

# SIMULATION OF THE NORTH ATLANTIC OCEAN DRIFT OF *ANGUILLA LEPTOCEPHALI*

JAMES H. POWER<sup>1</sup> AND JAMES D. MCCLEAVE<sup>2</sup>

## ABSTRACT

A numerical simulation model of surface current drift was developed in order to simulate the poorly understood drift migration of *Anguilla leptocephali* in the North Atlantic Ocean. The model was based upon the advection-diffusion equation, which was approximated by finite differences. Currents for the model were calculated from ships' drift data. Leptocephali were "started" at various points in the presumed American and European eel spawning areas, and the model produced spatiotemporal patterns of leptocephalus concentrations resulting from surface current drift and turbulent diffusion. In the American eel drift simulations the patterns followed a sequence of four phases: 1) Initial northwest drift on the presumed Antilles Current; 2) the formation of a "patch" of leptocephali offshore of Florida and the Gulf Stream; 3) dispersal along the North American coast resulting from the continued input of larvae into the Gulf Stream from the patch; and 4) transport eastward into the Atlantic on the Gulf Stream. In the European eel drift simulation, the leptocephali slowly spread throughout the Sargasso Sea region of the North Atlantic, and there was little Gulf Stream transport by the eighth month of drift. The patterns of distribution produced by the model correspond well with the limited collection data for both species, though it remains for future sampling efforts to verify whether the features present in the simulations actually occur.

Schmidt (1925) summarized over two decades of work to provide what has since become known as the "classical solution" to the Atlantic eel problem. Schmidt proposed that adult European eels, *Anguilla anguilla*, and American eels, *A. rostrata*, migrate in the fall from their freshwater habitats and travel to spawning areas in the Sargasso Sea. The adults spawn in the early months of the year and then die. The resulting larvae (termed leptocephali) are presumed to drift passively on surface currents toward their respective coasts. Schmidt stated that American eels, having a shorter distance to traverse, drift about a year as leptocephali before metamorphosing to the glass eel phase and commencing their migration toward freshwater. European eel leptocephali are presumed to take 3 yr to complete their journey. This scenario was challenged by Tucker (1959), who hypothesized that the two Atlantic anguillid eel species are in fact only one. Tucker proposed that all adult European eels die during their migration, that all anguillid leptocephali are the progeny of eels originating in North America, and that European eel stocks are replenished by leptocephali that simply drifted across the Atlantic after failing to

land on the North American coast. Tucker felt that differences in the vertebral counts used to discriminate between the two species could be explained by a thermal shock suffered by developing embryos in part of the spawning area. Tucker's hypothesis has been largely discounted, and recent electrophoretic (Jamieson and Turner 1980; Comparini and Rodino 1980) and karyotypic (Passakas 1981) evidences indicate the existence of two anguillid eel species in the North Atlantic and associated freshwaters.

Nonetheless, there are persistent unanswered questions concerning the migrations of larval, juvenile, and adult eels (Vladykov 1964; McCleave and Harden-Jones 1979). One of these questions concerns the location and timing of American and European eel spawning. Schmidt (1925) identified the European eel spawning area as lying between lat. 22° to 30°N and long. 48° to 65°W, and stated that spawning "commences in late winter or early spring and lasts well on in summer." He based these limits on the distribution of the smallest leptocephali (<10 mm) he collected. To the present time no adult eel has been captured away from the continental shelves, and no identified anguillid eel eggs have been collected. Schmidt did not collect many small American eel leptocephali, and consequently his delineation of the American eel spawning area and time is much less precise. Recently there have been several systematic sampling efforts for small leptocephali with the ob-

<sup>1</sup>Migratory Fish Research Institute and Department of Zoology, University of Maine at Orono, Orono, Maine; present address: Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

<sup>2</sup>Migratory Fish Research Institute and Department of Zoology, University of Maine at Orono, Orono, ME 04469.

jective of defining the spawning areas of the European eel (Tesch et al. 1979; Schoth and Tesch 1981) and the American eel (McCleave and Kleckner<sup>3</sup>). Kleckner and McCleave<sup>4</sup> have obtained evidence that recently hatched American eel leptocephali are associated with a thermal front in the Sargasso Sea.

Also, little is known regarding the time course of the leptocephalus drift migration. Following Schmidt's (1925) summary, several authors have compiled information on the spatiotemporal distribution of anguillid leptocephali, including Smith (1968), Vladykov and March (1975), Tesch (1980), and Kleckner and McCleave (1980). These studies only provide a broad outline of the course of the leptocephalus drift migration, as the number of identified leptocephali collected is still small, considering the scale of the migration in terms of distance and probable numbers. The available data are difficult to interpret and may better represent the distribution of sampling effort than the distribution of leptocephali (Kleckner and McCleave 1980). Unless sampling at a particular location was done systematically, the absence of leptocephali from collections can only be interpreted as negative evidence concerning the presence of leptocephali at that location. It is still not known how leptocephali are transported in the Florida Current-Gulf Stream system. How do American eel leptocephali cross the Gulf Stream to approach the North American coast, and why are substantial numbers of these leptocephali not transported across the Atlantic to populate Europe? Are any behavioral components necessary in the leptocephalus drift migration? In summary, where and when are leptocephali most likely to be found, and what implications does this distribution have for the eel's life history and migration patterns?

To answer some of these questions a simulation model of leptocephali drift in the North Atlantic surface currents was developed. The intent was to implement the simulation so that leptocephali started at points in the presumed Sargasso Sea spawning area would be transported in a way realistically approximating actual surface current transport. The objectives of the research were to generate patterns of distribution representing the likely time course of a passive drift migration and to compare and inter-

pret these distributional patterns with information about the actual leptocephalus distribution and the eel's life history. In this way the model serves an explanatory role, highlighting the factors important in generating a distribution of leptocephali, and also provides a framework for future research on the leptocephalus drift migration. Distributional patterns that developed during some of the simulations are presented here, with emphasis on the American eel; limited results for the European eel are also given.

## MATERIALS AND METHODS

*Anguilla* leptocephali are found in the top few hundred meters of the water column (Kleckner and McCleave 1980; Schoth and Tesch 1981), and therefore the model was developed with only two horizontal spatial dimensions. The model was based upon the time-dependent, two dimensional form of the advection-diffusion equation:

$$\frac{\partial P}{\partial t} + \frac{\partial}{\partial x} \left( uP - K_x \frac{\partial P}{\partial x} \right) + \frac{\partial}{\partial y} \left( vP - K_y \frac{\partial P}{\partial y} \right) = 0$$

where  $P$  = concentration of leptocephali;  
 $u$  and  $v$  = velocities in the respective  $x$  and  $y$  directions; and  
 $K_x$  and  $K_y$  = diffusivity coefficients for the respective directions.

Leptocephali were not assumed to have any directed swimming capability, so the velocities in the above equation represent simple water current velocities. The diffusivity coefficients express the dispersion of leptocephali by turbulence, eddies, and other phenomena not expressed by the advective terms (Okubo 1980).

The derivatives in the above continuous equation were approximated by finite differences. For example, to approximate the time derivative the following relation was used:

$$\frac{\partial P}{\partial t} \approx \frac{P^{t+1} - P^t}{\Delta t}$$

where  $P^t$  = concentration of leptocephali at the present time  $t$ ;  
 $P^{t+1}$  = concentration of leptocephali at time  $t + \Delta t$ ; and  
 $\Delta t$  = duration of the time step.

The derivatives with respect to the  $x$  and  $y$  directions were approximated by weighted finite differences. The method developed by Fiadeiro and Veronis

<sup>3</sup>J. D. McCleave, Professor of Zoology, and R. C. Kleckner, Research Associate in Zoology, Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469, pers. commun. July 1981.

<sup>4</sup>R. C. Kleckner, Research Associate in Zoology, and J. D. McCleave, Professor of Zoology, Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469, pers. commun. July 1981.

(1977) was followed for determining the weighting so as to provide increased numerical stability and to approximate more closely the solution to the continuous equation. Further details on the numerical methods used were presented elsewhere (Power 1982).

In approximating the advection-diffusion equation by finite differences, the region under study is partitioned by a grid, and a difference equation is derived for each cell formed by the grid. The difference equations express the concentration of the substance at the center of each cell formed by the grid in terms of fluxes between adjoining cells. The end result is a large system of simultaneous (difference) equations, which can be repeatedly solved to obtain the cell concentrations at successive time steps. The region included in this study was the Gulf of Mexico, Caribbean Sea, and the North Atlantic Ocean between lat.  $10^{\circ}$  and  $50^{\circ}$ N and west of long.  $40^{\circ}$ W (Fig. 1). Coastlines were approximated by cell boundaries, as were the Caribbean islands and shoal waters of the Bahamas. Flux of leptocephali across these boundaries was prohibited. Leptocephali approaching the Bay of Fundy, Gulf of St. Lawrence, and the long.  $40^{\circ}$ W boundary of the model were permitted to be transported out of the modeled area (dashed lines in Figures 2-9).

