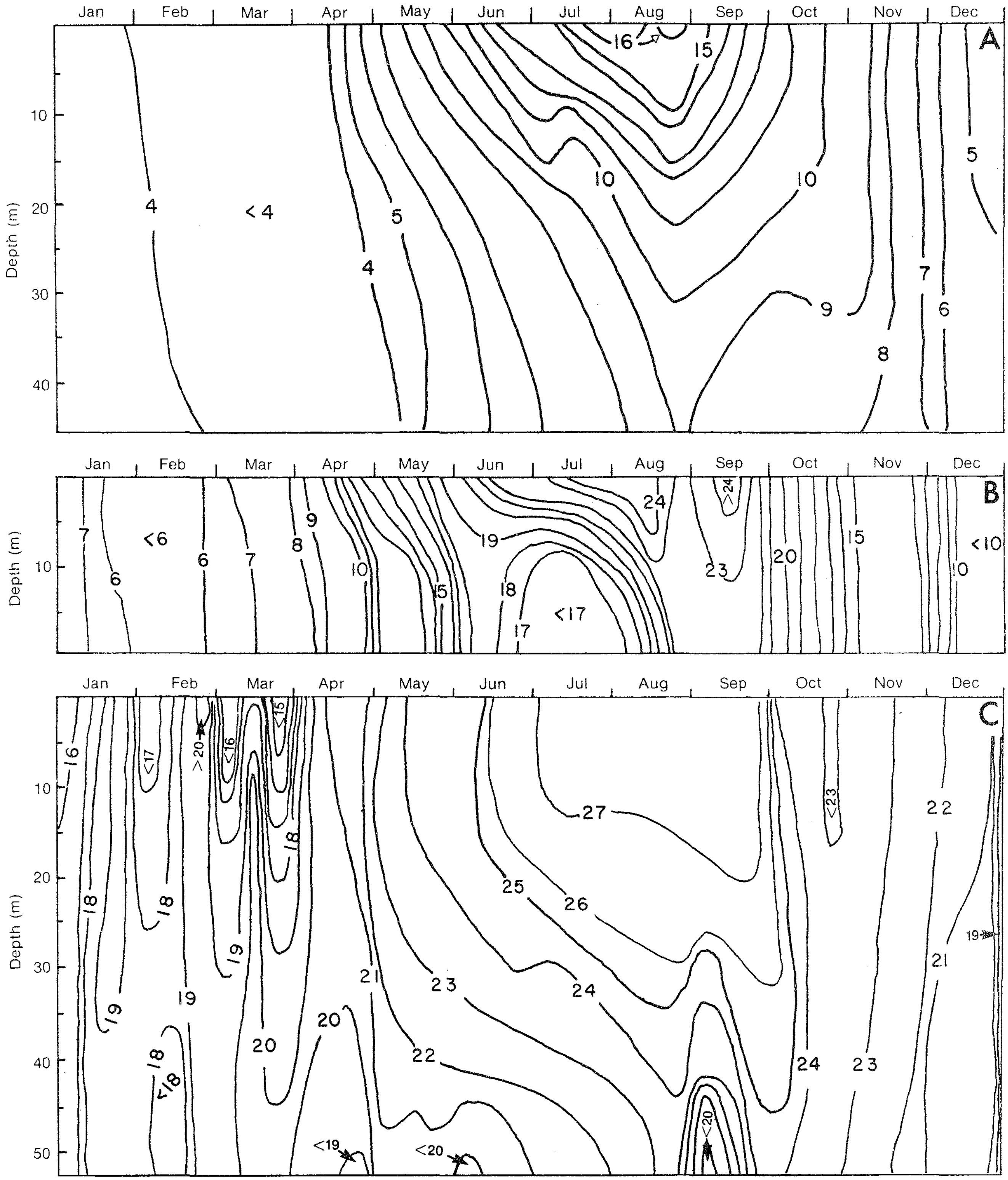

Fig. 2. Plots of time-depth temperature features in 1957 for (**A**) Portland Lightship, (**B**) Chesapeake Lightship, and (**C**) Diamond Shoals Lightship.

TABLE 1. Times when bottom temperatures exceeded 13°C at selected lightship stations during 1956-60 from the Gulf of Maine to Cape Hatteras.

Lightship	Depth of observation	Time when temperature: Increases to 13°C	Time when temperature: Decreases to 13°C	Maximum temperature °C	Month
Portland	46	(Never reaches 13°C)			
Boston	29	(Rarely reaches 13°C)			
Georges Shoals	17	Early July	Early Nov.	18°	Sep.
Nantucket	55	Late Sep.	Late Nov.	16°	Oct.
Ambrose	29	Early Aug.	Late Oct.	16°	Sep.
Chesapeake	20	Late May to early June	Late Nov.	21°	Aug.
Diamond Shoals	55	(Rarely <13°C; occasionally in Jan and Feb)		25°	Oct.

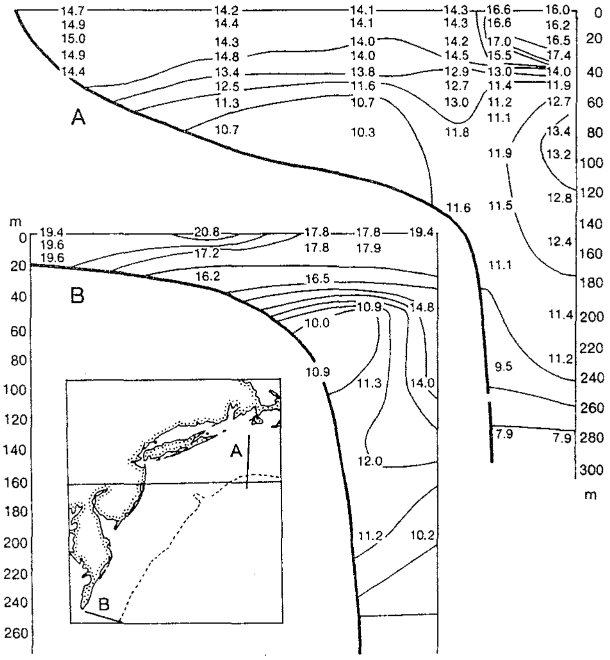

Fig. 3. Temperature profiles across the continental shelf: (**A**) off Martha's Vineyard, 19 October 1931; (**B**) off Chesapeake Bay, 30-31 October 1919 (From Bigelow, 1933).

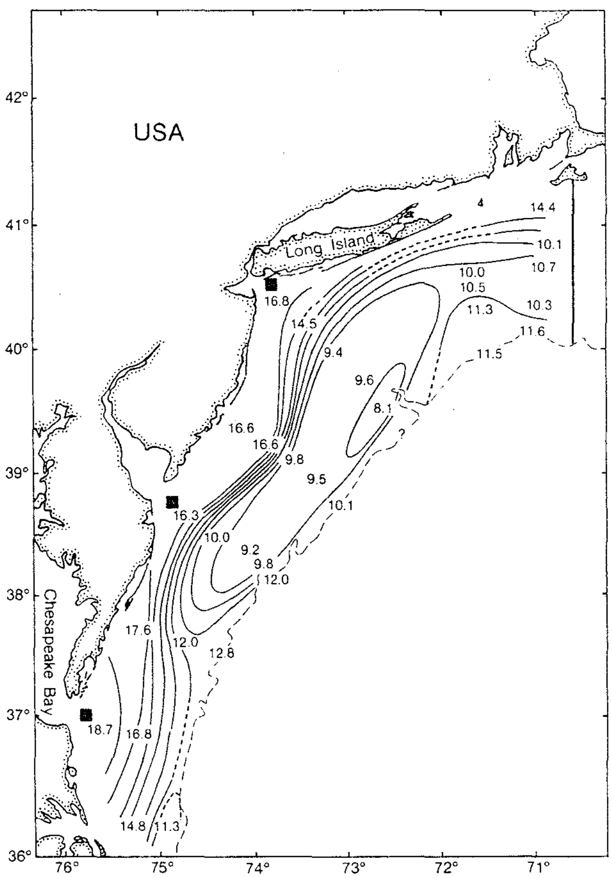

Fig. 4. Bottom temperatures at depths of 20-150 m on the continental shelf from Long island to Cape Hatteras, 19-29 October 1931 (from Bigelow, 1933).

show marked year-to-year variation. However, where depths exceed 20 m, the maximum bottom temperature under normal conditions does not exceed 13°C on the continental shelf north of about 42°N at any time during the year. At Nantucket Lightship, the bottom temperature generally exceeds 13°C for only about a 2-month period (late September-late November). There is a progressive increase in the period when bottom temperature exceeds 13°C from north to south, with the temperature at Diamond Shoals off Cape Hatteras rarely declining below 13°C.

Bigelow (1933), in his study of continental shelf waters from Cape Cod to Cape Hatteras, presented a series of temperature sections across the continental shelf at different seasons of the year, as well as maps showing bottom temperatures. Temperature sections south of Cape Cod and off Chesapeake Bay in October of 1931 and 1919 respectively (Fig. 3) show the general characteristics. Basically, the area where bottom temperatures exceed 13°C is confined to the shallow coastal waters and decreases toward the northeast. Bottom temperature contours for late October 1931 are shown in Fig. 4.

