

Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf

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Abstract

Larval fish originating south of Cape Hatteras, North Carolina, are frequently found on the continental shelf north of Cape Hatteras, even as far north as the Scotian shelf. The Gulf Stream and associated warm-core rings are hypothesized as the physical mechanisms responsible for the northward transport of larvae. Specifically, larvae spawned along the southeast U.S. continental shelf are entrained into the Gulf Stream, transported to the northeast, regularly incorporated in warm-core ring streamers, transported across the slope region, and released along the shelf edge north of Cape Hatteras. This proposed transport route was evaluated using hydrographic data and drifter tracks that were collected as part of other studies. Continental shelf water that originated south of Cape Hatteras was found

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along the edge of the Gulf Stream north of Cape Hatteras, and drifter tracks demonstrated each segment of the proposed transport route. A probability model was then developed to estimate transport times for larvae carried over the proposed transport route using a combination of sea surface temperature images, statistics of drifter transport speeds, and a larval mortality function. Modeled transport time distributions closely matched observed age distributions of larvae, further supporting the hypothesized transport route.

Two major oceanographic regimes occupy the eastern seaboard of the United States. The southeast U.S. continental shelf (SEUSCS) extends from the Straits of Florida to Cape Hatteras and contains relatively warm, salty water (Atkinson et al. 1983). The northeast U.S. continental shelf (NEUSCS) reaches from Cape Hatteras to Georges Bank and contains relatively cold, fresher water (Beardsley et al. 1985; Aikman et al. 1988; Churchill et al. 1993). (The terminology southeast and northeast U.S. continental shelves is used in the Large Marine Ecosystem literature [Sherman 1993] and is used here to avoid problems associated with the unofficial and inaccurate geographical names South and Middle Atlantic Bight [Richards 1999]. Both sets of place names refer to nearly identical geographic areas.) On the inner portion of the SEUSCS, circulation is predominantly wind and buoyancy driven (Blanton and Pietrafesa 1978; Lee et al. 1989; Werner et al. 1999). On the outer portion of the SEUSCS, circulation is dominated by the Gulf Stream, which flows northward along the shelf edge; flow direction at a given location, however, is variable owing to wavelike meanders (Lee et al. 1989). Large-scale circulation on the NEUSCS is not directly influenced by the Gulf Stream, which separates from the shelf edge in the vicinity of Cape Hatteras (Csanady and Hamilton 1988). The mean current over the NEUSCS and upper slope is directed southwestward, along isobaths, and is associated with an along-shore pressure gradient (Beardsley et al. 1985; Aikman et al. 1988). The NEUSCS and SEUSCS flows converge near Cape Hatteras, and most shelf and slope water is entrained into Gulf Stream flows and carried northeastward (Churchill and Berger 1998).

The water mass boundary near Cape Hatteras coincides with a boundary separating two distinct marine faunas: a warm-temperate fauna to the south and a cold-temperate fauna to the north (Briggs 1974). Members of these faunas, however, move between oceanographic regimes. Adults of some cold-temperate species are found south of Cape Hatteras (e.g., tautog, *Tautoga onitis*, Parker and Dixon 1998), and larvae of NEUSCS-spawning species can be transported south of Cape Hatteras via wind and buoyancy-driven intrusions into the SEUSCS (Stegmann and Yoder 1996; Grothues et al. 2002). Likewise, many warm-temperate species are found in the NEUSCS during late spring, summer, and early fall (Able and Fahay 1998). Some of these warm-temperate species migrate northward into the NEUSCS as adults in spring and return south with the onset of fall (e.g., Atlantic menhaden, *Brevoortia tyrannus*, Ahrenholz 1991). However, many warm-temperate species are transported north of Cape Hatteras as larvae or juveniles (Markle et al. 1980; Able and Fahay 1998). Larvae of some SEUSCS-spawned species use nursery habitats in the NEUSCS and migrate southward in fall to join adult populations (e.g., bluefish, *Pomatomus saltatrix*, Kendall and Walford 1979), whereas others are ex-

patriates and perish as water temperatures cool (e.g., spotfin butterflyfish, *Chaetodon ocellatus*, McBride and Able 1998).

The physical mechanisms that transport larvae from the SEUSCS to NEUSCS are important to the ecology of many warm-temperate species. For species whose larvae and juveniles successfully utilize NEUSCS habitats, the mechanisms responsible for northward transport could control larval supply to nursery habitats (Hare and Cowen 1996). For species whose larvae are expatriated to the NEUSCS, northward larval transport represents a loss of propagules from southern populations. Under a scenario of climatic warming, expatriation may provide a mechanism for warm-temperate species to colonize areas north of Cape Hatteras, similar to the recent spread of many tropical species into the northern SEUSCS (Parker and Dixon 1998). Larval transport from the SEUSCS to the NEUSCS might also be important in the northward dispersion of introduced species (Whitfield et al. 2002).

Several potential physical mechanisms could result in the transport of SEUSCS and Gulf Stream water, and their plankton, to the NEUSCS. Pietrafesa et al. (1994) found that strong northward winds can force SEUSCS water northward into the NEUSCS, in opposition of the NEUSCS's mean current. However, such wind-driven excursions have not been observed more than 100 km north of Cape Hatteras and cannot account for observations of SEUSCS-spawned fish larvae in the central or northern NEUSCS (Shima 1989; Hare and Cowen 1991; Cowen et al. 1993), or still further to the northeast over Georges Bank (Cowen et al. 1993) and the Scotian Shelf (Markle et al. 1980). Water discharged from Gulf Stream meanders often makes its way to the NEUSCS edge (Churchill and Cornillon 1991a, 1991b; Churchill et al. 1993). Using hydrographic data acquired quarterly over 11 yr, Churchill and Cornillon (1991b) determined that the probability of such transport decreases sharply going northwards from Cape Hatteras, and found no intrusions of discharged Gulf Stream water at the NEUSCS edge north of 39°N (off Delaware Bay).