Currents for the model were calculated using ships' drift data obtained from the National Oceanographic Data Center (Fig. 2). A ship's drift observation is the inferred surface current calculated by comparing the ship's true position after a given period of steaming with the navigator's dead reckoning position. Surface current charts of the North Atlantic are derived from the same data base used in this study. Each ship's drift observation was resolved into an east and north component, and the current component at the interface between two cells was calculated as the mean of all the appropriate current components recorded in the  $1^{\circ}$  of latitude and longitude bisected by the cell interface. The means were calculated by calendar months, so for each month in the simulations a different current regime was used. Using June as a representative month, the median number of observations used to calculate a current component was 10, and 75% of the components were calculated using five or more observations. The number of observations was greatest within  $5^{\circ}$  of the North American coast, with sample sizes  $>100$  commonly occurring. Sample sizes were poorest in the southeast portion of the modeled area. An average of 3% of the cell interfaces had no associated ships' drift observations. These points where data were completely missing were

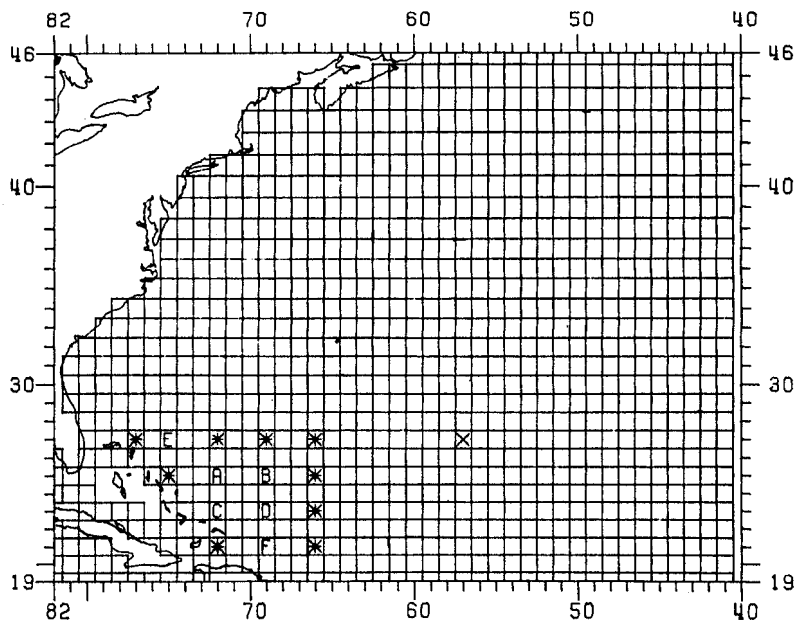


FIGURE 1.—Main portion of the geographic region included in the simulations, along with the  $1^{\circ}$  by  $1^{\circ}$  grid and coastline approximation. Lettered cells are the starting points for American eel leptocephalus drift simulations discussed in the text, and cells with stars are the starting points in other simulations not presented here. Note for comparative purposes that points A and C and points B, D, and F are the same meridians, while points A and B and points C and D share the same latitudes. Cell with an X is the starting point for the European eel drift simulation.

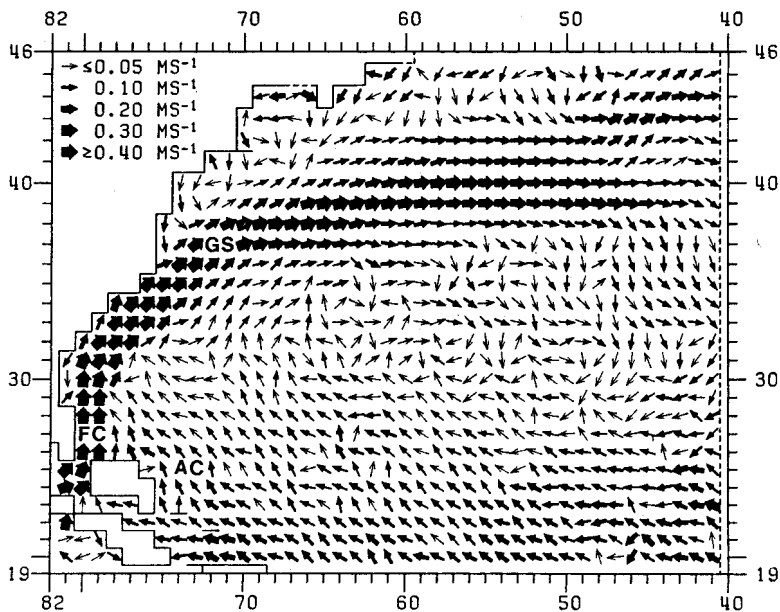


FIGURE 2.—Surface current vectors used in the simulations for the month of May. Vector in a cell was computed by taking the mean of the current components at the cell's edges and calculating the resultant vector. Key depicts representative current speeds. AC = Antilles Current; FC = Florida Current; GS = Gulf Stream.

irregularly spaced throughout the modeled area, so their components were calculated by interpolating between adjoining cells and months. Current velocities were necessarily taken as representative of the currents that occur throughout the depth range of *Anguilla* leptocephali. The leptocephali were assumed to maintain themselves continually in surface waters, so the finite differences were derived with no assumptions regarding fluid continuity. The effect of this is that leptocephali are concentrated in regions of net water convergence (downwelling) and dispersed from regions of divergence (upwelling).

The diffusivity coefficient ( $K$ ) was calculated as a function of grid spacing. Data from numerous dye diffusion experiments reviewed by Okubo (1971) were used in a least squares regression analysis to compute the equation  $K = (3 \times 10^{-4}) h^{1.1}$  relating the diffusivity parameter (in  $\text{m}^2/\text{s}$ ) to the length scale (grid spacing)  $h$  in meters. No spatial variation in diffusivity, other than that due to meridional grid narrowing in more northerly latitudes, was assumed. Diffusivities used ranged from 68 to 110  $\text{m}^2/\text{s}$ .

In carrying out the simulations, American eel leptocephali were considered to be "spawned" as point sources at the various locations designated by letters or stars in Figure 1. These starting locations cover most of the presumed geographic range of American eel spawning (Kleckner and McCleave 1980; Kleck-

ner<sup>5</sup>). Locations designated by letters are in the area which, on the basis of collections of very small leptocephali, represent the principal spawning area. The distributional patterns of leptocephali started at these lettered locations are discussed in detail in this paper, and the various simulation runs are referred to by these letters. The date 1 March is representative of the peak American eel spawning period (Kleckner and McCleave 1980; Kleckner footnote 5). That point in time was used as the starting date for the American eel drift simulations, with no additional input of leptocephali after that date. The center of the estimated European eel spawning area (Schmidt 1925; Scoth and Tesch 1981) is marked in Figure 1 with an  $\times$  at lat.  $27^\circ\text{N}$ , long.  $57^\circ\text{W}$ . The results of one simulation, in which leptocephali were started on 15 April at this point, are presented. The length of the time step in the simulations varied by month, but was always between 1.5 and 2.0 d. The simulation results are presented initially on a monthly basis and then later on a bimonthly basis.

There is little information regarding actual concentrations of leptocephali in the ocean. As the simulations progressed, individual cell concentrations were expressed as proportions of the start-

<sup>5</sup>R. C. Kleckner, Research Associate in Zoology, Department of Zoology, Murray Hall, University of Maine at Orono, Orono, ME 04469, pers. commun. July 1981.

ing concentration. No mortality of leptocephali was incorporated into the model, and the total number of leptocephali was conserved throughout the simulation except for the portion transported across the open boundaries discussed previously. A unitless number is given when referring to a concentration, so that reference to a concentration of  $10^{-3}$  refers to a concentration of leptocephali that is three orders of magnitude below the starting concentration. The concentration contours presented in Figures 3-9 were determined by linearly interpolating between the concentrations at the centers of the cells. Each contour represents an order of magnitude change in concentration relative to neighboring contours. Only leptocephalus concentrations  $>10^{-7}$  (proportion of the starting concentration) are shown. In Figures 3-9 the leptocephalus starting location is marked by a star.

The choice of contour intervals as orders of magnitude was arbitrary; in some cases, the display masked the spatial structure of the distributions. This can occur where the order of magnitude contours are widely spaced, and a discontinuity in the concentrations is between the contours. For this reason an agglomerative cluster analysis using a spatial autocorrelation coefficient, Moran's I (Cliff and Ord 1973), as the metric was carried out with cell concentrations as the variable. The weighting coefficient was the reciprocal of the distance between cells, and only immediately adjacent cells were linked (rook's moves). Examination of the equation for Moran's I indicates that when choosing among several coefficient values, the minimum I represents the most spatially uniform distribution. The clustering proceeded iteratively by examining all possible pairwise linkages of clusters of cells, and forming a new cluster from the pair that yielded the minimum value of I for the new cluster. Thus at any stage the clusters partition the distribution into "patches," i.e., regions in which the cells are most spatially uniform in concentration. The cell concentrations were logarithmically transformed for the analysis to minimize the effects of outliers on I. The results of these analyses are not explicitly presented, but are referred to when necessary to facilitate the interpretation of the contour plots.

## RESULTS

### Distribution of Leptocephali After 30 Days of Drift

The proximity of the starting point to the Gulf Stream, the Antilles Current northeast of the

Bahamas, and the Bahamas themselves all influenced the distributional patterns of American eel leptocephali that developed 1 mo after the 1 March starting date (Fig. 3). Capture of leptocephali by the Gulf Stream was already evident, and larvae started east and northeast of the Bahamas showed northwesterly drift on the Antilles Current.

Leptocephali begun at F mostly moved away from that location during the first month (Fig. 3F). The larvae were somewhat dispersed even at this early date, as cluster analysis indicated a large patch east of the Bahamas between lat.  $21^{\circ}$  and  $26^{\circ}$ N. Concentrations declined sharply to the east and south, as they did in all runs, indicating little transport in those directions. To the west, leptocephali were split by the Bahamas, approaching the Gulf Stream by both the route north of the islands and through the channel between the Bahamas and Cuba. Some passed completely through this channel to be caught in the Florida Current and carried northward, so that the  $10^{-7}$  contour extended to lat.  $32^{\circ}$ N.