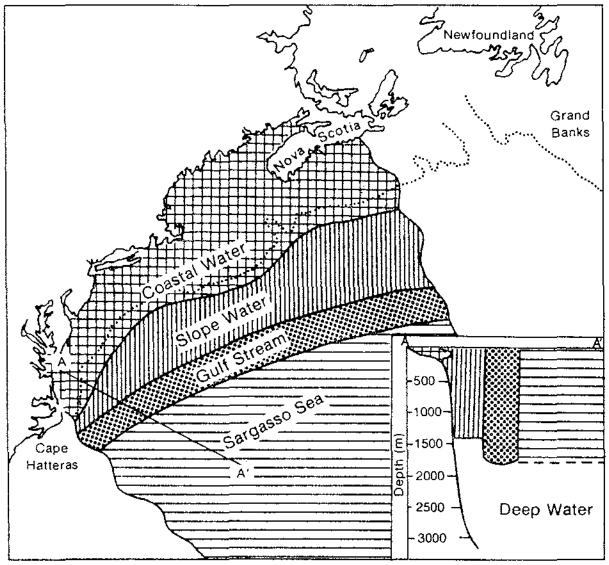

Fig. 5. Schematic representation of water masses in the Nova Scotia-Bermuda-Cape Hatteras triangle (from Iselin, 1936).

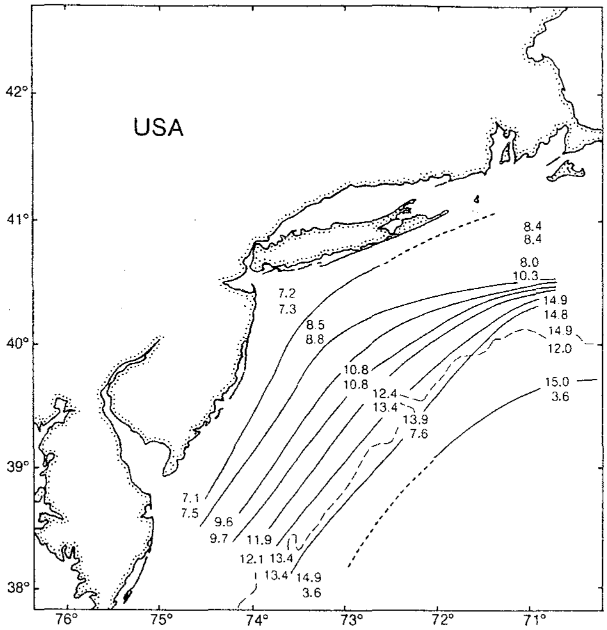

Fig. 6. Surface temperature contours off the U. S. coast from observations during 19-21 December 1932 (from Bigelow, 1933). (The upper value of each pair is the surface temperature and marks the station position, and the lower value is the bottom temperature.)

Surface temperatures over the continental shelf typically reach maximum values during August. However, the maximum values are normally reached at progressively later times at greater depths in the water column, generally several months later at 100 m.

Although the water on the continental shelf from Cape Hatteras to the Grand Bank is generally classed as "Coastal Water" or "Shelf Water", it is bounded on the seaward side by a water mass termed "Slope Water". Iselin (1936) presented a good schematic illustration of the general structure of the water masses in the Nova Scotia-Cape Hatteras-Bermuda triangle (Fig. 5). The boundaries or fronts between these water masses are convoluted and are regions of continual change, with strong temperature and salinity gradients. In the Mid-Atlantic Bight north of Cape Hatteras, the boundary between Coastal Water and Slope Water is located on the bottom near the shelf break at about 100 m (Wright, 1976) and slopes upward to intersect the surface at approximately 50 km farther seaward. Thus, the seasonal pattern of bottom temperatures in the shelf-slope area is markedly different from that of the shelf area nearer to the coast. The net effect of the Slope Water is to produce maximum bottom temperatures along the edge of the shelf in the autumn-winter period. Bottom temperature data, reported by Bigelow (1933) for 19-21 December 1932, show Slope Water along the edge of the shelf near the 100-m isobath (Fig. 6).

Northern Spawning Area Limits for *I. illecebrosus*

If *I. illecebrosus* spawns on the bottom at temperatures higher than 13° C, the northern limit of the region with suitable physical conditions for spawning is the Cape Cod-Georges Bank area. The continental shelf from Cape Hatteras southward is suitable for year-round spawning in terms of meeting the minimum temperature criterium. In the area north of Cape Hatteras, the period when conditions are suitable for spawning diminishes to about 6 months off Chesapeake Bay, 3 months off New York, 2 months on Nantucket Shoals and zero within the Gulf of Maine and farther northeastward. During October-November, the 13° C isotherm at the bottom in coastal waters recedes rapidly southward toward Cape Hatteras (Fig. 7). However, the Shelf Water-Slope Water boundary zone along the edge of the shelf behaves differently from the coastal area. Wright (1976) studied the thermal features of the shelf-slope area between 69° W and 72° W from 32 years of data and showed that the boundary, identified by the 10° C isotherm, intersected the bottom within 16 km of the 100-m isobath about 80% of the time. Maximum temperature of Slope Water on the bottom varied about 2° C seasonally and averaged about 13.2° C annually, the maximum occurring in December, although water with temperatures about 13° C was present from August to February. Although Wright (1976) did not give statistical limits for the areal extent of >13° C bottom water, examination of Bigelow's (1933) data indicates that it is unlikely to extend much deeper than the 200-m isobath. In Fig. 7, it has been assumed that water >13° C is confined to the 100–200 m depth zone in the shelf-slope area between Cape Hatteras and Cape Cod.

Lange and Sissenwine (MS 1981) indicated that *I. illecebrosus*, in the area off northeastern United States, probably spawns to some extent throughout most of

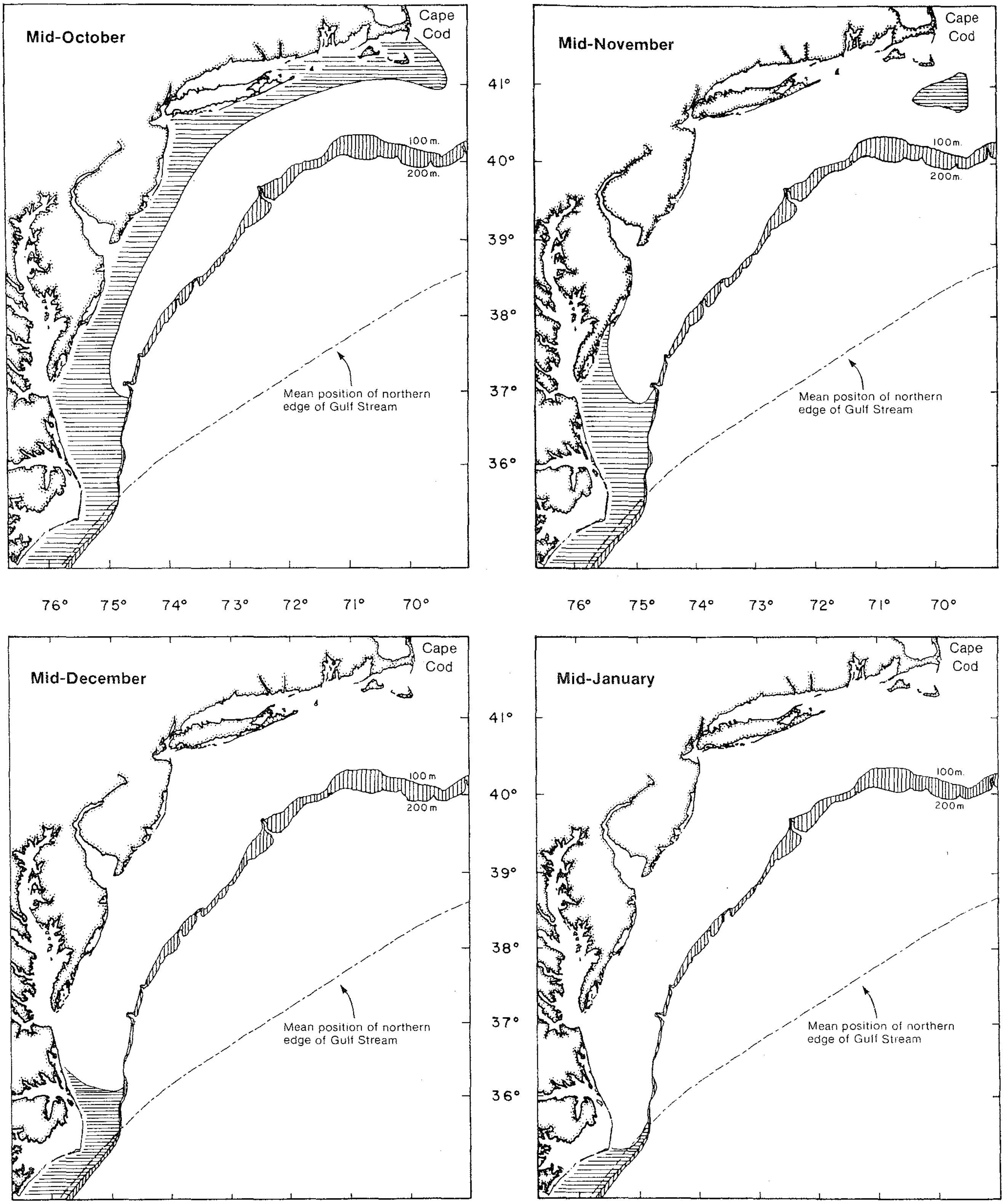

Fig. 7. Maps of the Cape Cod-Cape Hatteras region showing approximate areas (shaded) where bottom temperatures are expected to normally exceed 13°C in the period from mid-October to mid-January.