Many investigators have postulated that warm-core rings (WCRs), which are mesoscale eddies that form when Gulf Stream meanders "pinch-off" (Joyce et al. 1984), transport subtropical and warm-temperate plankton, including larvae, to the northeast North American shelf edge (Cox and Wiebe 1979; Markle et al. 1980). Specifically, Hare and Cowen (1991, 1996) and Cowen et al. (1993) proposed four segments for northward larval transport associated with WCRs (Fig. 1). Larvae that are spawned on the continental shelf south of Cape Hatteras are (1) entrained into the Gulf Stream, (2) transported to the northeast along the edge of the Gulf Stream, (3) carried in WCR streamers from the Gulf Stream and across the Slope Sea (i.e., the region between the Gulf Stream and the shelf edge north of Cape Hatteras), and (4) ejected from WCR streamers at the shelf edge where

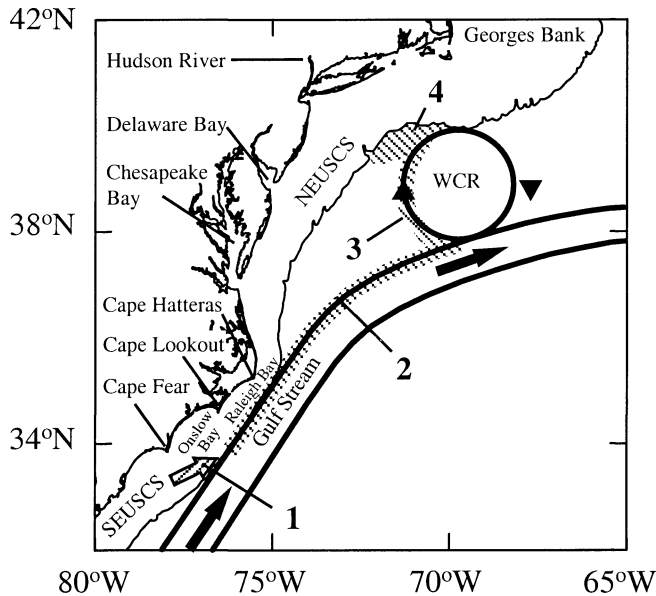


Fig. 1. Transport route proposed by Hare and Cowen (1991, 1996) and Cowen et al. (1993) for the movement of larvae spawned along the southeast U.S. continental shelf (SEUSCS) to the northeast U.S. continental shelf (NEUSCS) edge. Larvae that are spawned on the northern SEUSCS are (1) entrained into the Gulf Stream, (2) transported to the northeast along the edge of the Gulf Stream, (3) carried in WCR streamers from the Gulf Stream across the slope region between the Gulf Stream and the shelf edge north of Cape Hatteras, and (4) ejected from WCR streamers at the shelf edge, where they enter the NEUSCS/slope frontal region. Coastline and 200-m isobath are plotted, and place names used in the text are indicated.

they enter the shelf/slope frontal region. WCR streamers are composed of Gulf Stream-derived water that moves around the western periphery of the WCRs and result from a WCR–Gulf Stream interaction (Evans et al. 1985; Nof 1988). Ages of larval fish derived from otolith increments suggest that transport over the proposed route can occur in as little as 8 d (Hare and Cowen 1991). Although founded in a general understanding of the physical oceanography of the region, there is no direct physical evidence for the proposed transport route (see discussion by Epifanio and Garvine 2001); nor is there independent verification of the speed over which water and larvae can travel over the proposed route.

The purpose of the present study was to evaluate the transport route proposed by Hare and Cowen (1991, 1996) and Cowen et al. (1993) through an examination of water properties and Lagrangian drifter tracks. These observations reveal transport along each of the four segments of the proposed transport route, as well as transport connections joining the segments. To further assess the likelihood that SEUSCS-spawned larvae observed on the NEUSCS were carried along this route, a probability model was developed that estimated the age distribution of larvae arriving at the NEUSCS edge at the endpoint of the route. Model input included all the available measurements of drifter speed along the various segments of the proposed route, distances for each segment extracted from satellite-derived sea surface temperature (SST) images, and estimates of larval mortality