There was gradual northwesterly dispersal of leptocephali started at more northerly (Fig. 3B, D) and northwesterly (Fig. 3A, C) locations than those at F. The larvae in these runs are more concentrated, with most remaining near the starting points. In runs A-D larvae are impinging upon the Bahamas, and in C the concentrations offshore of the Bahamas are particularly high. This is due to the clearly evident Antilles Current transport in run C, and this current also facilitated the entry of run C larvae into the Gulf Stream. Runs A and E also show Gulf Stream transport, but this is more by virtue of their starting point's proximity to the Gulf Stream. Gulf Stream transport is pronounced in E, with the  $10^{-7}$  contour reaching north to lat.  $39^{\circ}$ N and east to long.  $65^{\circ}$ W.

### Distribution of Leptocephali After 60 Days of Drift

By 30 April, 2 mo after the 1 March start, leptocephali had spread and most moved northwest of their starting locations (Fig. 4). There were now broader areas of more moderate concentration, typified by the area enclosed by the  $10^{-2}$  contour east of the Bahamas. Gulf Stream transport was now evident in all runs A through F.

Run F is notable for the substantial distance traversed by the larvae, considering the position of point F (Fig. 4F). This was primarily caused by continued transport between the Bahamas and Cuba, entry into the Florida Current, and then rapid Gulf Stream transport. Antilles Current transport also contributed. Concentrations in run F fell into three

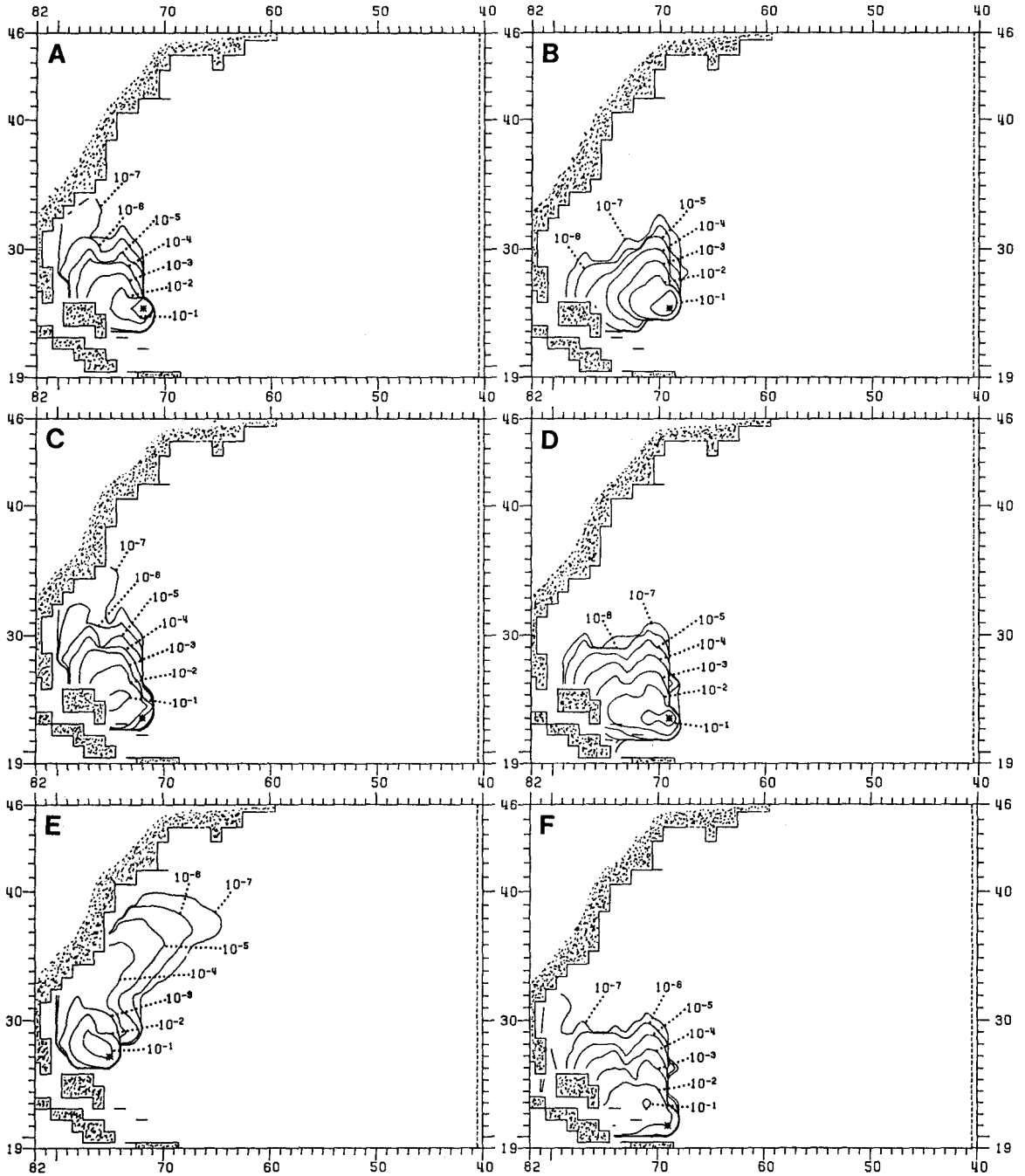


FIGURE 3.—Concentration contours of American eel leptocephali, expressed as a proportion of the starting concentration, for 30 March. Each lettered plot corresponds to the same lettered starting location in Figure 1. In this and subsequent figures stars mark the starting points. 30 March is 1 mo after the 1 March starting date.

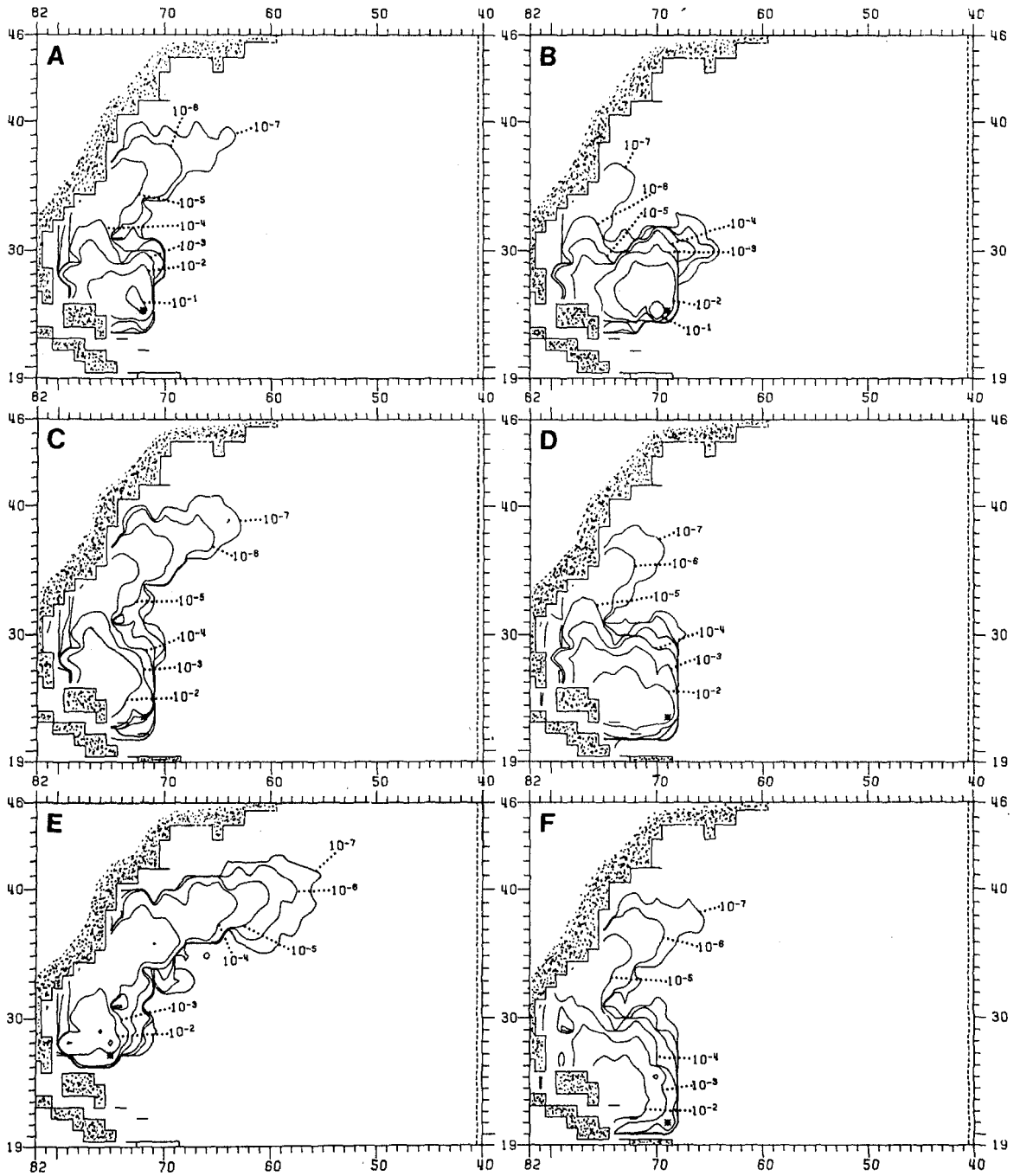


FIGURE 4.—Concentration contours after 60 d of American eel leptocephalus drift. Corresponding date is 30 April.

groupings: 1) High concentrations east of the Bahamas containing most leptocephali, 2) lower concentrations flanking this patch, and 3) Gulf Stream larvae.

Leptocephali started north and northwest of F (runs A through D) showed more uniform distributions than the previous month, although the sharp eastern and southern gradients were maintained. There was transport between the Bahamas and Cuba only in run D, and leptocephali in run B showed lesser dispersal when compared with other runs. Run C again showed most clearly the effects of Antilles Current transport, while run A showed a similar but less developed pattern. Leptocephali in runs A and C reached lat.  $39^{\circ}\text{N}$  and long.  $65^{\circ}\text{W}$  at concentrations  $>10^{-7}$ .