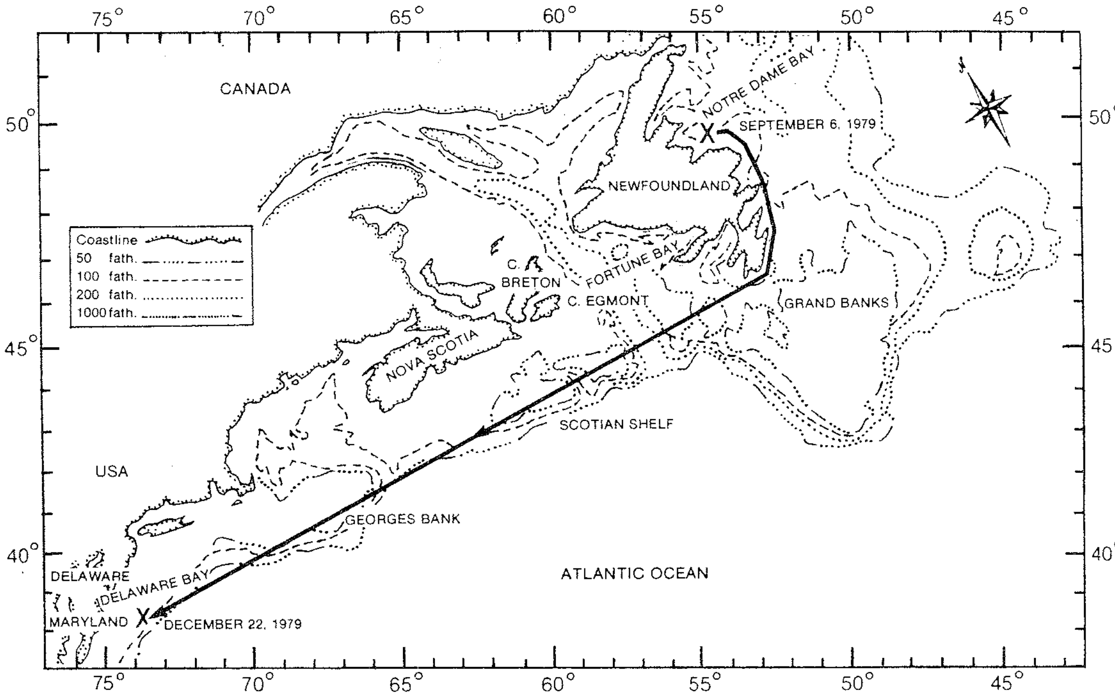

Fig. 8. Map showing the shortest possible migration route for a squid tagged in northeastern Newfoundland and recaptured off Maryland (from Dawe *et al*., 1981).

the year, although samples from autumn catches contained the highest proportion of mature individuals in most years. No spawning has been observed in waters off Nova Scotia or Newfoundland, and this is consistent with the assumption that bottom temperatures in these areas are always subcritical. The departure of maturing *I. illecebrosus* from the Canadian continental shelf waters in autumn is noteworthy. Of particular significance is the fact that squid can travel long distances in comparatively short periods. Dawe *et al*. (1981) reported the recapture off Maryland of a short-finned squid tagged in Notre Dame Bay, Newfoundland. This migrant travelled at least 2,300 km in 107 days (Fig. 8). This squid, when recaptured in the 100-200 m depth zone, may have already reached the area where bottom temperatures exceeded 13° C. On the other hand, if it were to spawn in shallower depths, it would have to continue southward almost to Cape Hatteras before encountering 13° C bottom water.

Juvenile *I. illecebrosus* (10-30 mm mantle length) have been captured during February-March in the Slope Water-Gulf Stream frontal zone (Fedulov and Froerman, MS 1980; Dawe *et al*., MS 1981). Although growth rates during the larval and juvenile stages are unknown, Squires (1967) concluded that *I. illecebrosus* probably matures within the first year of life, with an average growth rate of 2.8 cm/mo over a 12-month period and 4.7 cm/mo during the first 3 months. On that basis, 10-30 mm juveniles taken in February-March are probably less than 2 months old. Thus, peak spawning may occur during December-January, with the highest probability in the area south of Chesapeake Bay and possibly south of Cape Hatteras, where bottom temperatures in winter exceed 13° C.

Assumed Spawning in the Chesapeake Bay-Cape Hatteras Area

If *I. illecebrosus* larvae are "released" from the bottom in the Chesapeake Bay-Cape Hatteras area, what pattern of dispersion might one expect? If the larvae are neutrally buoyant and immobile, they would be expected to behave much like the surrounding water mass. In winter, the water is virtually homogeneous from surface to bottom (Fig. 2B, 2C). Bumpus (1973), in his summary of a 10-year study of drift-bottle and seabed-drifter releases, concluded that a mean alongshore flow of 5 cm/sec occurs from Cape Cod to Cape Hatteras. Beardsley *et al*. (1976) determined the "mean" or residual current field from current meters in the Mid-Atlantic Bight (Fig. 9). Only records with a duration of 1 month or longer were used, and the mean currents are plotted as vectors with magnitude equal to average speed. The flow near Section III is southerly at all depths, and in both summer and winter at the three outermost stations, at speeds of 10-20 cm/sec.

It would be expected, therefore, under the foregoing conditions, that larvae would be mixed throughout the water column on the shelf within a matter of hours

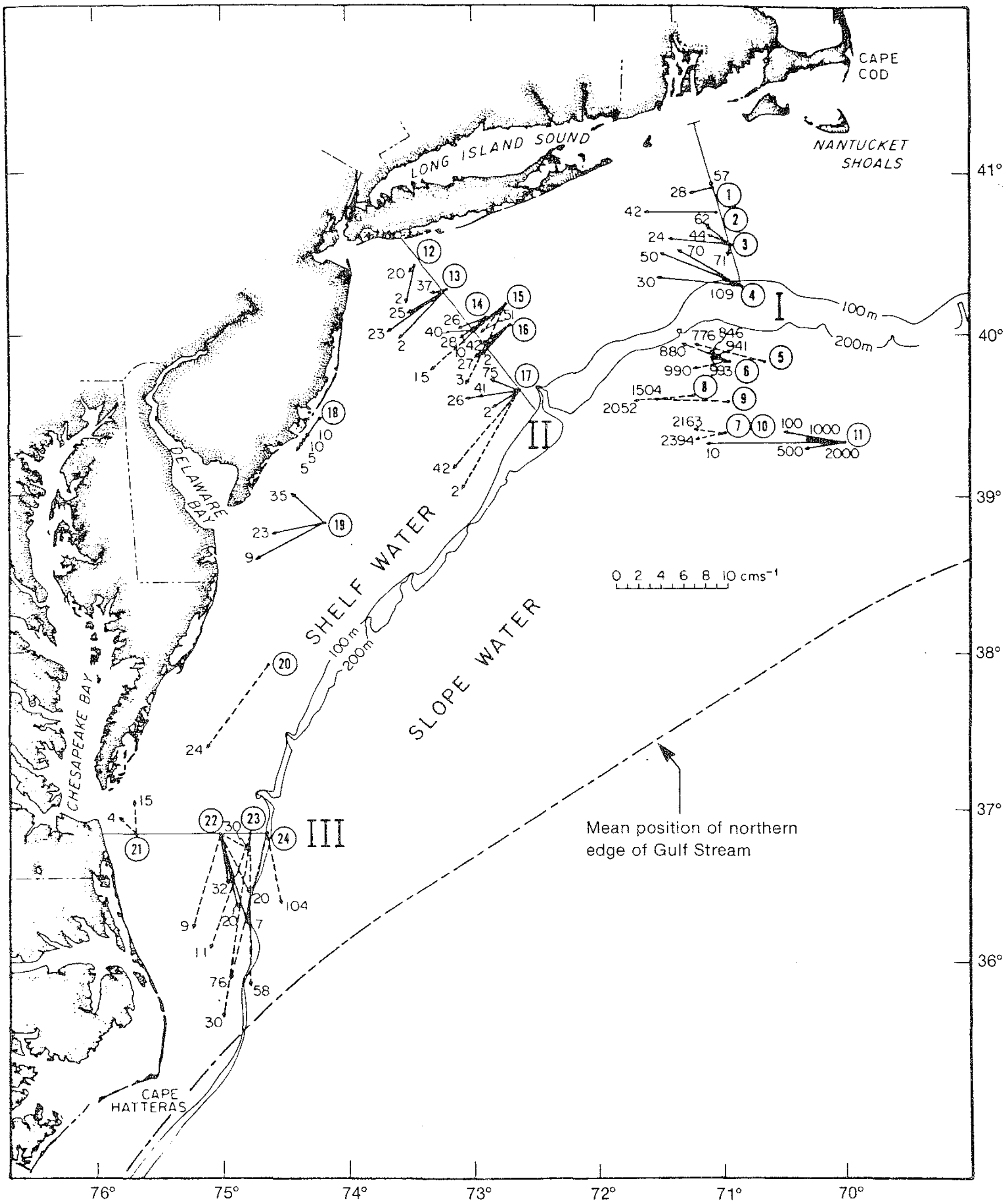

Fig. 9. Mean velocities (cm/sec) at various depths in the Cape Cod-Cape Hatteras region, as measured by moored current meters (from Beardsley *et al.*, 1976). [Solid and dashed arrows indicate winter and summer velocities respectively; station numbers are inside the circles and depths (m) are indicated at the heads of the arrows.]

after their release. Advection southward would transport them to Cape Hatteras within a matter of days. Because Cape Hatteras is a barrier to continued southward alongshore flow, the current turns seaward and becomes entrained in the Gulf Stream (Beardsley *et al.*, 1976). Before considering specifically the northeastward transport of larvae in the Gulf Stream system, it is necessary to give a theoretical review of particle diffusion and dispersion in shear flow.