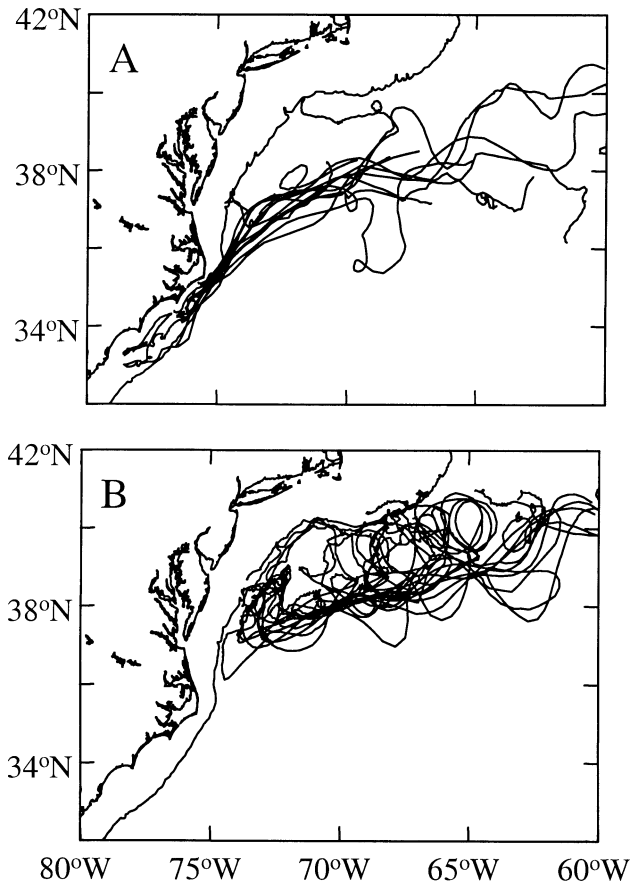


Fig. 2. (A) Tracks of 13 satellite-tracked drifters released in the northern portion of the SEUSCS as part of three separate field programs (see Data sources). These drifter tracks were used to examine segments 1 and 2 of the proposed route (Fig. 1, Table 1). (B) Tracks of 11 drifters released in the slope region of the NEUSCS (see Data sources). These drifter tracks were used to examine segments 3 and 4 of the proposed route (Fig. 1, Table 1). Coastline and 200-m isobath are plotted with drifter tracks.

rate. Model results were then compared with measured age distributions of SEUSCS-spawned larvae captured at the NEUSCS edge to assess the validity of the proposed transport route.

Materials and methods

Data sources—Hydrographic data: Hydrographic measurements taken along a cross-slope transect east of Virginia during May 1984 as part of the Mid-Atlantic Slope and Rise (MASAR) project (Csanady and Hamilton 1988) provided a view of SEUSCS water at the edge of the Gulf Stream, north of Cape Hatteras. CTD (conductivity, temperature, depth) casts and XBT (expendable bathythermograph) drops were made, and observed temperature–salinity (TS) properties were compared to the TS properties of the water masses typically observed in the SEUSCS and southern NEUSCS during springtime (Atkinson et al. 1983; Churchill et al. 1993). To gain a sense of the speed of entrained SEUSCS

Table 1. Summary of drifters used in this study including original project, transmitter number, release date, water depth at release, drogue type and depth, general release location (see Fig. 1), and transport route segments for which the drifter was included in analysis. Drogue type refers to holey sock (HS), surface (S), and window shade (WS). Drogue depth refers to depth of the center of the drogue.

Project	Transmitter no.	Release date	Water depth at release (m)	Drogue		Release location	Segment
				depth (m)	type		
FRED	8772	23 May 87	130	10	HS	Onslow Bay	1,2
FRED	8773	22 May 87	270	10	HS	Onslow Bay	1,2
FRED	8775	12 May 87	30	10	HS	Raleigh Bay	1,2
FRED	8776	12 May 87	35	10	HS	Raleigh Bay	1,2*
SABRE	9806	1 Feb 94	30	0	S	Onslow Bay	1,2
SABRE	17543	1 Feb 94	30	0	S	Onslow Bay	1,2
SABRE	2600	17 Dec 94	30	19	WS	Onslow Bay	1†
SABRE	4563	17 Dec 94	30	9	WS	Onslow Bay	1,2
MMS-CHFS	3537	5 May 92	25	2.25	HS	Raleigh Bay	1,2
MMS-CHFS	3540	26 Aug 92	25	2.25	HS	Raleigh Bay	1,2
MMS-CHFS	3774	30 Oct 93	25	2.25	HS	Raleigh Bay	1,2
MMS-CHFS	3590	8 Nov 92	25	2.25	HS	Raleigh Bay	1,2
MMS-CHFS	3593	12 May 93	25	2.25	HS	Raleigh Bay	1,2
SEFCAR‡	23112	27 Feb 96		2.25	HS	Florida Bay	
DWDS-EPA	22734	3 May 91	>2000	10	HS	106 DWDS	3,4
DWDS-EPA	12738	4 May 90	>2000	10	HS	106 DWDS	3§
DWDS-EPA	12742	6 Jul 90	>2000	10	HS	106 DWDS	3§
DWDS-EPA	12745	21 Jul 90	>2000	10	HS	106 DWDS	3,4
DWDS-EPA	12750	13 Sep 90	>2000	10	HS	106 DWDS	3,4
DWDS-EPA	12761	3 Dec 90	>2000	10	HS	106 DWDS	3,4
DWDS-EPA	12762	8 Dec 90	>2000	10	HS	106 DWDS	3§
DWDS-EPA	12763	4 Nov 90	>2000	10	HS	106 DWDS	3,4
DWDS-EPA	12768	8 Nov 90	>2000	10	HS	106 DWDS	3,4
DWDS-EPA	12769	20 Jan 91	>2000	10	HS	106 DWDS	3,4
DWDS-EPA	12771	3 Feb 91	>2000	10	HS	106 DWDS	3,4

* Crossed from the Gulf Stream to the northeast U.S. continental shelf edge in a discharge of water emanating from a Gulf Stream meander.

† After release, drifter moved southwest and was stranded on Frying Pan Shoals. This drifter was omitted from the residence time on the southeast U.S. continental shelf (segment 2).

‡ Released off south Florida, subsequently became entrained into Gulf Stream flows, and moved north of Cape Hatteras, where it was incorporated into a WCR during ring formation.

§ One of three EPA-DWDS drifters that circuted around the periphery of a WCR and was not detained in the vicinity of the shelf/slope front north of Cape Hatteras.

water, the geostrophic velocity component normal to the transect line was calculated using the CTD station at which SEUSCS water was encountered and the adjacent XBT stations (the tight TS relation observed in the transect data allowed us to infer salinity from the XBT data).