Run E continued to show the most widespread distribution, and while offshore of Florida there were still concentrations  $>10^{-2}$ , the  $10^{-3}$  contour enclosed a considerable area offshore of the mid-Atlantic coast.

### Distribution of Leptocephali After 90 Days of Drift

Runs A, C, D, and F became similar by the third month of drift (Fig. 5; 30 May). The cluster analyses for these simulations at day 90 are of interest, because in each a distinct geographic grouping of cells emerged consistently. These clusters did not combine with others until forced to do so at the final stages of clustering. This indicated that the cell groupings represented by the clusters had spatial distributions of leptocephali (as measured by Moran's I) which were internally more uniform than if cells external to the groupings had been included during clustering. This characterized (independently of concentration contour plots) an important feature in the spatial structure of the leptocephali at day 90. The clusters of cells in runs A, C, D, and F formed patches east of Florida and the Gulf Stream, north to northwest of the Bahamas, and northwest of the starting points (roughly between lat.  $24^{\circ}$  to  $28^{\circ}\text{N}$  and long.  $71^{\circ}$  to  $77^{\circ}\text{W}$ ). These patches had mean cell concentrations of 0.015 to 0.025, and patch limits were approximated by the  $10^{-2}$  contours (Fig. 5). The bulk of the starting concentrations was contained within these patches.

Another feature common to the A, D, and F runs was the large area of concentrations between  $10^{-3}$  and  $10^{-4}$  that paralleled the mid-Atlantic coast and then extended offshore at about lat.  $38^{\circ}\text{N}$ . Run C had an identical pattern, except that its concentrations in this area were an order of magnitude higher. This difference can be attributed to starting point C's loca-

tion and the enhanced Antilles Current-Gulf Stream transport mentioned earlier.

Run B's pattern was similar to that of runs A, C, D, and F, but was not as fully developed. This is because run B leptocephali were started farther into the Sargasso Sea, where currents are weaker. The main patch of concentration was present, but it covered a broader area and had a slightly lower mean concentration of 0.01. The  $10^{-5}$  contour along the North American coast in run B took the place of the  $10^{-4}$  contour in runs A, D, and F. In B there were still high concentrations near the starting point.

Run E continued to exhibit the most extensive pattern of leptocephalus distribution (Fig. 5E). There was a patch offshore of Florida and the Gulf Stream with a mean cell concentration of 0.012, but it was smaller and farther north than the corresponding patch in other runs. More than half of the starting concentration lay north of lat.  $31^{\circ}\text{N}$  and within the  $10^{-3}$  contour. Concentrations  $>10^{-2}$  were well north of lat.  $32^{\circ}\text{N}$  in run E.

### Distribution of Leptocephali After 150 Days of Drift

The patterns of distribution below lat  $32^{\circ}\text{N}$  persisted during the next several months in the simulations, while to the north there was an increase in the concentrations and continued Gulf Stream transport. The main patches of concentration offshore of the Gulf Stream and Florida remained in runs A, C, D, and F after 5 mo of drift (Fig. 6; 29 July). The patches moved slightly to the northwest, and lay between lat.  $25^{\circ}$  to  $30^{\circ}\text{N}$  and long.  $70^{\circ}$  to  $78^{\circ}\text{W}$ . This region still contained more than half of the total starting concentration in runs A, C, D, and F, and the mean cell concentration in this area was about 0.005.

The broad bands of concentration along the mid-Atlantic coast also persisted and increased in concentration to between  $10^{-3}$  and  $10^{-2}$ . This was a consequence of the patches offshore of Florida just mentioned. It appears the patches slowly introduced larvae into the Gulf Stream system. The subsequent transport in the Gulf Stream quickly spread larvae parallel to the coast, then offshore and out into the Atlantic. The patches in simulations A, C, D, and F formed in the same general location, so that for larvae carried north of lat.  $30^{\circ}\text{N}$  the starting location had a lesser effect on the distribution. This is illustrated by the fact that the  $10^{-3}$  contours are virtually identical in position north of lat.  $30^{\circ}\text{N}$  in runs A, D, and F at 5 mo after starting. Run C formed the patch earlier, so more larvae had entered the Gulf Stream and were therefore more widely dispersed. Leptocephali at



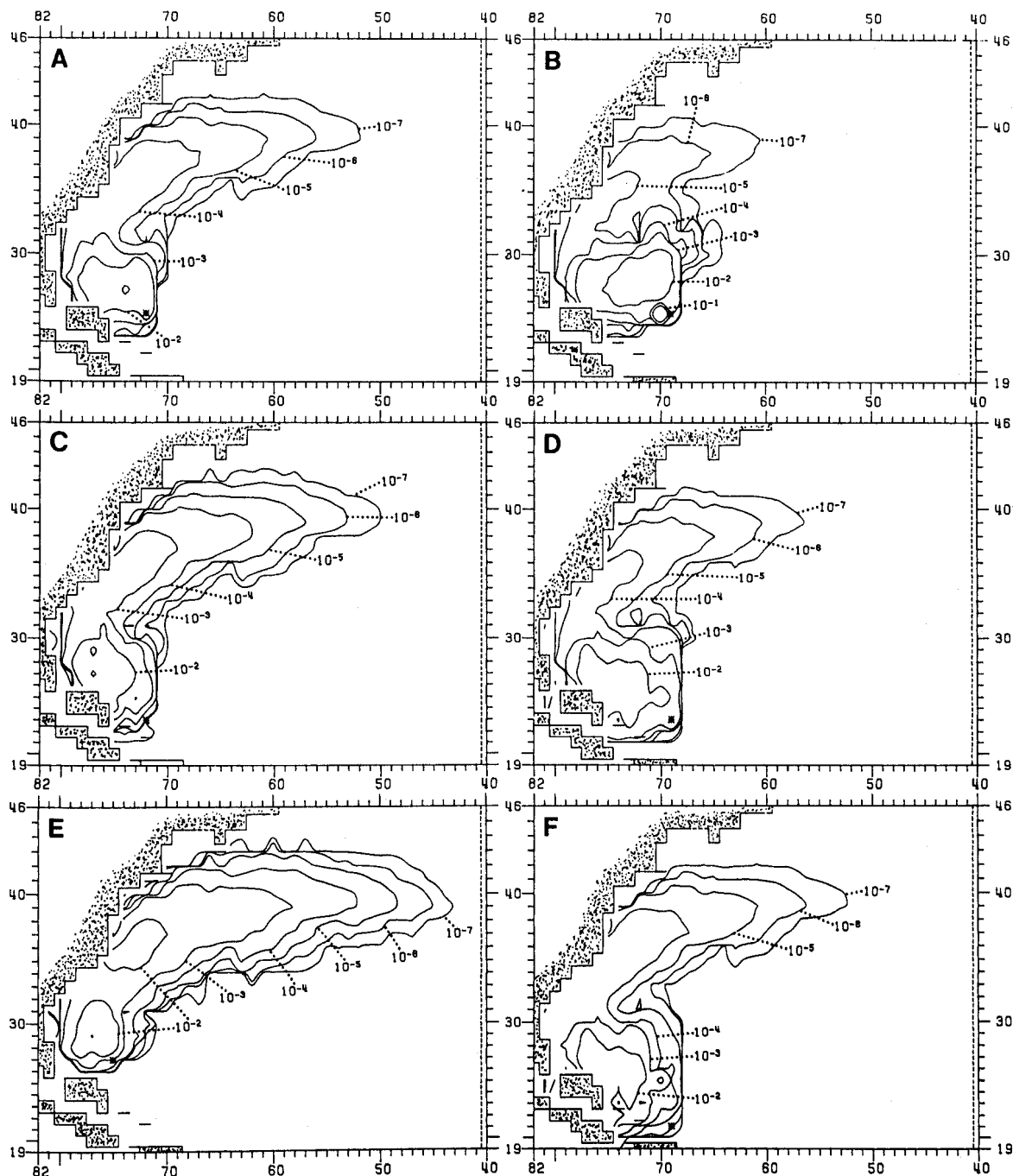


FIGURE 5.—Concentration contours of American eel leptocephali after 90 d of drift (30 May).

concentrations  $> 10^{-7}$  were now being advected past the long,  $40^{\circ}\text{W}$  border of the modeled area.

Run B's pattern at 5 mo was similar to those just discussed, but the main concentration of leptocephali was farther offshore of Florida and more broadly dis-

tributed (Fig. 6B) because the larvae were started in a region of weaker currents. There was a greater degree of northward transport from the main concentration, so that leptocephali joined the Gulf Stream at higher latitudes than in other runs.

The very large area enclosed by the  $10^{-3}$  contour was the striking aspect of the pattern for run E at 5 mo (Fig. 6E). Cells in this area had a mean concentration of 0.002 and contained in total a concentration of 0.9. This region formed an exaggerated example of

the results of prolonged leptocephalus entry into the Gulf Stream. In this case, the observed distribution is because larvae began close to the Gulf Stream, in the region where the main patch of concentration formed in other runs.