Diffusion and Dispersion Processes

General characteristics

The process of oceanic diffusion is complex and there is no single theory that can explain or interpret the entire diffusion pattern. In practice, therefore, progress in understanding oceanic diffusion depends greatly on an empirical approach by means of tracer experiments.

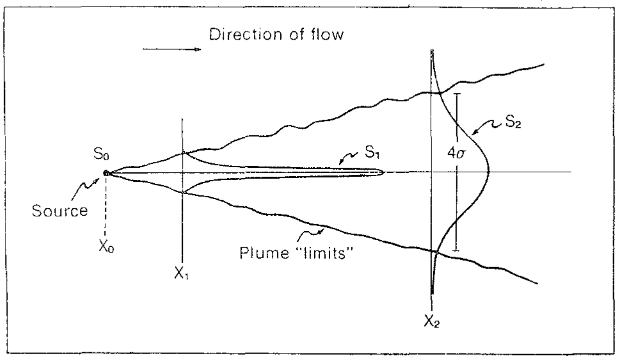

Fig. 10. Schematic illustration of the diffusion of a substance away from a continuous point source in a uniform flow. Typically "Gaussian" profiles of the concentration of the diffusing substance are shown for two cross-sections through the plume downstream from the source. The patch width is defined as four standard deviations (4σ).

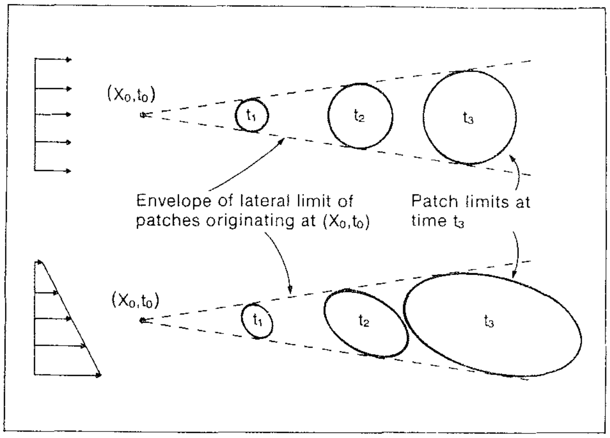

Fig. 11. Schematic illustration of the shape of a patch of diffusing substance in a uniform flow field (upper) and in a shear flow field (lower). Patch limits are shown for three different times (t_1 , t_2 and t_3).

If a substance S with concentration S_o was continuously introduced at position X_o in water moving uniformly with velocity U_o in the x-direction, the substance typically spreads out into an ever-broadening plume and the concentration decreases as the distance from the source increases. This phenomenon is illustrated schematically in Fig. 10. Typically, the distribution of the concentration across the plume is Gaussian, and, in practice, the variance (σ^2) is used to describe the diffusion characteristics and the plume width is taken as 4σ, which encompasses about 95% of the diffusing substance.

In addition to the diffusion of a substance through the turbulent or eddying water motion, its spread is further enhanced if there is a gradient (shear) in the mean flow field. The effect of horizontal velocity shear is illustrated schematically in Fig. 11. In a no-shear situation, diffusion away from a point would be radially symmetric, with the limits of the patch size increasing with time. In the presence of horizontal shear, however, the substance will be stretched out in the direction of the flow, because material diffusing into the area of higher velocity will be advected faster than the mean and material diffusing into the area of lower velocity will be advected slower than the mean.

The distribution of a conservative property (S) in the sea can be represented in terms of the differential equation:

$$\frac{\partial S}{\partial t} = u\frac{\partial S}{\partial t} + v\frac{\partial S}{\partial y} + w\frac{\partial S}{\partial z} = \frac{\partial}{\partial x}\left(A_x\frac{\partial S}{\partial x}\right) + \frac{\partial}{\partial y}\left(A_y\frac{\partial S}{\partial y}\right) + \frac{\partial}{\partial z}\left(A_z\frac{\partial S}{\partial z}\right) \qquad (1)$$

where S = S(x,y,z,t) = concentration; x = eastward direction; y = northward direction; z = downward direction; t = time; u, v and w are velocities in the x, y and z directions respectively; and A_x, A_y and A_z are eddy diffusion coefficients. The eddy diffusion coefficients are considered to be analogous with molecular diffusion coefficients but many orders of magnitude larger because they incorporate the effect of turbulent mixing.

Some simplifying assumptions must be made to enable a solution to Equation 1. Specifically, it is assumed that diffusion is confined to the horizontal direction and is independent of position, that the water is homogeneous over depth (d), that the flow is only in the x direction, and that the shear (Ω) is constant so that $u = u_o - \Omega_y$ where u_o is the mean velocity. Equation 1 thus becomes

$$\frac{\partial S}{\partial t} + (u_o - \Omega_y)\frac{\partial S}{\partial x} = A_x\frac{\partial^2 S}{\partial x^2} + A_y\frac{\partial^2 S}{\partial y^2} \qquad (2)$$

Since the mean velocity has nothing to do with the dispersion of S (which for convenience is considered to be a concentration of squid larvae), u_o can be eliminated from equation 2, with the understanding that the coordinate system (x,y,z) is moving with the center of gravity of the patch of squid larvae. If a mass of squid larvae (Q) is introduced at an instantaneous point source into the water column under initial conditions of t = 0 and x = y = 0, the solution of equation 2, as shown by Carter and Okuba (1965), is

$$S(s,y,t) = \frac{Q}{4t(A_xA_y)^{\frac{1}{2}}\left\{1 + \frac{\Omega^2 Ay}{12A_x}t^2\right\}^{\frac{1}{2}}} \,.\, \exp(B) \qquad (3)$$

$$\text{Where } B = \frac{x^2 + \Omega xyt + \frac{A_x}{A_y}\left\{1 + \frac{\Omega^2 A_y}{3A_x}t^2\right\}y^2}{4tA_x\left\{1 + \frac{\Omega^2 A_y}{12A_x}t^2\right\}}$$

TABLE 2. Form of dispersion parameters for Equation 3 at long times after release of larvae from an instantaneous point source.

Peak concentration (Sp)	Inflow direction variance (σ_x^2)	Normal to flow variance (σ_y^2)	Stretching factor, σ_x/σ_y (ρ)
$\frac{3t^{-2}Q}{2\pi A_y \Omega}$	$\frac{2 A_y \Omega^2 t^3}{3}$	$2 A_y t$	$\frac{\Omega t}{\sqrt{3}}$

Equation 3, having a quadratic form in x and y, indicates that the contours of concentration are a set of ellipses with common principal axes whose orientation varies with time. Thus, the larval squid patch is elongated in the direction of flow. The variance in the major principal axis increases as the cube of the time (t^3) and the square of the shear (Ω^2). After a sufficiently long time, the patch of larvae will line up in the direction of mean flow.

On the basis of Equation 3, a number of diffusion characteristics can be computed, such as the peak concentration (S_p), the variances σ_x^2 and σ_y^2), and the stretching factor (ρ), i.e. the ratio of the major axis to the minor axis of the ellipse. Since only very long diffusion times (days to weeks) are of interest, the forms of these parameters can be simplified as shown in Table 2.

Dispersion from a continuous source

The foregoing model, although providing insight into the nature of dispersion from an instantaneous point source, is not realistically applicable to larval squid dispersion, because spawning and hatching occurs over an interval of time. A model is needed that predicts subsequent distribution from a larval squid source that is continuous over a period of several weeks.

Okuba and Karweit (1969) dealt with the application of the shear-diffusion solution for a continuous release of a passive contaminant in a flow with uniform shear both laterally and vertically. Basically, the solution assumes that a plume may be assembled by the superposition of an infinite number of patches released from a fixed origin and translated by the mean flow. Figure 11 is a schematic representation of individual patches and the envelope surrounding them for both a uniform and a shear flow. Okuba and Karweit (1969), in their numerical solution, found that the cross-sectional distributions of concentration became skewed about the maximum, at increasing distances from the source, to the side where the velocity was lower (Fig. 12). They explain that, in general, the lateral spread at a given distance from the source is determined by the time required for the flow to cover the

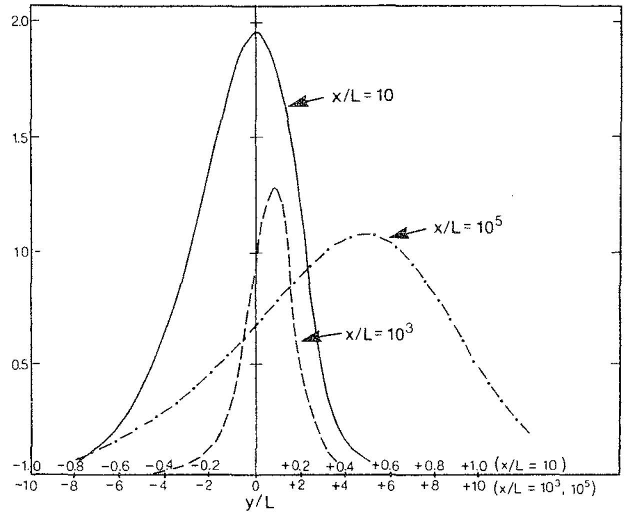

Fig. 12. Concentration distribution across a plume in a shear flow field (from Okuba and Karweit, 1969).

distance, this time being longer at the site where the velocity of the flow is lower and shorter where the velocity is higher. Hence, the lateral spread will be wider at the site of the lower mean velocity.