Drifter data: Tracks of 13 drifters released in the northern SEUSCS during three separate experiments (Fig. 2A, specifics of drifters and their release are provided in Table 1) were used to examine movements along segments 1 and 2 of the proposed transport route (Fig. 1). Four of the tracks were from the Frontal Eddy Dynamics (FRED) experiment, which examined Gulf Stream frontal eddies between Cape Fear and Cape Hatteras (Glenn and Ebbesmeyer 1994a, 1994b). Four tracks were from the South Atlantic Bight Recruitment Experiment (SABRE), which examined biological and physical processes involved in the recruitment dynamics of estuarine-dependent fishes that spawn on the SEUSCS (Werner et al. 1999). The final five drifter tracks were ac-

quired as part of the Mineral Management Service–Cape Hatteras Field Study (MMS-CHFS), which evaluated the potential effect of oil and gas exploration over the shelf region between Chesapeake Bay and Cape Lookout (Churchill and Berger 1998).

Drifter tracks from the Environmental Protection Agency's (EPA) Monitoring, Research, and Surveillance Study of the 106-mile Deep Water Dumpsite (EPA-DWDS) were used to evaluate segments 3 and 4 of the proposed transport route (Fig. 1). The EPA-DWDS evaluated the potential effects of sewage sludge dumping at a site on the continental slope east of New Jersey and south of New York (Berger et al. 1996; Dragos et al. 1996). During the study, 58 drifters were deployed in and around the 106-mile site. Tracks of 11 drifters, which were entrained in the Gulf Stream and then into a WCR west of 65°W, were used in this study (Table 1, Fig. 2B).

Location data from all drifters were quality checked and linearly interpolated to produce tracks at evenly spaced in-

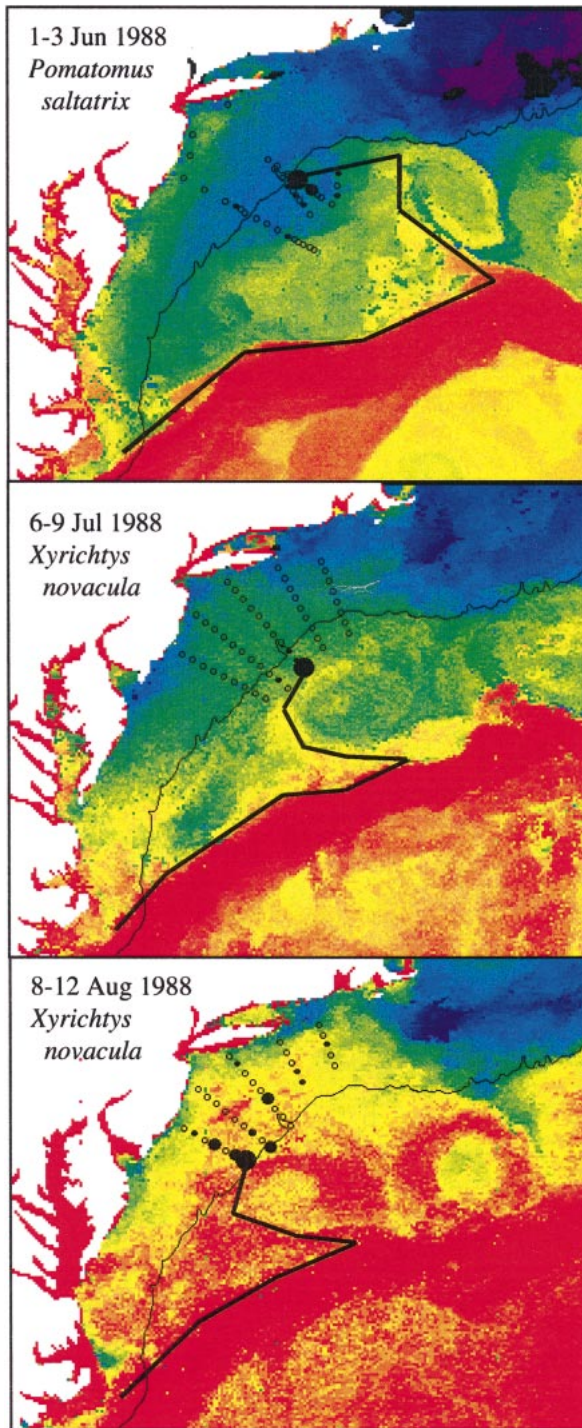


Fig. 3. Five-day composite satellite-derived SSTs from June, July, and August 1988. Station locations are plotted where *P. saltatrix* pelagic juveniles were captured in June 1988 and *X. novacula* larvae were captured in July and August 1988. Symbol size represents concentration of larvae—zero larvae are denoted with an open circle. The proposed transport route is indicated by a black line, and distances were extracted from these lines for use in a probability model. Red indicates warmer water and blue indicates cooler water. Land is shown as white, and the 200-m isobath is plotted.