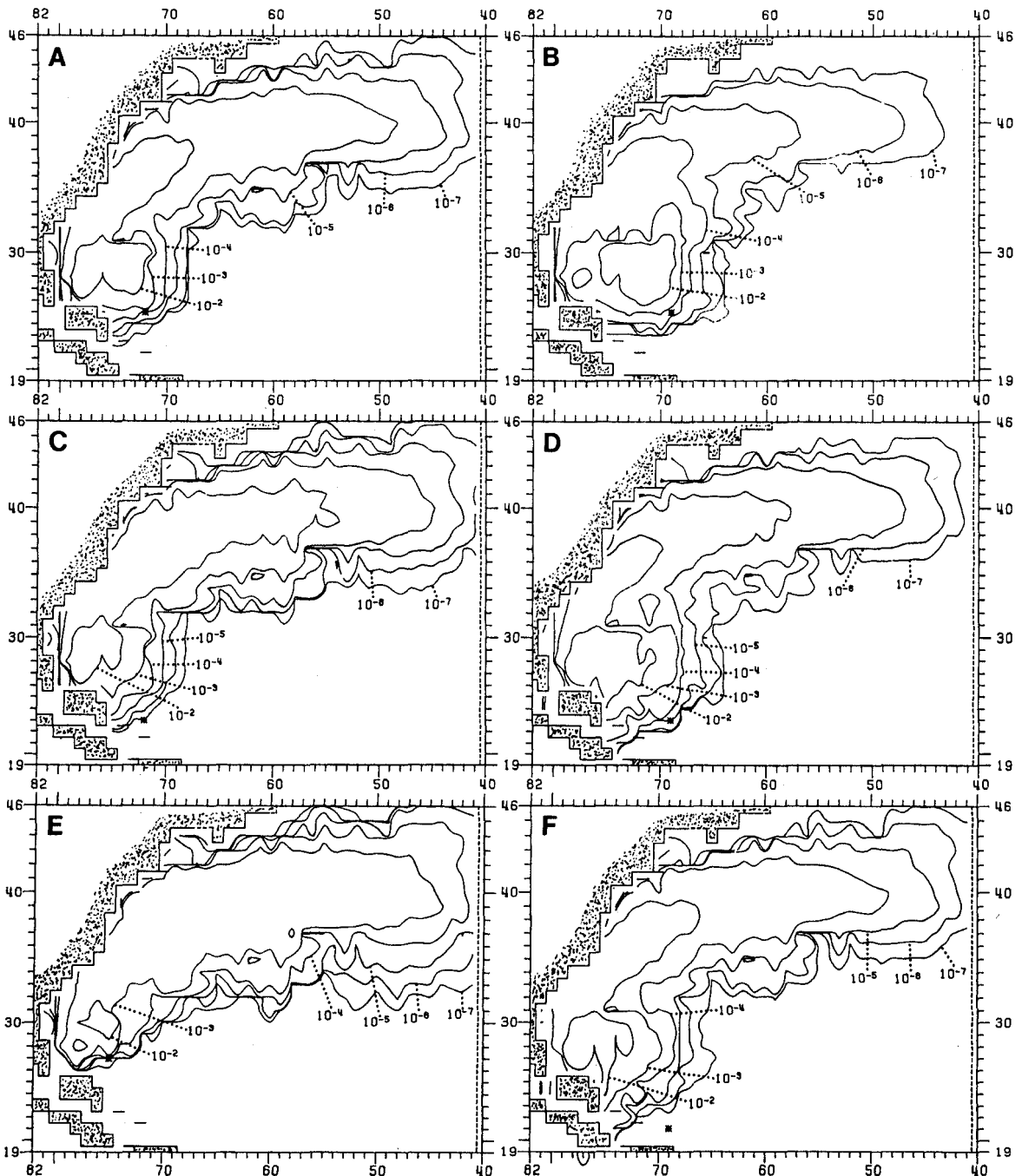


FIGURE 6.—Concentration contours of American eel leptocephali after 150 d of drift (29 July).

### Distribution of Leptocephali After 210 Days of Drift

The patches of higher concentration persisted offshore of Florida and the Gulf Stream in all runs

during the remainder of the summer (except E) and up to 7 mo after drift began, although they were beginning to dissipate (Fig. 7; 27 September). The cluster analyses still discriminated unequivocally between the patches and the lower concentrations to

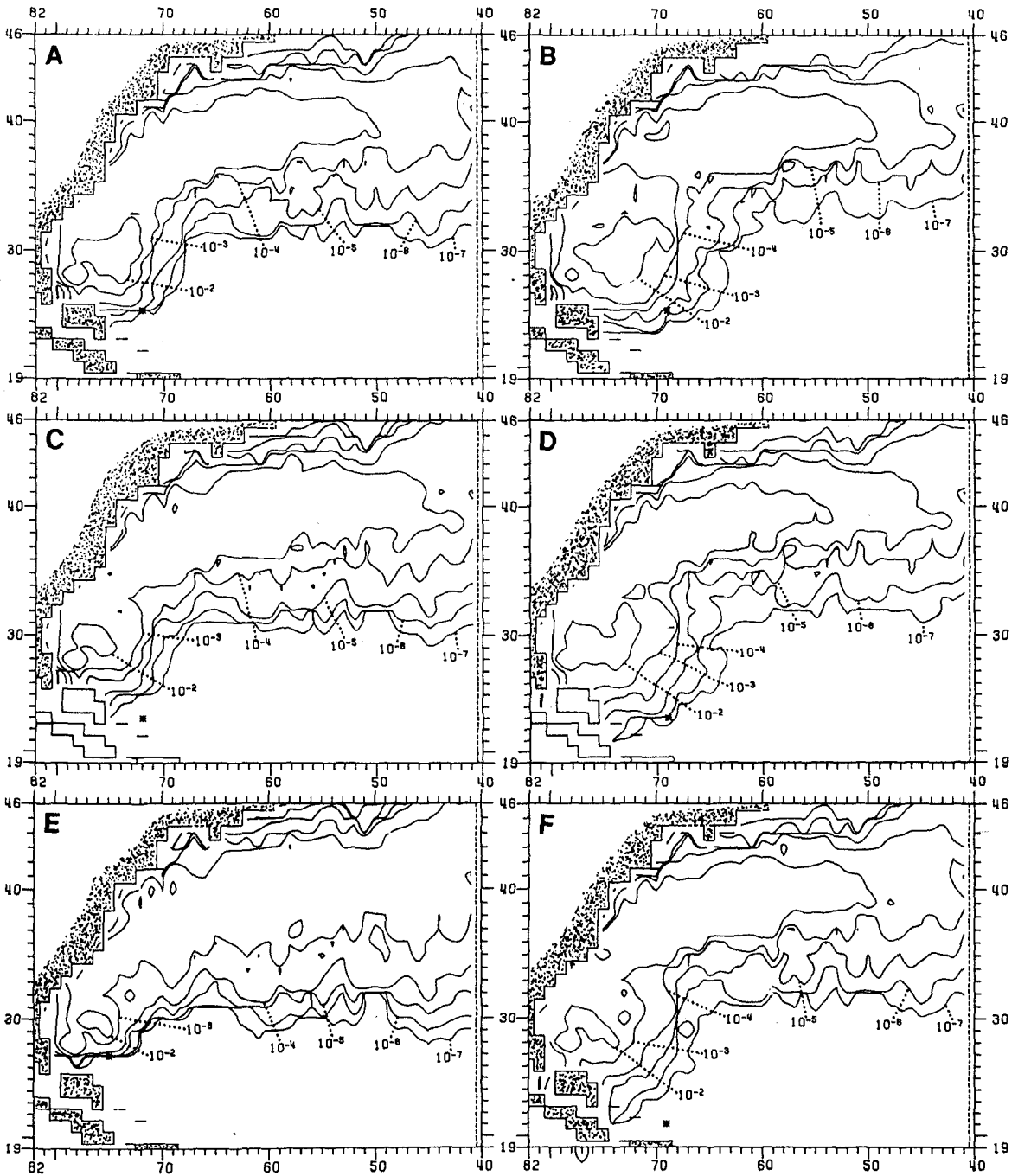


FIGURE 7.—Concentration contours of American eel leptocephali after 210 d of drift (27 September).

the immediate north in runs A and B and, to a lesser extent, in runs C, D, and F.

North of the patches the broad areas of uniform concentration were maintained and expanded by the continued entry of leptocephali into the Gulf Stream.

This region extended along the North American coast to lat.  $38^{\circ}\text{N}$ , at which point it curved out into the Atlantic. It was best represented by the  $10^{-3}$  contours in runs A, C, D, and F. The pattern was similar for run B, but the radial expansion of the main patch