As indicated by the concentration isopleths illustrated schematically in Fig. 13, the maximum concentration is seen to bend initially in the direction where the mean velocity is smaller, but, at longer distances when the shear effect becomes relatively important in mixing, it bends in the direction of increasing velocity. The overall rate of decrease in the peak concentration is nearly inversely proportional to the distance away from the source. Another interesting observation is that, if the horizontal velocity decreases with depth, the maximum concentration occurs at the sea surface.

Although lines of constant concentration are of interest with respect to larval dispersion, knowledge of how the age-distribution curves should vary geographically is of equal interest. It is not the intent to develop an analytical model of the precise distribution, but a semi-quantitative interpretation will be attempted. If larvae are released into the water column over a period of, say, 100 time units, the larvae which have reached the furthest downstream location at t = 100 will be all age 100 but at exceedingly low concentration whereas the age 0 larvae at the source will be highly concentrated. The mode of the age distribution will shift smoothly from 0 to 100 along the axis of peak concentration. On any cross-section, normal to the locus of peak concentration, the age will be highest at the most northerly point where the velocities are lowest and lowest at the most southerly point where the velocities are highest. Under certain conditions of shear and horizontal eddy diffusion, the isopheths of age might appear as in Fig. 14.

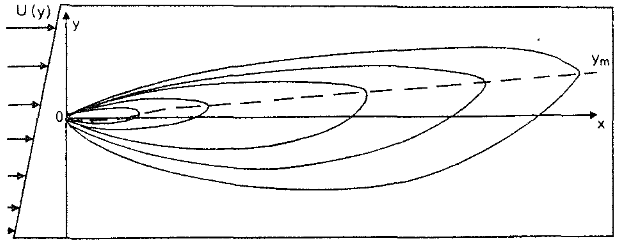

Fig. 13. Lines of equal concentration for a continuous plume in a shear flow field (from Okuba and Karweit, 1969). Y_m is the locus of maximum concentration.)

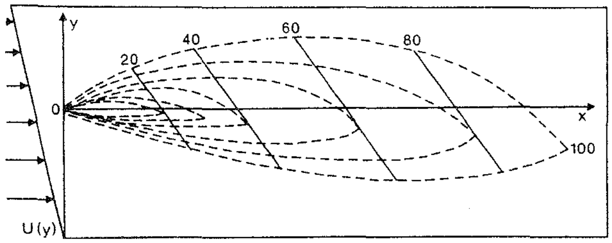

Fig. 14. Schematic illustration of the way in which the age frequency of larvae may vary geographically. (The numbers used are arbitrary and would vary markedly depending on the shear and diffusion coefficients selected.)

Flow characteristics in the Gulf Stream

Before evaluating the various parameters identified in the preceding sections, some of the important features of the flow pattern in the Gulf Stream must be considered. Currents in the Gulf Stream have been measured or computed by a variety of techniques: time-distance observations of ship drift (Loran), surface current measurements with geomagnetic-electrokinetographs (GEK), and dynamic computations from temperature and salinity data. More recently, satellite-tracked droqued buoys have provided frequent and accurate information on drift over many months.

In the Gulf Stream, peak velocities of 200–250 cm/sec are commonly observed. Worthington (1954) measured and computed velocities through three sections across the Gulf Stream in October–November 1950 in the vicinity of 68°–69° W (Fig. 15). The results from all three methods (GEK, Loran, and dynamic computation) are in relatively good agreement and show that, on the average, the horizontal shear is strongest near the northern edge of the Gulf Stream. Shear in this part of the flow ranged from 3×10^{-5} to 8×10^{-5}/sec with a mean of 6×10^{-5}/sec. Mean current velocity through this shear zone was about 100 cm/sec. The mean maximum velocity of the current was about 200 cm/sec. It should be noted as well that the northern edge of the Stream, on a water-mass basis may not be at the zero velocity position, since Slope Water and various admixtures of Slope Water-Coastal Water-Gulf Stream Water may also be moving in the direction of the Stream.

Geostrophic currents, assuming no motion at 2,000 m, were computed by Worthington (1954) for the three sections noted above (Fig. 16). Although the Gulf Stream appears to be composed of a series of jets, the important consideration is the broadscale picture, i.e. the core of maximum current is confined to depths less than 200 m, and velocities >20 cm/sec are confined to the upper 1,000 m.

The advent of satellite technology for tracking drifting buoys has enabled the acquisition of much new data on the kinematics of the Gulf Stream. Kirwan *et al*. (1976) reported the results of a buoy (drogued with a parachute at the end of 35 m of wire) launched off Florida on 20 July 1975 and tracked for 5 months (Fig. 17). Of particular interest is the trajectory from off Cape Hatteras to about 55° W, the distance being covered in 15 days at an average speed well over 150 cm/sec. The mean straight-line transit velocity was in excess of 140 cm/sec. For a short period, the maximum drift velocity was in excess of 250 cm/sec.

Other buoys, deployed in the Northwest Atlantic for different purposes, have become entrapped in the Gulf Stream for part of their periods of deployment (Fig. 18). Buoy 0252, with a drogue at 200 m, travelled from just off Cape Hatteras to 60° W in 14 days (Fig. 18A) at a mean straight-line velocity of about 120 cm/sec. Buoy 0512 (Fig. 18B) made a similar journey in 38 days, but, during this period, it spent 24 days making three circuits of a warm-core eddy before continuing eastward. The mean velocity, excluding time in the eddy, averaged about 120 cm/sec. Buoy 1301 (Fig. 18C), originally deployed on Browns Bank off Southwest Nova Scotia, was caught in the Gulf Stream south of Georges Bank and averaged 50 cm/sec during its eastward transit from 60° W to 50° W.

The general picture emerges that, although the flow velocities in the Gulf Stream tend to decrease towards the east, particularly east of 60° W, the average speed in the region from Cape Hatteras to about 60° W is typically in the range of 120–150 cm/sec.

Larval dispersion in the Gulf Stream system

From the results of Worthington (1954) and the satellite-tracked buoys, the simple velocity profile depicted in Fig. 19 is assumed for use in the larval dispersion model. It is further assumed that the Gulf Stream flows smoothly without meanders and that the velocity profile does not change between 75° W and 50° W. With realistic velocity and shear values, the simplified equation of particle dispersion in shear flow from an instantaneous point source, can be solved for a point source located off Cape Hatteras.

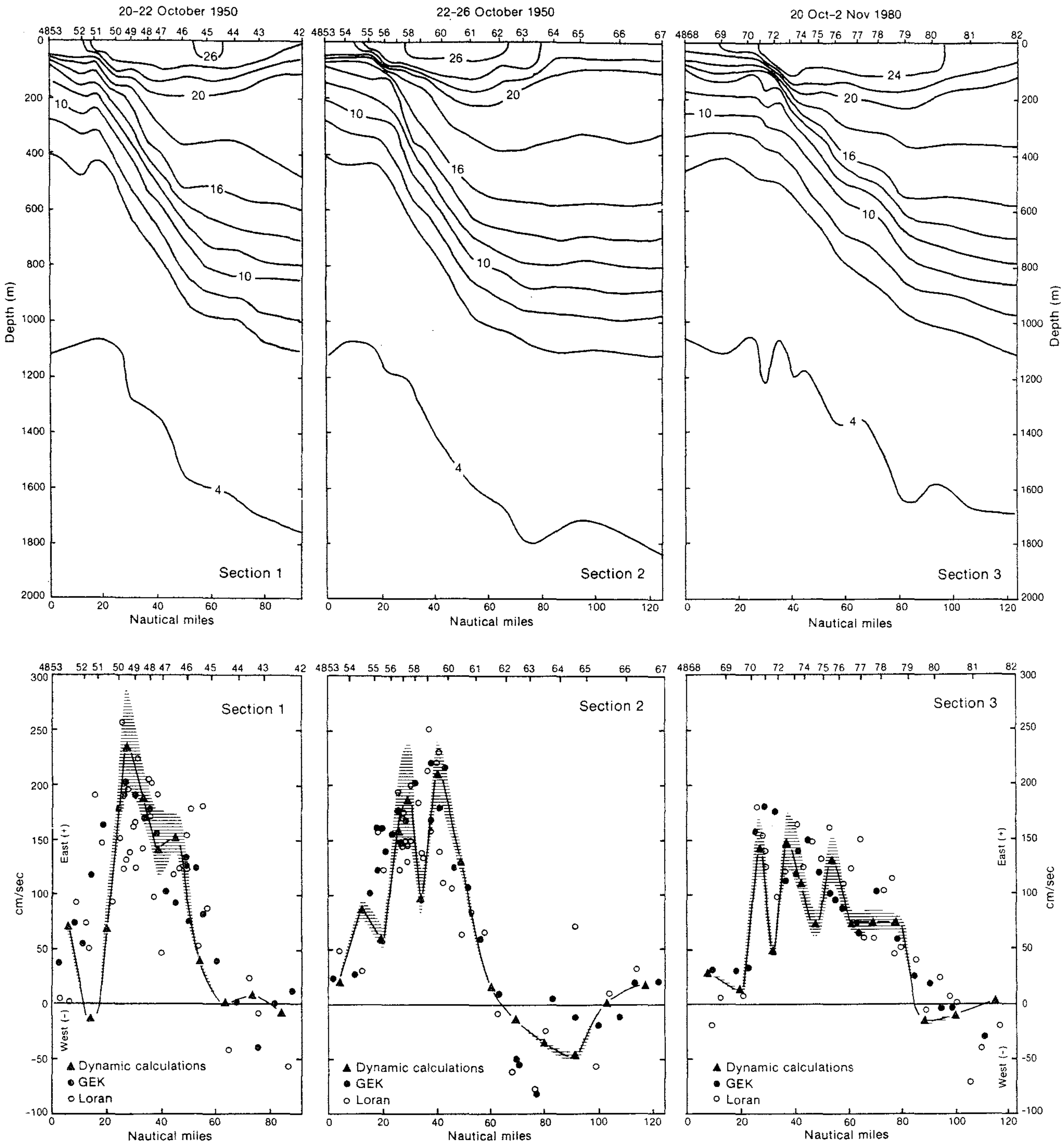

Fig. 15. Temperature profiles (upper) for three sections across the Gulf Stream (68° to 70° W) in October–November 1950, and the corresponding surface velocities (lower) for GEK, Loran and Dynamic calculations (from Worthington, 1954).