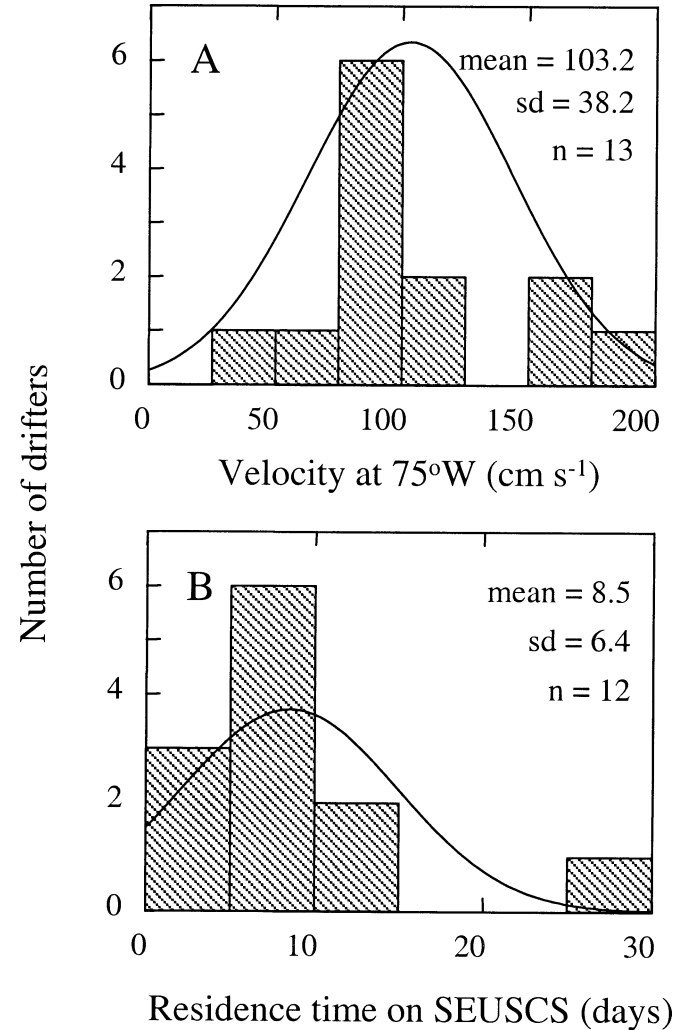


Fig. 4. (A) Distribution of speeds as drifters crossed out of the SEUSCS. (B) Distribution of residence times of drifters released on the SEUSCS. All drifters released on the SEUSCS were entrained into Gulf Stream flows and moved rapidly to the northeast. One drifter that was stranded on Frying Pan Shoals for about 1 week (Table 1) was not included in the determination of residence time.

intervals (6 h). Velocities were then estimated from the tracks by dividing the distance traveled in an interval by time.

Satellite-derived SSTs: Drifter tracks were superimposed on concomitant satellite-derived images of SSTs to relate surface temperature features with movement of drifters over different segments of the proposed transport route. Satellite-derived SST images were obtained from the Southeast CoastWatch Program at the NOAA Center for Coastal Fisheries and Habitat Research, from the Remote Sensing Laboratory at the University of Rhode Island, and from a data set of 5-d composite imagery developed for NOAA by Brown and Podesta (1989).

Probability model—Conceptual framework: A probability model was developed to give estimates of the age distribution of larvae that traveled along the proposed route to arrive

at a specified location on the NEUSCS edge. Specific scenarios were developed for the model to correspond to specific times when SEUSCS-spawned larvae were collected on the outer NEUSCS. Modeled age distributions were then compared to observed age distributions, which were determined through otolith aging of captured larvae. If actual larval ages appeared at very low probabilities in the modeled age distribution, then transport along the proposed route could be deemed unlikely. Conversely, coincidence of actual ages with modeled ages of high probability supports the assertion that larvae had traversed the proposed route.

Conceptually, the model consists of two components: (1) probability distributions of transport times over the four segments of the proposed route and (2) a larval mortality function. To determine component 1, a transit time probability function was defined for each route segment (Fig. 1). For route segment i , this is denoted as $p_i(t)$, where $p_i(t)dt$ is the probability that larvae are transported the length of the segment in the forward direction (leading to the NEUSCS) over a period between t and $t + dt$. Consider transport across the first two segments. If $p_1(t)$ and $p_2(t)$ are independent and the probability of going from one segment to the next is 1, then the likelihood per unit time that a larva may transit the two segments in a period t is simply the sum of all possible combinations of $p_1(t_1) p_2(t_2)dt$, with t_1 and t_2 summing to t . This can be expressed as a convolution integral,

$$p_{1-2}(t) = \int_0^t p_1(t - \varepsilon)p_2(\varepsilon) d\varepsilon \quad (1)$$

where $p_{1-2}(t)dt$ is the probability of being carried in the forward direction over segments 1 and 2 within a period of t to $t + dt$, and ε is a dummy variable for integration. With the inclusion of additional segments, the above is expanded to nested convolution integrals. The transit time distribution for the four segments of the specified route is

$$p_{1-4}(t) = \int_0^t \int_0^\psi \int_0^\varepsilon p_1(t - \psi)p_2(\psi - \varepsilon)p_3(\varepsilon - \kappa)p_4(\kappa) d\kappa d\varepsilon d\psi \quad (2)$$

with κ and ψ also dummy variables of integration.

A survival probability $S(t)$ was defined to account for the effect of mortality on the final transit time distribution (component 2). This gives the likelihood of survival for larvae that cover the route in a time t . The transit time probability function with mortality included then becomes Eq. 3.

$$P(t) = p_{1-4}(t)S(t) \quad (3)$$

Residence time on the SEUSCS, $p_1(t)$: This segment was represented as a normal distribution of the expected residence time of water on the SEUSCS. This distribution was fully specified by the mean and standard deviation of residence time of drifters deployed on the SEUSCS. Residence time was defined as the period between a drifter's release and its crossing of 75°W. FRED, SABRE, and MMS-CHFS drifters were used, but the SABRE drifter that grounded on Frying Pan Shoals was excluded from the calculation (Table

1). Larvae were assumed to be spawned in the northern portion of the SEUSCS, and leaving the shelf is the first segment of transport to the NEUSCS.