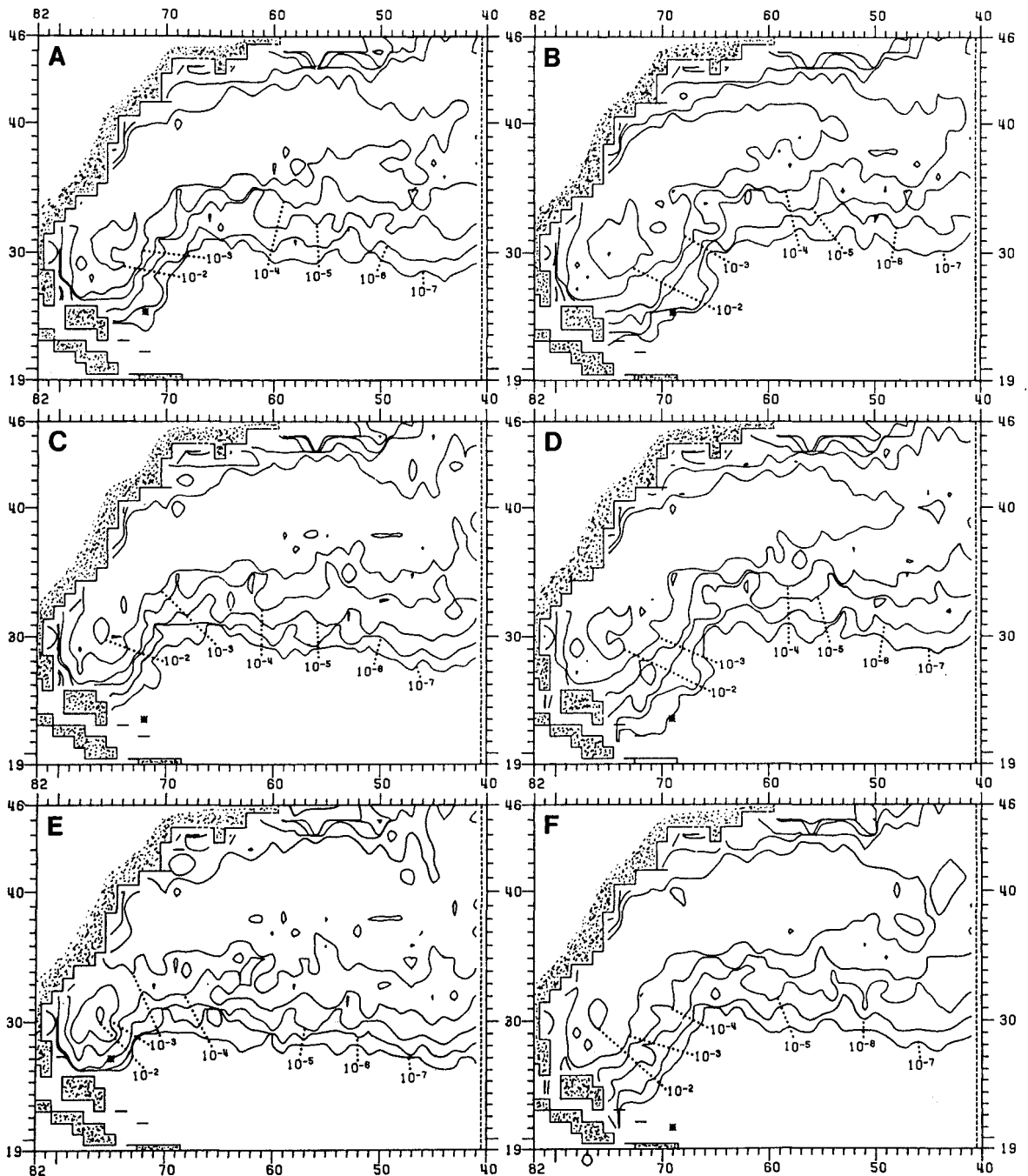


FIGURE 8.—Concentration contours of American eel leptocephali after 270 d of drift (26 November).

had continued. In most runs the plumes of leptocephali in the Gulf Stream had widened, so that concentrations  $>10^{-7}$  were present across the modeled area between lat.  $31^{\circ}$  and  $46^{\circ}$ N. In run E the  $10^{-3}$  concentrations extended completely from the patch area offshore of Florida to the right border of the modeled area.

### Distribution of Leptocephali After 270 Days of Drift

Nine months after starting the leptocephali in runs A, C, D, and F had been distributed completely along the course of the Gulf Stream (Fig. 8; 26 November). There were very large areas with concentrations between  $10^{-3}$  and  $10^{-2}$  that spanned the modeled area from offshore of Florida to near the eastern border at long.  $40^{\circ}$ W. Run B still appeared to be in the process

of developing the same distributional pattern as the others, because its pattern resembled those of the others 2 mo earlier. Leptocephali had progressed farthest in run E, in which the  $10^{-3}$  concentrations were moving away from the mid-Atlantic coast.

At day 270 the simulations were halted, as some leptocephali would have begun metamorphosis to the glass eel phase by late November (Kleckner and McCleave 1980). It is unknown what behavioral components a glass eel or large leptocephalus may contribute during oceanic transport.

### European Eel Drift Simulation

A simulation of European eel leptocephalus drift was done with the starting point at lat.  $27^{\circ}$ N and long.  $57^{\circ}$ W, and the starting date as 15 April. After 45 d of drift the larvae had spread to the northwest (Fig. 9A;

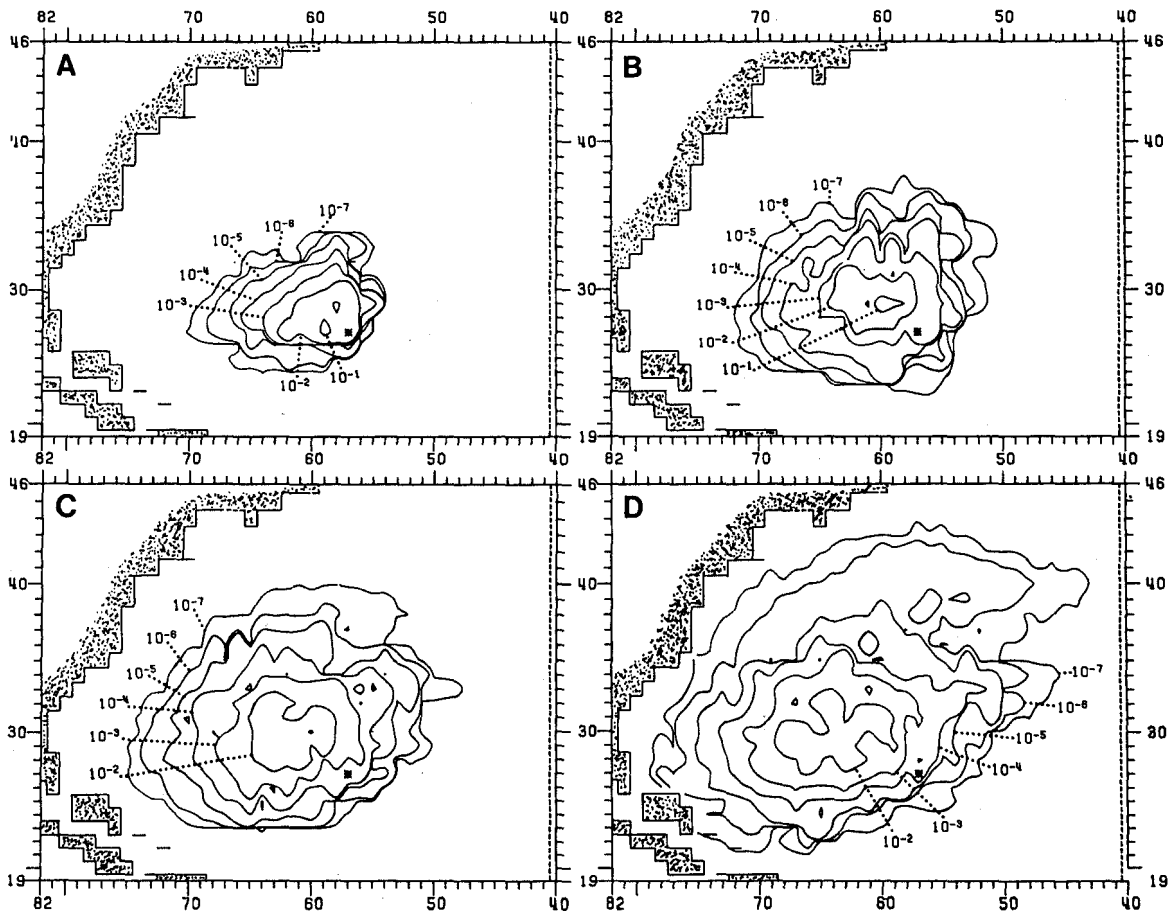


FIGURE 9.—Concentration contours of European eel leptocephali, expressed as a proportion of the starting concentration. Leptocephali were begun at the point marked with an X in Figure 1. A: contours for 30 May, 45 d after the 15 April start. B: contours for 29 July, 105 d after starting. C: contours for 27 September, 165 d after starting. D: contours for 26 November, 215 d after starting.

30 May). Two months later the  $10^{-2}$  enclosed about the same area as before, but it had moved a few degrees to the northwest of the starting location (Fig. 9B; 29 July). The lower concentrations continued to spread, and dispersal occurred in most compass directions. By day 165, the lower concentrations had expanded still further, although concentrations  $>10^{-2}$  maintained approximately the same position (Fig. 9C; 27 September). This same pattern of dispersal continued to day 215 of drift, at which point the concentrations  $<10^{-5}$  at the northern limits of the distribution showed signs of being captured by the Gulf Stream (Fig. 9D; 26 November). The simulation was halted at day 215.

## DISCUSSION

The simulations revealed several previously unsuspected features of the leptocephalus drift migration, such as the patch formation offshore of Florida and the Gulf Stream. This is in spite of the simplifications and assumptions that were made in a model encompassing such a large geographic area. The boundaries, currents, and eddy diffusivities all provided only an approximation to the physical system. Nonetheless, interpreting the simulation output using the available information on leptocephalus distribution and the eel's life history indicates that the model has realistically reproduced the large-scale features of the drift migration.

The simulated drift of American eel leptocephali can be divided into four phases, the first being initial northwest transport following spawning. This transport was largely on the Antilles Current, which flows northwesterly on a course parallel to the north-eastern border of the Bahama Islands chain (Fig. 2). The extent of the initial larval transport depended on the starting location's position with respect to this current. Larvae started farther northeast in the Sargasso Sea (point B and other simulations not shown here) showed less unidirectional movement than those started in or nearer the Antilles Current. This current clearly appeared in ships' drift data for May (Fig. 2) and other late winter and spring months, so its effects in the simulations were no surprise. However, there are questions concerning the existence of the Antilles Current (Ingham 1975; Gunn and Watts 1982). Gunn and Watts (1982) showed that the Antilles Current was present in January-February 1973, but that the region was dominated by eddies in July-August 1972. They speculated that the Antilles Current may only exist seasonally. Its presence in January-February 1973 must have dominated the drift of newly hatched leptocephali from early spawn-

ing in that year. If the Antilles Current is seasonal, the question important to eel biology is how long does it persist through the spring and summer? The Antilles Current was important in the simulations from the time of spawning up to May-June. After that its influence on the distribution of 0-group leptocephali diminished, and by July-August, when Gunn and Watts (1982) did not find the current, most of the larvae were north of lat.  $25^{\circ}$ N. A study like that of Gunn and Watts is clearly needed for the months between February and July, and particularly for April and May.