Patch dispersion characters are computed for two larval "injection" points (Table 3). In the first example, the larvae are assumed to be injected as an instantaneous pulse where the velocity is assumed to be zero at the northern edge of the Gulf Stream. Patch length in the direction of flow is given by

$$2\ [(\sigma_x)_t + (\sigma_y)_t]$$

In the second example, larvae are assumed to be injected at a point 12 km inside the shear zone where

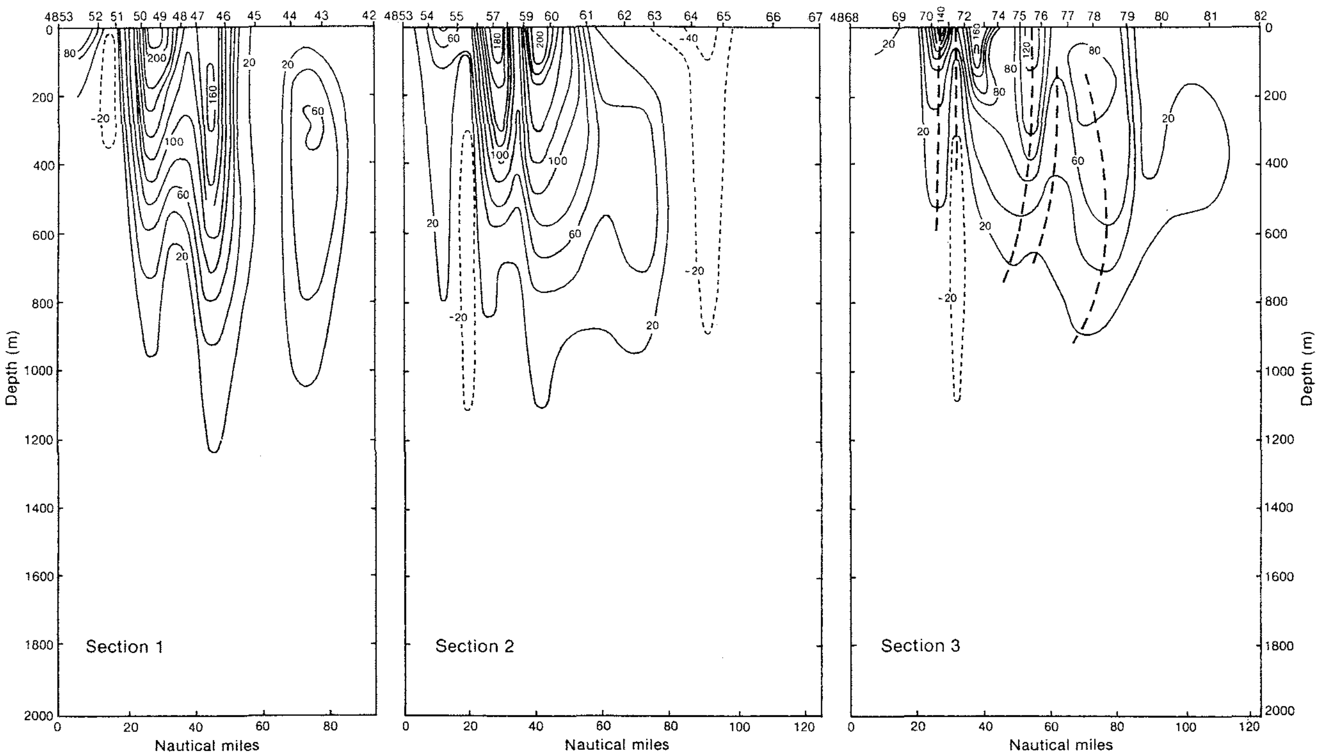

Fig. 16. Geostrophic currents for the three sections across the Gulf Stream depicted in Fig. 15 (from Worthington, 1954).

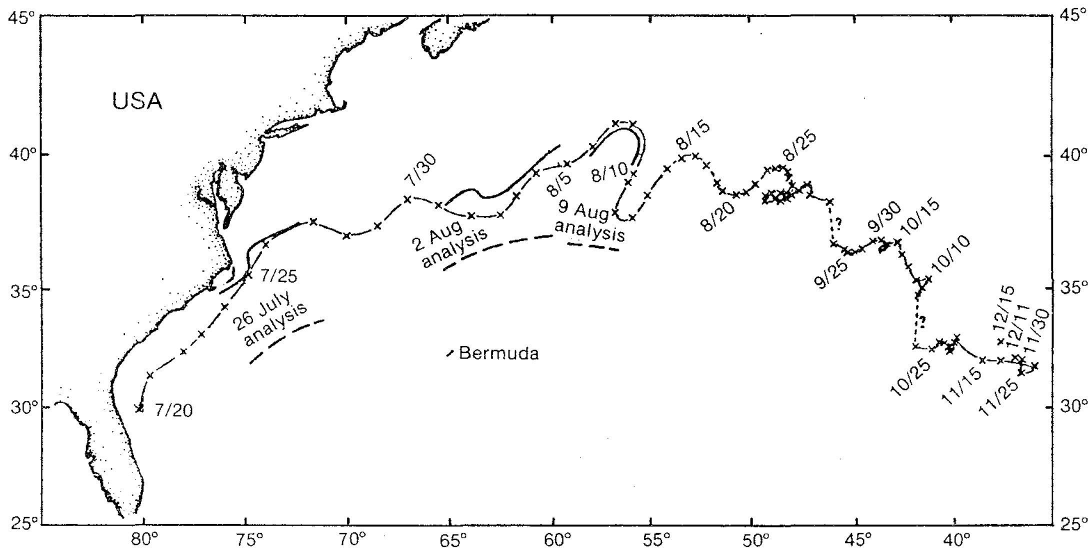

Fig. 17. Trajactory of a satellite-tracked buoy, with a parachute and 35 m of cable, deployed in the Gulf Stream and tracked for 5 months in 1975 (from Kirwan *et al*., 1976).

the velocity is 72 cm/sec. In this example, the larvae will remain entirely within the shear zone for 10 days. At this time, some larvae will have reached the northern boundary where the current vanishes. At times longer than 10 days, the along-flow patch size is assumed to be

$$2\ [(\sigma_x)_t + (\sigma_x)_{10} - (\sigma_y)_{t-10}]$$

Several features are evident in the plots of patch location and size for a simple Gulf Stream system with a width of 100 km (Fig. 20). Firstly, the shear is responsible for stretching the patch greatly in a direction nearly parallel to the direction of flow of the Gulf Stream, the patch length to width ratio being about 50 after 30 days. Secondly, the patch length in Example 1