Transport time along the Gulf Stream's edge, $p_2(t)$: For this, and the subsequent route segments, transit time probability was determined from (1) the segment length and (2) the distribution of speeds along the segment. Segment length was determined for three specific scenarios (June, July, and August 1988), times when SEUSCS-spawned fish were collected on the outer shelf of the NEUSCS. The procedure involved tracing the proposed route over SST images that coincided with larval collections (Fig. 3) and then determining the distances along the edge of the Gulf Stream (segment 2), from the Gulf Stream to the NEUSCS edge around a WCR (segment 3), and along the NEUSCS edge from the WCR to larval collection locations (segment 4).

The speed distribution for segment 2 was determined from the tracks of drifters that moved from 75 to 71°W (range chosen to include maximum number of drifters). The along-Gulf Stream speed was taken as the ratio of the length of the line connecting the crossings of these longitudes for each drifter and the time difference between the crossings. This method was necessary to give a representative speed because movement of drifters along the edge of the Gulf Stream often was not unidirectional. Speeds were computed from FRED, SABRE, and MMS-CHFS drifters.

The mean and standard deviation of the drifter speeds were used to specify a normal transport speed distribution. This was defined as $q_2(v)$, where $q_2(v)dv$ is the likelihood that larvae traverse segment 2 with a mean speed between v and $v + dv$. Because our interest was confined to transport in the forward direction along the route, this distribution was converted to one defined for speeds in the forward direction only. To ensure that the "forward speed" distribution would integrate to unity, it was determined as

$$q'_2(v) = \frac{q_2(v)}{\int_0^\infty q_2(v) dv} \quad (4)$$

Conversion of $q'_2(v)$ to a transit time probability was done by noting that the equation

$$q'_2(v)dv = p_2(t)dt \quad (5)$$

is satisfied for $v = D_2/t$, where D_2 is the segment 2 length. Evaluating dv/dt gives Eq. 6.

$$p_2(t) = D_2q'_2(v)/t^2 \quad (6)$$

Warm-core ring transport time to the shelf edge, $p_3(t)$: None of the 13 drifters released in the SEUSCS were incorporated into WCR streamers, and only two of these drifters passed a WCR. Thus, these drifters could not be used to examine segments 3 and 4 of the proposed transport route (Table 1).

Examination of drifter tracks with concomitant SST images indicated that at least 23 of the EPA-DWDS drifters moved from the edge of the Gulf Stream into the circulation of a WCR before reaching 60°W. Analyses herein were con-