There was little eastward transport from the starting locations in all American eel simulations, including those in which larvae were started along long.  $66^{\circ}$ W (not pictured in this paper). Scoth and Tesch (1981) collected American eel leptocephali east of long.  $69^{\circ}$ W (the longitude of the easternmost starting points in the simulations presented here), although the numbers of larvae they caught declined rapidly east of long.  $65^{\circ}$ W. Transport to the south was also minimal in the simulations, and few leptocephali entered the Caribbean. The simulations do not adequately explain the presence of leptocephali that have been collected in the Caribbean and Gulf of Mexico, and in particular the presence of young leptocephali near the Yucatan peninsula (Kleckner and McCleave 1980) was not reproduced. American eel spawning in the Caribbean remains a viable explanation for these collections.

The simulated drift of leptocephali south and west of the Bahamas must be interpreted cautiously, because this region's complicated bathymetry and currents were not well represented in the model. However, there were some striking correspondences between the simulations and the actual collection data for this region. Smith (1968) reported 10 May as the earliest collection date for 0-group leptocephali in the Straits of Florida between the Bahamas and Florida; Figure 3F shows larval concentrations of  $10^{-6}$  (proportion of the starting concentration) had arrived in the Straits of Florida around 30 March, and by 30 April the concentration had increased to  $10^{-4}$  (Fig. 4F). Kleckner and McCleave (1980) reported the collection of 0-group leptocephali in the Bahama Island chain in April to June, and the first collections of larvae in the Straits of Florida in May. Smith (1968) gave 28 August as the latest collection date of 0-group larvae in the Straits of Florida, and by that date most of the leptocephali in the simulations had departed the area as well.

The formation and maintenance of a patch of leptocephali north of the Bahamas and east of Florida and the Florida Current-Gulf Stream system were the

second phase in the simulated drift migrations. Regardless of starting location, most larvae converged upon the area and became part of this patch, except those that entered the Florida Current by the route south of the Bahamas. Gunn and Watts (1982) found evidence in the January-February 1973 data of a large anticyclonic eddy in the region of this patch formation (cf their figure 3D). If this eddy is a permanent or seasonal feature, it has substantial implications for American eel *leptocephalus* drift. It could be reasonably assumed that *leptocephali* collect in the eddy each year and that this patch phase is an integral part in the transport of most American eel *leptocephali*.

Transport of larvae from the patch and into the Gulf Stream seems to have been a result of turbulent diffusion, rather than advection, since currents east of the Florida Current are weak (Fig. 2). In the model, entry into the Gulf Stream was an example of large-scale shear induced diffusion, where large differences in adjoining northward current velocities resulted in concentration gradients down which a diffusive flux occurred. Whether this is the phenomenon that facilitates actual entrainment of *leptocephali* into the Gulf Stream is problematic. Alternatively, Gulf Stream cold-core rings occur in this area (The Ring Group 1981), and it may be that Gulf Stream eddies and meanders act to capture larvae.

The *leptocephalus* collection data are still inadequate to confirm the presence of a *leptocephalus* patch offshore of Florida and the Gulf Stream. However, there is empirical evidence that this is indeed the region where most *leptocephali* enter the Gulf Stream system. Kleckner and McCleave (1982) studied near synoptic collections of *leptocephali* taken on four transects of the Florida Current and Gulf Stream between 26 July and 16 August 1978. There were substantially higher concentrations of *leptocephali* in the waters sampled on the northern transects than there were in the southern ones (Fig. 10), indicating a significant input of *leptocephali* from the western Sargasso Sea. Combined with the present work, the studies of Kleckner and McCleave (1982) and Gunn and Watts (1982) indicate that processes important to the *leptocephalus* drift migration occur east of Florida and that further research should concentrate on this region.

The prolonged existence of the *leptocephalus* patch offshore of Florida and the Gulf Stream and the continuous capture of larvae by the Gulf Stream resulted in the broad and surprisingly uniform distribution of *leptocephali* along the North American coast. This transport along the North American coast formed the third phase of the drift migration. The patch can be viewed as a mechanism causing a more uniform distribution of *leptocephali* than would otherwise occur. Before developing the simulation model it had been

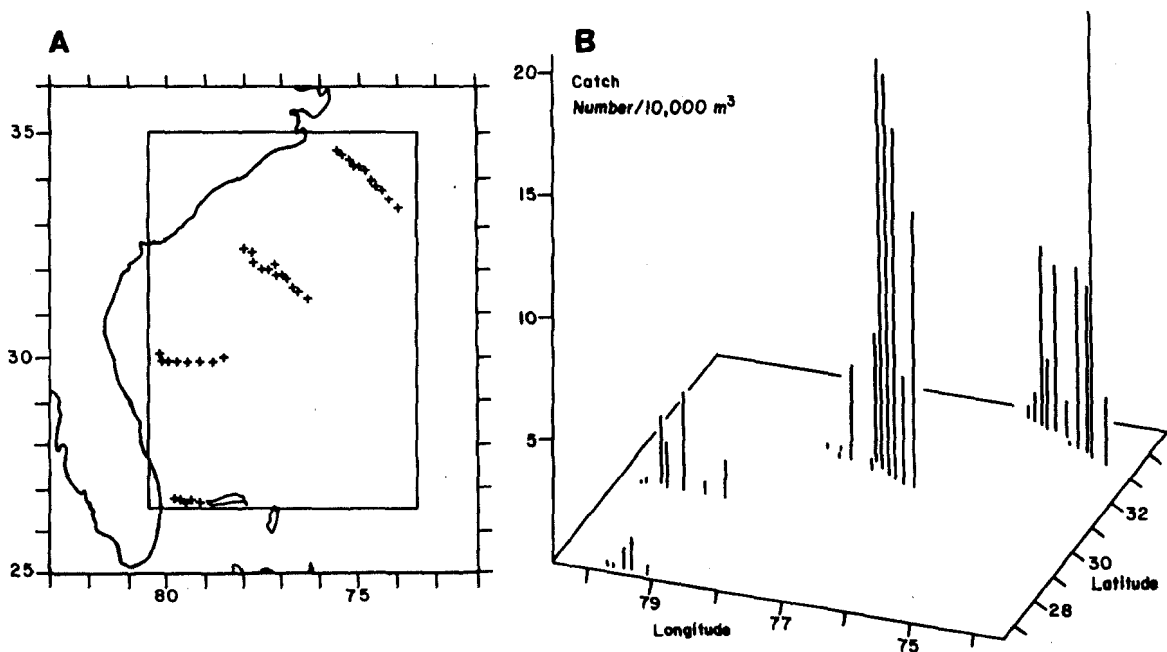


FIGURE 10.—A: Station positions on transects where American eel *leptocephali* were taken in the Gulf Stream system. B: Catches of *leptocephali* on the transects. Data from Kleckner and McCleave (1982).

assumed that leptocephali were quickly captured by the Gulf Stream and carried north and east, and it had been unclear how significant numbers of larvae remained in the southern portion of the eel's range. It is remarkable that a majority of the larvae remained so far south for such a prolonged period of time in the simulations.

Leptocephalus collections have not been made as systematically north of lat. 30°N as they have to the south, so it is difficult to compare the simulation results with the collection data north of this latitude. Kleckner and McCleave (1980, 1982<sup>6</sup>) stated that American eel leptocephali are abundant in the Gulf Stream from July through September, and the distributions of leptocephali they presented for these months correspond well with the simulation distributions (Fig. 11).

Up to about lat. 38°N the simulated concentrations formed wide bands along the coast; however, the simulations did not indicate how leptocephali in the eastern edges of the bands would move west towards the coast. The possibility of a behaviorally based, directed movement cannot be dismissed as unnecessary. Alternatively, it could be that these larvae are transported to Europe, or simply perish. McCleave and Kleckner (1982) demonstrated that in the tidal portion of an estuary American glass eels achieved upstream transport by selectively rising in-

to the water column during flood tides. This has also been demonstrated for European eels (Creutzberg 1961), and it is certainly possible that larval and juvenile eels could utilize this mechanism in offshore tidal areas such as Georges Bank (Magnell et al. 1980).

There are abundant examples in the literature of stochastic events whereby leptocephali could also be transported inshore. Recent examples include Gulf Stream intrusions off St. Augustine, Fla. (Atkinson et al. 1978) and in Onslow Bay (Blanton 1971), Gulf Stream frontal eddies off Jacksonville, Fla. (Yoder et al. 1981), and Gulf Stream intrusions along the New York Bight (Judkins et al. 1980). Cox and Wiebe (1979) discussed the mechanisms by which oceanic plankton are transported into the Mid-Atlantic Bight, such as Gulf Stream warm-core rings and meanders. These meso- and finer scale features all surely transport leptocephali, but they were not directly incorporated into the model, except as their effects were represented with other turbulent motions by the eddy diffusivity terms. It seems maladaptive for leptocephali to rely upon such unpredictable features to facilitate a migration that occurs with annual regularity.