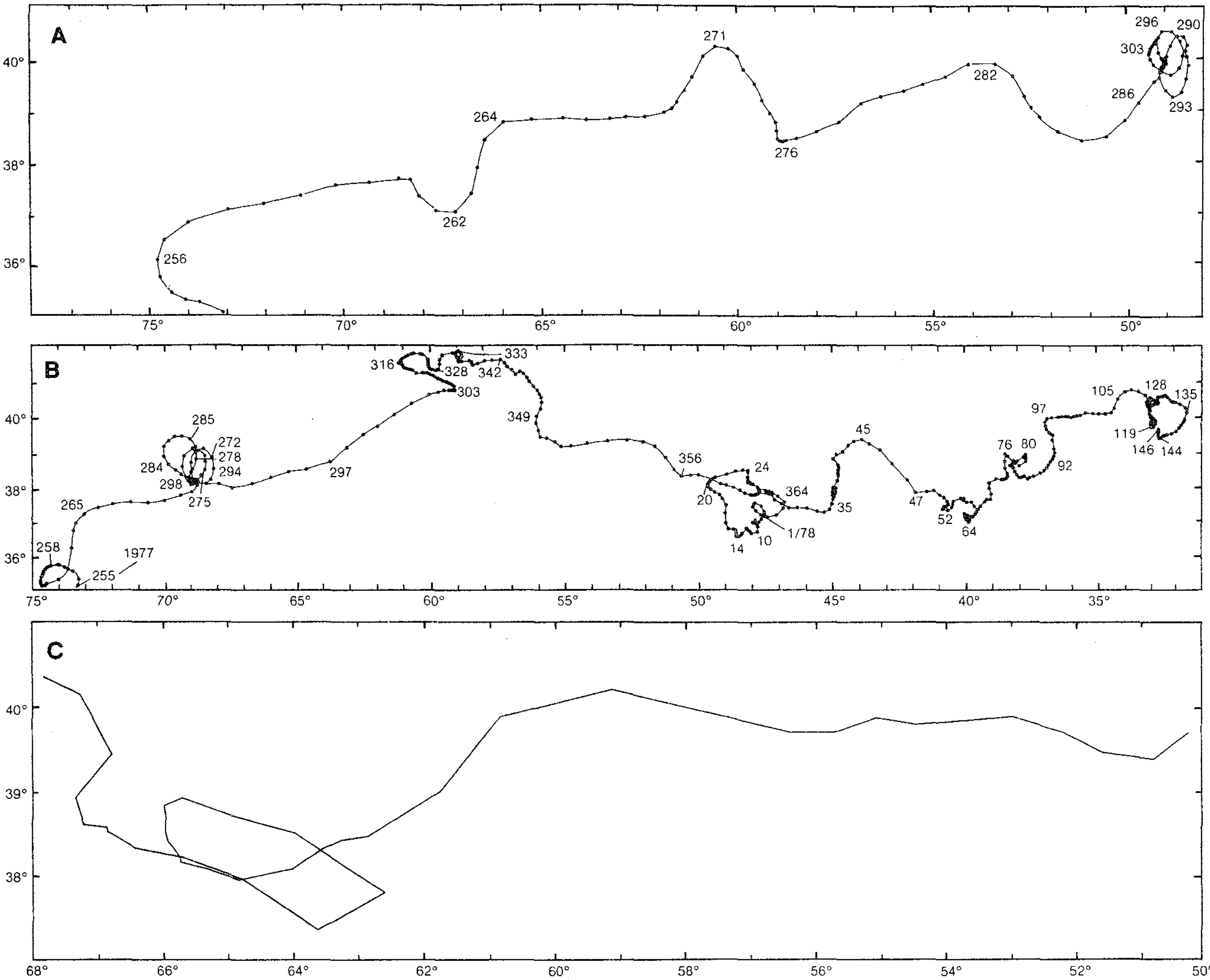

Fig. 18. Trajectories of three satellite-tracked buoys in the Gulf Stream system: **A**, buoy 0252 from day 253 to day 305 (10 September–1 November 1957); **B**, buoy 0512 from day 254 (11 September 1957) to day 146 (26 May 1958); **C**, buoy 1301 released on Browns Bank in October 1979 by the Bedford Institute of Oceanography. (**A** and **B** from Richardson *et al.*, 1979.)

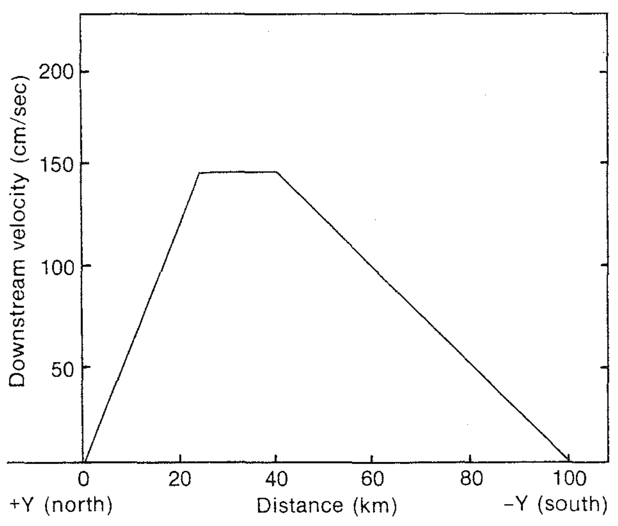

Fig. 19. Assumed surface distribution of mean velocity of the Gulf Stream from Cape Hatteras to the southern tip of the Grand Bank, for use in predicting larval squid patch size and location.

after 20 days extends from a point west of 75° W along the northern edge of the Gulf Stream to approximately 60° W. For Example 2, the patch extends to about 57° W in the same time period. Thirdly, the patch width, even after 30 days is little more than half the width of the Gulf Stream. In Example 1, the patch limits penetrate equal distances (normal to the flow) into the Gulf Stream and the Slope Water (assuming the Gulf Stream boundary to be the zero-velocity line), whereas, in Example 2, the ratio of the relative distances is 71:29.

For a continuous point source of new larvae over a 30-day period, the larval distribution is essentially contained within the envelope of a 30-day ensemble of patches, with (on theoretical grounds) a slight bending of the line of peak concentration toward the zone of maximum velocity in the Stream. The shear produces major assymetry in terms of the geographic variation in age distribution. The isopleths of the age frequency mode will, in Example 2, extend obliquely across the Stream at a very small angle. Thus, at any given time

TABLE 3. Patch dispersion characteristics for two geographic positions of an instantaneous point source, with velocity profile as shown in Fig. 19.

Time (days)	Diffusion coefficient A_y ($cm^{-1} x10^{-5}$)	Mean distance travelled by patch center (km)	Patch width (B) (km)	Patch length (L) (km)	L/B $= \rho$
		Example 1[a]			
5	1	0	12	94	8
10	2	0	24	363	15
15	3	0	35	809	23
20	4	0	47	1,432	31
30	4	0	58	2,615	45
		Example 2[b]			
5	1	311	12	176	15
10	2	622	24	704	29
15	3	933	35	1,149	33
20	4	1,244	47	1,771	38
30	4	1,866	58	2,963	51

[a] Point source is located at northern edge of the shear zone with mean velocity of zero at a longitude of 75° W ($\bar{u} = 0$, $x = 0$, $y = 0$).

[b] Point source is located 12 km inside the shear zone where the mean velocity is 72 cm/sec ($\bar{u} = 75$, $x = 0$, $y = 12 \times 10^5$ cm).

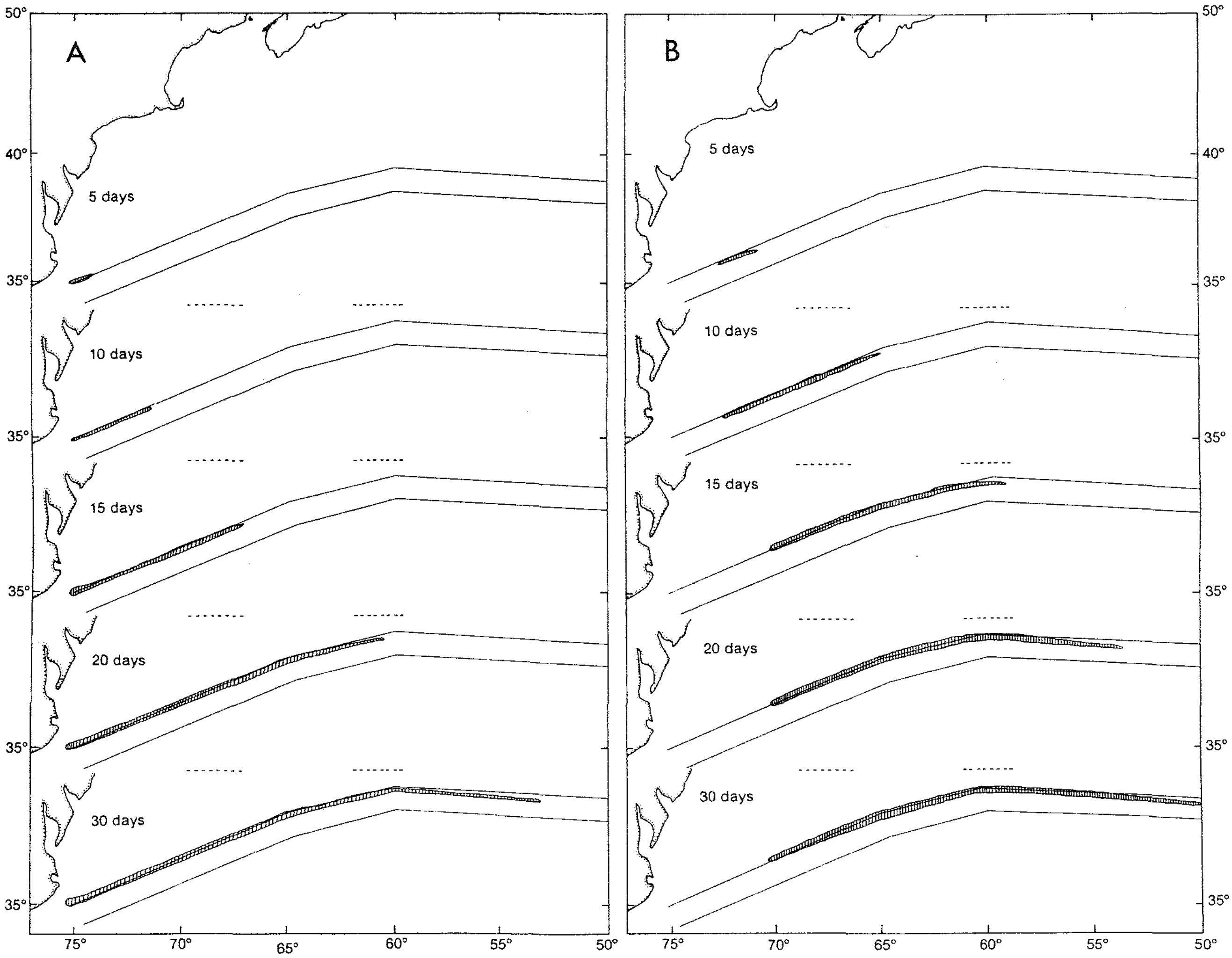

Fig. 20. Schematic illustration of patch location and size during 5, 10, 15, 20 and 30 days after a point source release of larvae (**A**) at the edge of the shear zone of the Gulf Stream, and (**B**) 12 km inside the shear zone.

and for any given section across the Stream, the proportion of younger larvae should increase in a section from the northern limit of distribution in Slope Water to the southern boundary in the Gulf Stream. In this idealized situation, the larvae are all confined to a relatively narrow section which is unlikely to exceed 60 km in width.