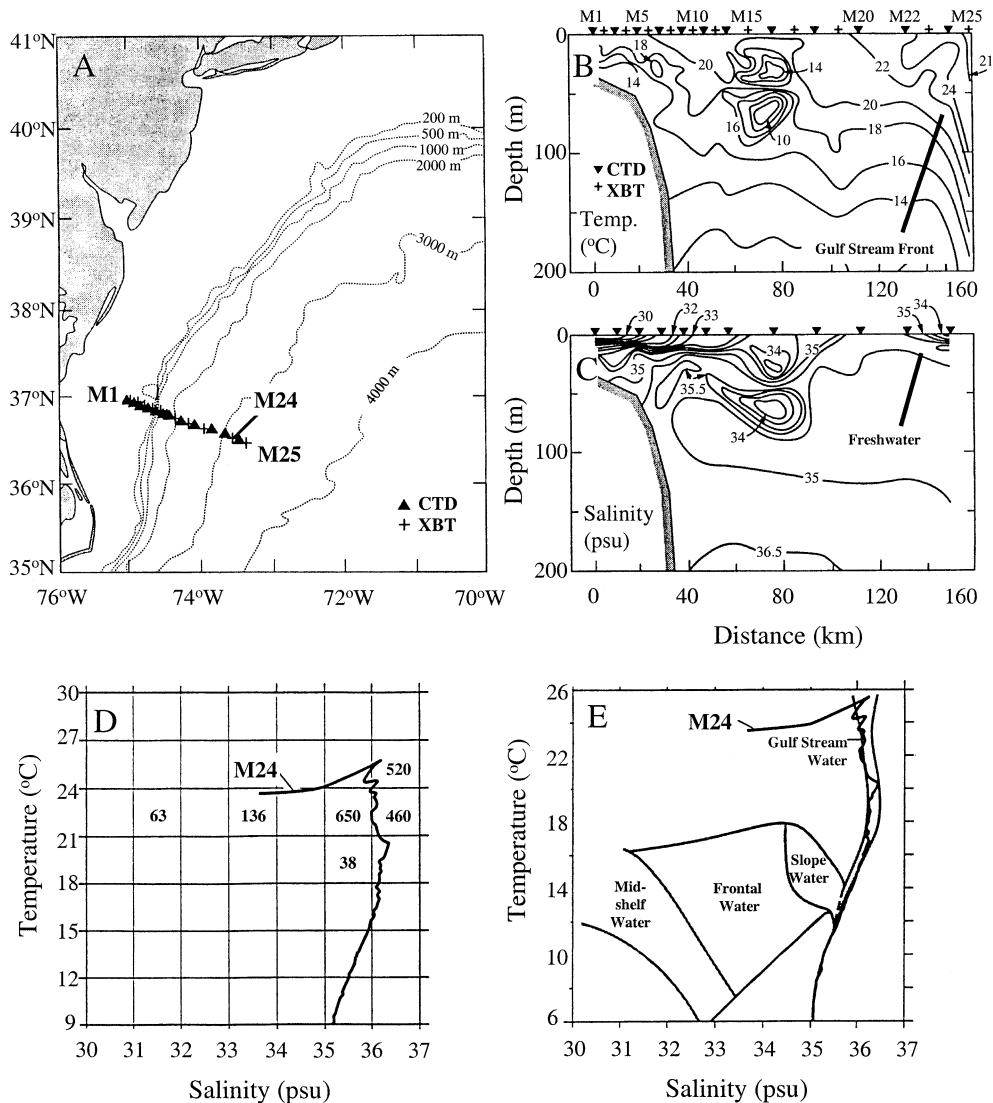


Fig. 5. (A) Location of hydrographic stations sampled during MASAR cruise 2 (Csanady and Hamilton 1988). (B) Section of temperature and (C) salinity along the MASAR transect extending from the southern portion of the outer NEUSCS to the edge of the Gulf Stream. (D) Volumetric TS diagram of water found over the SEUSCS during May (from Atkinson et al. 1983). The number in each square gives the volume (km^3) of SEUSCS water with TS characteristics falling within the box's range. Also shown is the TS profile of water encountered at station M24. The near-surface portion of the M24 trace overlaps with data from the SEUSCS. (E) TS regimes of various water masses found in the southern portion of the NEUSCS during late May and early June 1984 (from Churchill et al. 1993). TS profile from station M24 is overlain. The near-surface portion of the M24 trace does not overlap with data from the NEUSCS.

ducted on only the 11 drifters that entered WCR circulation west of 65°W (Fig. 2B). WCR streamer speed was calculated as the average of a drifter's speed while in a WCR streamer. The resulting ensemble of drifter speeds was used to specify $p_3(t)$ in the manner as described above for $p_2(t)$.

Transport time along the NEUSCS edge, $p_4(t)$: Transport speed along the NEUSCS edge were calculated from EPA-DWDS drifters that exited WCR streamer circulation and moved to the west-southwest parallel to the NEUSCS edge ($n = 8$). For each drifter, along-shelf edge speed was calculated as its average speed while it traveled parallel to the shelf edge. The speed ensemble was used to specify $p_4(t)$ in the manner as described above for $p_2(t)$.

Mortality: Following Peterson and Wroblewski (1984), larval fish survival probability was modeled as an exponential function. The decline of a population with an initial N_0 individuals can be expressed as $N(t) = N_0 e^{-zt}$, where $N(t)$ is the number of individuals surviving to time t and z is the instantaneous larval mortality rate. The survival probability function was expressed relative to the overall survival likelihood (for all transit times) as

$$S(t) = e^{-zt} / \left[\int_0^\infty p_{1-N}(t) e^{-zt} dt \right] \quad (7)$$

Scenario-specific mortalities were calculated from the slope of the natural logarithm-transformed age distribution (Ricker 1975). For *Xyrichtys novacula* larvae (the July and August 1988 scenarios), mortality rate was estimated using