Eastward transport into the North Atlantic on the Gulf Stream was the fourth and final phase evident in the simulations. These last simulation phases may not have accurately represented the eel's migration, because leptocephali begin metamorphosis to the glass eel stage as early as October (Kleckner and McCleave 1980), and it becomes questionable as to whether the eels were still drifting passively. Unless the loss of eels due to transport out into the Atlantic is substantial, it seems that by this point the eels must modify their drift in some way if they are to avoid transport to Europe. A small number of American eel are in fact found in European waters (Boëtius 1980). In the passive drift simulations, only a small portion of the larvae entered the Gulf of Maine, although this region also has complicated currents not accurately represented in the model. Meanders of the Gulf Stream will carry some larvae near the northeastern North American coast, as it has for other species (Colton et al. 1962; Markle et al. 1980). The transport of leptocephali out into the Atlantic was centered on lat. 40°N, and this agrees well with the results of Richardson (1981), who tracked buoys drifting on the Gulf Stream.

The European eel spawns in a region of weak and indeterminate currents, and in the simulation this resulted in a slow spreading of the leptocephali throughout the Sargasso Sea. It is clear that if the simulation presented in Figure 9 were continued, the

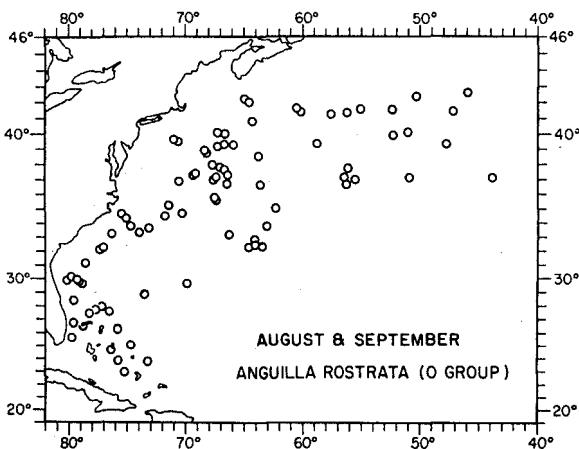


FIGURE 11.—Locations in the North Atlantic Ocean where one or more *Anguilla* leptocephali have been collected during August and September. Compare with Figures 6 and 7. From Kleckner and McCleave (text footnote 6).



leptocephali would simply have continued to spread, with those moving west and north gradually entering the Gulf Stream. This simulation result agreed with the "moderate to rich" catches of 1-group European eel leptocephali reported by Tesch et al. (1979) as being present north of lat. 26°N and between Bermuda and Europe. Such gradual dispersal also makes it not surprising that the European eel spends 3 yr as a leptocephalus before reaching Europe.

In summary, the simulations have reproduced the important features of the leptocephalus drift migration. Some of the features, such as the patch formation offshore of Florida, were previously unsuspected, but seem highly plausible when considered in combination with the hydrographic data and the leptocephalus collection data for that region. This patch, and the remainder of the predicted leptocephalus distribution, remains to be verified by intensive and systematic sampling.

## ACKNOWLEDGMENTS

We thank Robert C. Kleckner, John M. Ringo, Bruce D. Sidell, Irving L. Kornfield, John R. Moring, and the journal reviewers for their comments and criticisms. Computer time was provided by Computing and Data Processing Services, University of Maine. Funding for this research was provided by the National Science Foundation (Grant OCE77-19440) and by the National Geographic Society.

## LITERATURE CITED

- ATKINSON, L. P., G.-A. PAFFENHÖFFER, AND W. M. DUNSTAN.  
1978. The chemical and biological effect of a Gulf Stream intrusion off St. Augustine, Florida. *Bull. Mar. Sci.* 28:667-679.
- BLANTON, J.  
1971. Exchange of Gulf Stream water with North Carolina shelf water in Onslow Bay during stratified conditions. *Deep-Sea Res.* 18:167-178.
- BOËTIUS, J.  
1980. Atlantic *Anguilla*. A presentation of old and new data of total numbers of vertebrae with special reference to the occurrence of *Anguilla rostrata* in Europe. *Dana* 1:93-112.
- CLIFF, A. D., AND J. K. ORD.  
1973. Spatial autocorrelation. *Pion*, Lond., 176 p.
- COLTON, J. B., JR., R. F. TEMPLE, AND K. A. HONEY.  
1962. The occurrence of oceanic copepods in the Gulf of Maine-Georges Bank area. *Ecology* 43:166-171.
- COMPARINI, A., AND E. RODINO.  
1980. Electrophoretic evidence for two species of *Anguilla* leptocephali in the Sargasso Sea. *Nature* (Lond.) 287:435-437.
- COX, J., AND P. H. WIEBE.  
1979. Origins of oceanic plankton in the Middle Atlantic Bight. *Estuarine Coastal Mar. Sci.* 9:509-527.
- CREUTZBERG, F.  
1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. *Neth. J. Sea Res.* 1:257-338.
- FIADDEIRO, M. E., AND G. VERONIS.  
1977. On weighted-mean schemes for the finite-difference approximation to the advection-diffusion equation. *Tellus* 29:512-522.
- GUNN, J. T., AND D. R. WATTS.  
1982. On the currents and water masses north of the Antilles/Bahamas arc. *J. Mar. Res.* 40:1-18.
- INGHAM, M. C.  
1975. Velocity and transport of the Antilles Current north-east of the Bahama Islands. *Fish. Bull., U.S.* 73:626-632.
- JAMIESON, A., AND R. J. TURNER.  
1980. Muscle protein differences in two eels *Anguilla anguilla* (Linnaeus) and *Anguilla rostrata* (Le Seuer). *Biol. J. Linn. Soc.* 13:41-45.
- JUDKINS, D. C., C. D. WIRICK, AND W. E. ESAIAS.  
1980. Composition, abundance, and distribution of zooplankton in the New York Bight, September 1974-September 1975. *Fish Bull., U.S.* 77:669-683.
- KLECKNER, R. C., AND J. D. MCCLEAVE.  
1980. Spatial and temporal distribution of *Anguilla rostrata* and *Anguilla anguilla* leptocephali found in North American ichthyoplankton collections. *ICES C.M.* 1980/M:21.  
1982. Entry of migrating American eel leptocephali into the Gulf Stream system. *Helgol. Wiss. Meeresunters.* 35:329-339.
- MAGNELL, B. A., S. L. SPIEGEL, R. I. SCARLET, AND J. B. ANDREWS.  
1980. The relationship of tidal and low-frequency currents on the north slope of Georges Bank. *J. Phys. Oceanogr.* 10:1200-1212.
- MARKLE, D. F., W. B. SCOTT, AND A. C. KOHLER.  
1980. New and rare records of Canadian fishes and the influence of hydrography on resident and nonresident Scotian Shelf ichthyofauna. *Can. J. Fish. Aquat. Sci.* 37:49-65.
- MCCLEAVE, J. D., AND F. R. HARDEN-JONES.  
1979. Eels: New interest in an old problem. *Nature* (Lond.) 278:782-783.
- MCCLEAVE, J. D., AND R. C. KLECKNER.  
1982. Selective tidal stream transport in the estuarine migration of glass eels of the American eel (*Anguilla rostrata*). *J. Cons. Int. Explor. Mer.* 40:262-271.
- OKUBO, A.  
1971. Oceanic diffusion diagrams. *Deep-Sea Res.* 18:789-802.  
1980. Diffusion and ecological problems: Mathematical models. Springer-Verlag, Berl., 254 p.
- PASSAKAS, T.  
1981. Comparative studies on the chromosomes of the European eel (*Anguilla anguilla* L.) and the American eel (*Anguilla rostrata* Le Seuer). *Folia Biol. (Cracow)* 29:41-57.
- POWER, J. H.  
1982. A numerical method for simulating plankton transport and simulation of the North Atlantic Ocean drift of *Anguilla* leptocephali. Ph.D. Thesis, University of Maine, Orono.
- RICHARDSON, P. L.  
1981. Gulf Stream trajectories measured with free-drifting buoys. *J. Phys. Oceanogr.* 11:999-1010.

## RING GROUP, THE.

1981. Gulf Stream cold-core rings: Their physics, chemistry, and biology. *Science* (Wash., D.C.) 212:1091-1100.

## SCHMIDT, J.

1925. The breeding places of the eel. *Annu. Rep. Smithsonian Inst.* 1924:279-316.

## SCHOTH, M., AND F.-W. TESCH.

1981. Spatial distribution of the 0-group eel larvae (*Anguilla* spec.) 1979 in the Sargasso Sea. ICES C.M. 1981/M:8.

## SMITH, D. G.

1968. The occurrence of larvae of the American eel, *Anguilla rostrata*, in the Straits of Florida and nearby areas. *Bull. Mar. Sci.* 18:280-293.

## TESCH, F.-W.

1980. Occurrence of eel *Anguilla anguilla* larvae west of the European continental shelf, 1971-1977. *Environ. Biol. Fish.* 5:185-190.

## TESCH, F.-W., R. KRACHT, M. SCHOTH, D. G. SMITH, AND G. WEGNER.

1979. Report on the eel expedition of FRV "Anton Dohrn"

and R. K. "Friedrich Heincke" to the Sargasso Sea 1979. ICES C.M. 1979/M:6.

## TUCKER, D. W.

1959. A new solution to the Atlantic eel problem. *Nature* (Lond.) 183:495-501.

## VLADYKOV, V. D.

1964. Quest for the true breeding area of the American eel (*Anguilla rostrata* Le Seuer). *J. Fish. Res. Board Can.* 21:1523-1530.

## VLADYKOV, V. D., AND H. MARCH.

1975. Distribution of leptocephali of the two species of *Anguilla* in the western North Atlantic based on collections made between 1933 and 1968. *Sylogus* 6:3-38.

## YODER, J. A., L. P. ATKINSON, T. N. LEE, H. H. KIM, AND C. R. MCCLAIN.

1981. Role of Gulf Stream frontal eddies in forming phytoplankton patches on the outer southeastern shelf. *Limnol. Oceanogr.* 26:1103-1110.