Role of Gulf Stream eddies

The formation of eddies begins when the Gulf Stream starts to meander as it flows northeastward and away from the coast at Cape Hatteras. The meander may develop into a major loop which subsequently becomes detached from the Gulf Stream. The result is an eddy (ring) of high velocity Gulf Stream water circulating around a core of water of different origin. An eddy which forms north of the Gulf Stream rotates clockwise; it has a core of water drawn from the Sargasso Sea and is called a "warm-core" eddy. Conversely, an eddy which forms south of the Gulf Stream rotates anticlockwise; it has a core of water (Slope Water) drawn from north of the Gulf Stream and is called a "cold-core" eddy.

Eddies have a wide range of lifetimes from barely a week to possibly 3 years. The average lifetime of cold-core eddies has been estimated to be 1.0–1.5 years (Wiebe, 1982). A census of warm-core rings, reported by Mizenko and Chamberlin (1979), Ceylone and Chamberlin (1980), and others, indicates that 5–8 eddies were formed per year during 1976–80 in the region west of 60°W. Satellite imagery reveals that eddies also form east of 60°W, but there is as yet little documentation on their number and duration. The warm-core eddies formed west of 60°W generally move southwestward and may not be absorbed into the Gulf Stream until they reach Cape Hatteras. Their lifetimes are shorter than for cold-core eddies, with most of them disappearing in the first year of life. Eddies formed east of 60°W appear to have much shorter lifetimes than those formed west of 60°W.

It was noted in the preceding section that the dispersion of larvae, from releases at the edge of, or just within, the Gulf Stream off Cape Hatteras, tends to be confined to the area near the northern edge of the Stream. A simplified scenario for a sequence of small patches being carried by the Gulf Stream during the formation of a warm-core and a cold-core eddy is illustrated in Fig. 21. Shear is ignored, and the center of the patch is considered to be moving at a velocity of about 120 cm/sec. The mean larval age in days is shown inside the circles. The scenario depicts the formation of both types of eddy at about 65°W over a 10-day period. The following points should be noted: larvae tend to be found on the exterior boundary of a warm-core eddy and in the central part of a cold-core eddy;

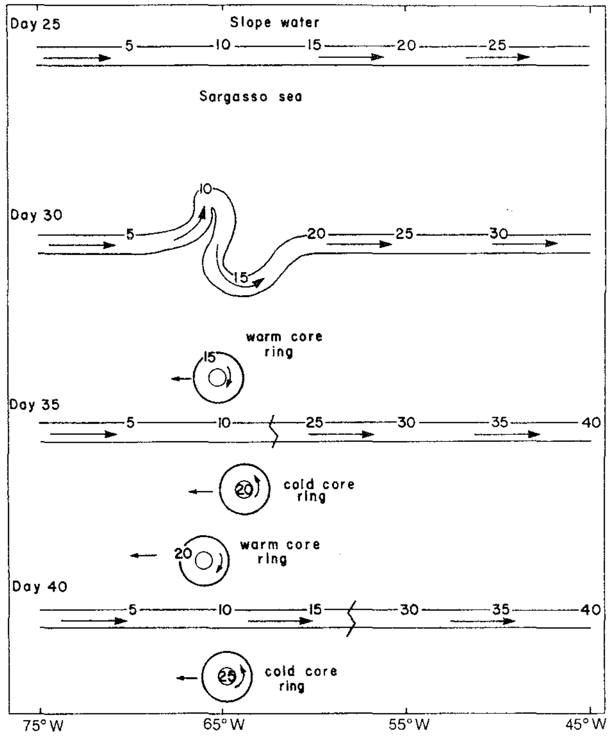

Fig. 21. Schematic illustration of the larval distribution during and following the formation of Gulf Stream eddies.

the effect of eddy formation is to produce a discontinuity, in terms of increasing age, along the Gulf Stream; with a lapse of time, the mean age of larvae in the eddies will be much higher than that of larvae in the Gulf Stream at the same longitude.

Some additional comments about eddies and their importance in larval transfer from the northern edge of the Gulf Stream into Slope Water and the Sargasso Sea are warranted. Given a constant concentration of larvae per unit length of Gulf Stream prior to the onset of a meander and subsequent development of a warm-core and a cold-core eddy of equal size, would the total number of larvae incorporated in each eddy be the same? Unfortunately, the dynamics and kinematics are not well enough understood to answer this question. If there were no important secondary motions and if there was no "stretch" or "compression", more larvae should be contained in a warm-core eddy than in a cold-core one.

Regardless of the possible asymmetry in larval distributrion within warm-core and cold-core eddies, they must be recognized as an important mechanism in laterally "ejecting" larvae from the Gulf Stream–Slope Water boundary zone. If two warm-core eddies, each with a diameter of 200 km formed during a period when larvae were concentrated along the northern edge of the Gulf Stream, as much as a 1,200 km "length" of Gulf Stream could be transported into Slope Water by the two eddies. This represents about 50% of the straight line distance between Cape Hatteras and the southern tip of the Grand Bank.

Discussion

If spawning reaches a peak that is largely contained within a period of a few weeks, the larval distribution will change during the "decay" period, when the supply has diminished to near zero. At any given longitude, larvae would be expected to disappear first from the high velocity part of the Gulf Stream and remain for a longer time in the low velocity areas north of the Stream.

The analysis of larval dispersion and concentration has assumed that larvae drift passively with the surrounding water and can be treated as a conservative scalar quantity. The role of larval mortality has not been considered, but the effect could be included readily by assuming that the proportion of larvae lost due to mortality is a constant (k). Equation 1 would have an additional term (kS), and the solution (Equation 3) would be multiplied by e^{-kt}. A high mortality rate would have a major effect on concentration levels, but it would not change the pattern of the dispersing patch.

The assumption that larvae behave as inert, neutrally-buoyant particles is probably a reasonable one for recently-hatched larvae in a highly turbulent regime, but it eventually will become totally untenable at some later stage in their growth and development. Vertical movements of a few decameters may produce important differences in distributional pattern due to vertical variation in currents and turbulence. If the sustained swimming speed (mm/sec) is assumed to be roughly equal to their length (mm), a 10-mm larvae could achieve a vertical migration of 100 m in less than 3 hr. When juveniles reach a size where sustained swimming speeds of 5–10 cm/sec are possible, their horizontal distribution outside the high velocity areas of the Gulf Stream system is likely to be more dependent on their swimming activity than on current patterns.

The model developed here is based on the assumption that newly-hatched larvae become entrained into the northern edge of the Gulf Stream in the vicinity of Cape Hatteras and are rapidly advected northeastward and dispersed. Although a long strip of the continental shelf between Cape Hatteras and Cape Cod, within the 100–200 m depth zone, appears likely to have temperatures exceeding 13° C in the August-February period and hence might be considered as a suitable spawning area, most of it has a low probability of being a source area for larvae subsequently found in the Gulf Stream-Slope Water area in January-March. The southwestward current along the shelf and slope northeast of Chespeake Bay commonly flows at less than 10 cm/sec, and larvae released in this area would have become juveniles before reaching Cape Hatteras and the Gulf Stream. Satellite imagery shows that, from time to time, a tongue of shelf water may extend offshore and be in direct contact with the Gulf Stream. Such a tongue is generally associated with the presence of a warm core eddy in the area. One therefore cannot rule out the possibility that some larvae could be transferred intermittently from the edge of the continental shelf directly across the Slope Water area to the Gulf Stream. Available information on larval-juvenile squid distribution, however, lends little support to this scenario. Therefore, on the assumption that squid, *Illex*, spawn on or near the bottom where temperatures are higher than 13° C and that the larvae subsequently become entrained into the Gulf Stream, the principal geographical areas meeting these criteria are located south of Chesapeake Bay.

The model, using lateral diffusion coefficients derived from a wide range of oceanic dye diffusion experiments and a simple unidirectional flow regime with linear shear, indicates that larvae entering the shear zone of the Gulf Stream should, during a period of 30 days, be distributed in a narrow band about 60 km wide at the broadest point and nearly 3,000 km long. However, the dynamic and kinematic features of the Gulf Stream-Slope Water system are extremely complex and not, as yet, well understood. The meandering nature of the Stream and the creation and reabsorption of eddies provide a "real world" situation which is much more complex than the simple model considered here. Nevertheless, the model does point to some basic features that should be testable with existing field data and future observations.

Existing data on the distribution of squid larvae were collected during various cruises in the winter and spring months of 1979–82: USSR vessel *Belegorsk* in March-April 1979, *Atlant* in February-May 1981, and *Evrika* in February-April 1982; Canadian vessels *Gadus Atlantic* in February-March 1981 and 1982, and *Lady Hammond* in February-March 1982; and the Japanese vessel *Kaiyo Maru* in January-March 1982. Most of the data from these cruises have yet to be published, but preliminary reports of some cruises indicate that larvae are most commonly found in Slope Water near the northern edge of the Gulf Stream (Fedulov and Froerman, MS 1980; Dawe *et al.*, MS 1981).

A critical area in which a detailed search for spawning *I. illecebrosus* should be conducted is the shelf-slope region southwest of Chesapeake Bay during December-January, because the model indicates this area and time to be the most probable ones where adults, eggs and larvae might be found. As far as can be determined from the literature, there are almost no existing data on either the presence or absence of squid in this time and space domain, because the traditional seasonal surveys have seldom been conducted in this area during December-January.

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