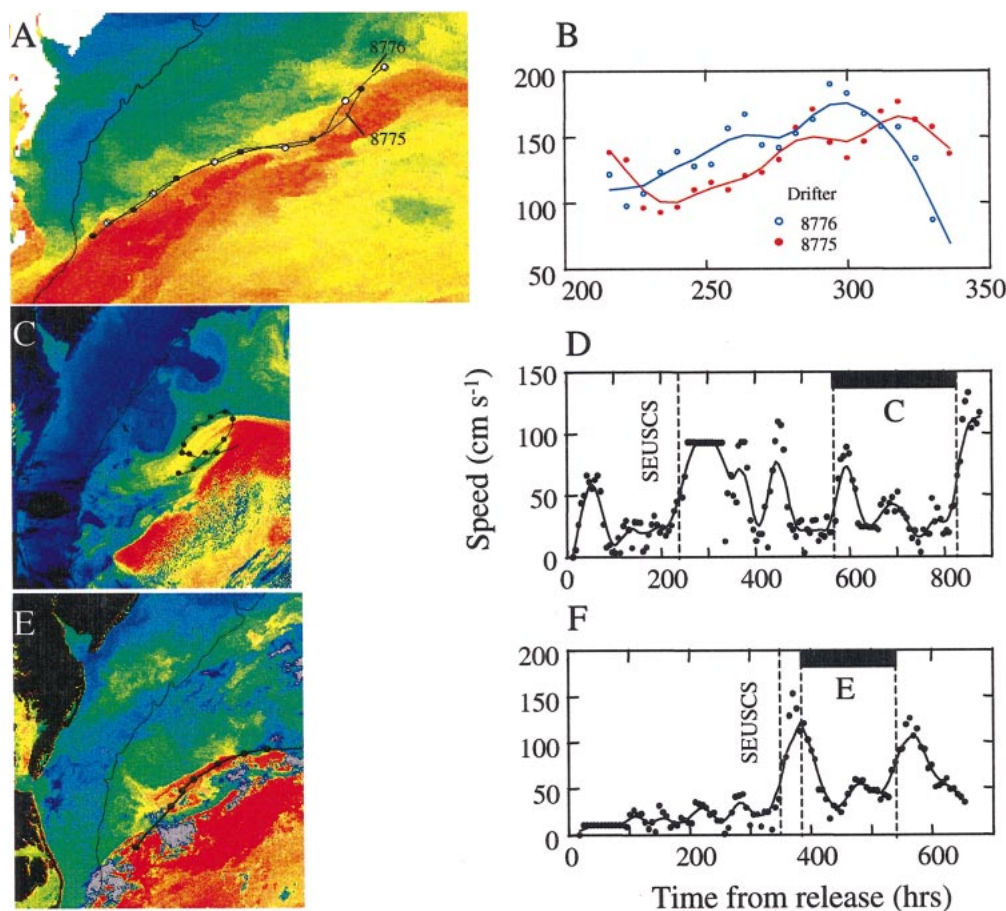


Fig. 6. (A) Tracks of two FRED drifters released in the northern SEUSCS. Track time is coincident with the underlying satellite SST image. Circles indicate locations at 24-h intervals. (B) Speed time series derived from the two drifter tracks shown in panel A. Both drifters moved east-northeastward in association with the Gulf Stream front at speeds between 100 and 200 cm s^{-1} . (C, E) Tracks of two MMS-CHFS drifters released in Raleigh Bay. Both drifters exit the SEUSCS in association with the Gulf Stream; however, both are detrained from the main Gulf Stream current downstream of Cape Hatteras in association with meander crests. Both were then re-entrained. Track time is coincident with the underlying satellite SST images. Circles indicate locations at 24-h intervals. (D, F) Speed time series derived from the two drifter tracks shown in panels C and E, respectively. Time at which drifter leaves SEUSCS is indicated by vertical line labeled SEUSCS. Periods that correspond to positions and images shown in panels C and E are indicated by black bars.

data presented in Hare and Cowen (1991). Estimated instantaneous mortality was $0.12 \pm 0.01 \text{ d}^{-1}$ (mean \pm SE, $r^2 = 0.89$). For *P. saltatrix*, the age distributions of *P. saltatrix* larvae collected in the SEUSCS during April 1989 and March 1990 were used (Hare and Cowen 1996, unpubl. data). Estimated *P. saltatrix* mortality was $0.11 \pm 0.02 \text{ d}^{-1}$ ($r^2 = 0.67$).

Analysis of model results: The probability model estimated larval age distributions for three scenarios in which SEUSCS-spawned larvae were collected over the outer NEUSCS. Shima (1989) reported the ages of SEUSCS-spawned *P. saltatrix* pelagic juveniles that were collected in the vicinity of the Hudson Canyon during June 1988. Hare and Cowen (1991) reported the ages of expatriated *X. novacula* larvae that were captured in the Hudson Canyon region during July and August 1988 (only larvae collected at the outer three stations of the cross-shelf sampling grid were included in the comparison with model results).

Sensitivity analyses were conducted to evaluate the effect

of various model parameters on predicted larval age distributions. Larval mortality rate (z) was varied for each of the three time periods modeled: June, July, and August 1988. Values of z used in the sensitivity analyses were 0.05, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 1.0 d^{-1} , which covers the range of larval mortality rates commonly reported (Peterson and Wroblewski 1984; Morse 1989). Distance of the route, mean speed, and standard deviation of speed were also varied for each of the three time periods modeled. Values were varied by ± 10 , 25, 50, 75, and 100%. Values were varied as an ensemble; for example, all distances were increased by 10% or all speeds were decreased by 25%. The number of observed ages that were in the lower and upper 5% tails of each modeled distribution was then calculated.

Results

Entrapment of water from the SEUSCS into the Gulf Stream—Upon release on the SEUSCS, most drifters moved to the northeast ($n = 10$); however, some initially moved to

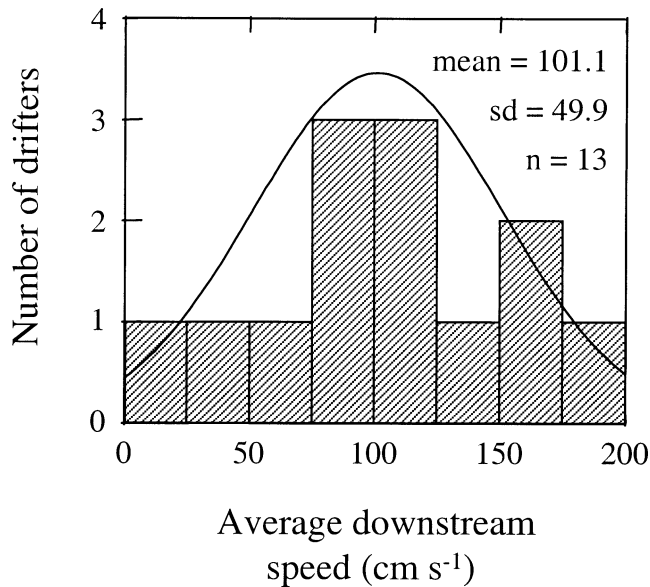


Fig. 7. Distributions of Gulf Stream-associated speeds for drifters released on the SEUSCS.

the southwest before turning to the northeast ($n = 3$) (Fig. 2A). All drifters eventually exited the SEUSCS into the vicinity of the western Gulf Stream front and exit speeds were typical of reported Gulf Stream and Gulf Stream frontal velocities (~ 100 cm s⁻¹; Fig. 4A; Glenn and Ebbesmeyer 1994a, 1994b). No particular SST feature could be linked to the process of Gulf Stream entrainment owing to cloud cover during entrainment events. Defining 75°W as the eastern extent of the SEUSCS, the mean drifter residence time on the outer SEUSCS was 8.5 d (Fig. 4B).

SEUSCS water at the Gulf Stream's edge north of Cape Hatteras—The temperature distribution along the MASAR transect (Fig. 5A) showed the Gulf Stream front approximately 130 km east of the shelf edge (Fig. 5B). A surface layer of relatively fresh water extending to a depth of about 10 m was situated along the western edge of the Gulf Stream front (station M24; Fig. 5C). TS characteristics identified this layer as entrained SEUSCS water and were within the range of TS properties of water found on the SEUSCS during May (Fig. 5D) but were far outside the range of TS properties of NEUSCS and slope water during May–June (Fig. 5E).

Estimates of geostrophic velocity normal to the transect indicated that this entrained SEUSCS water was traveling at

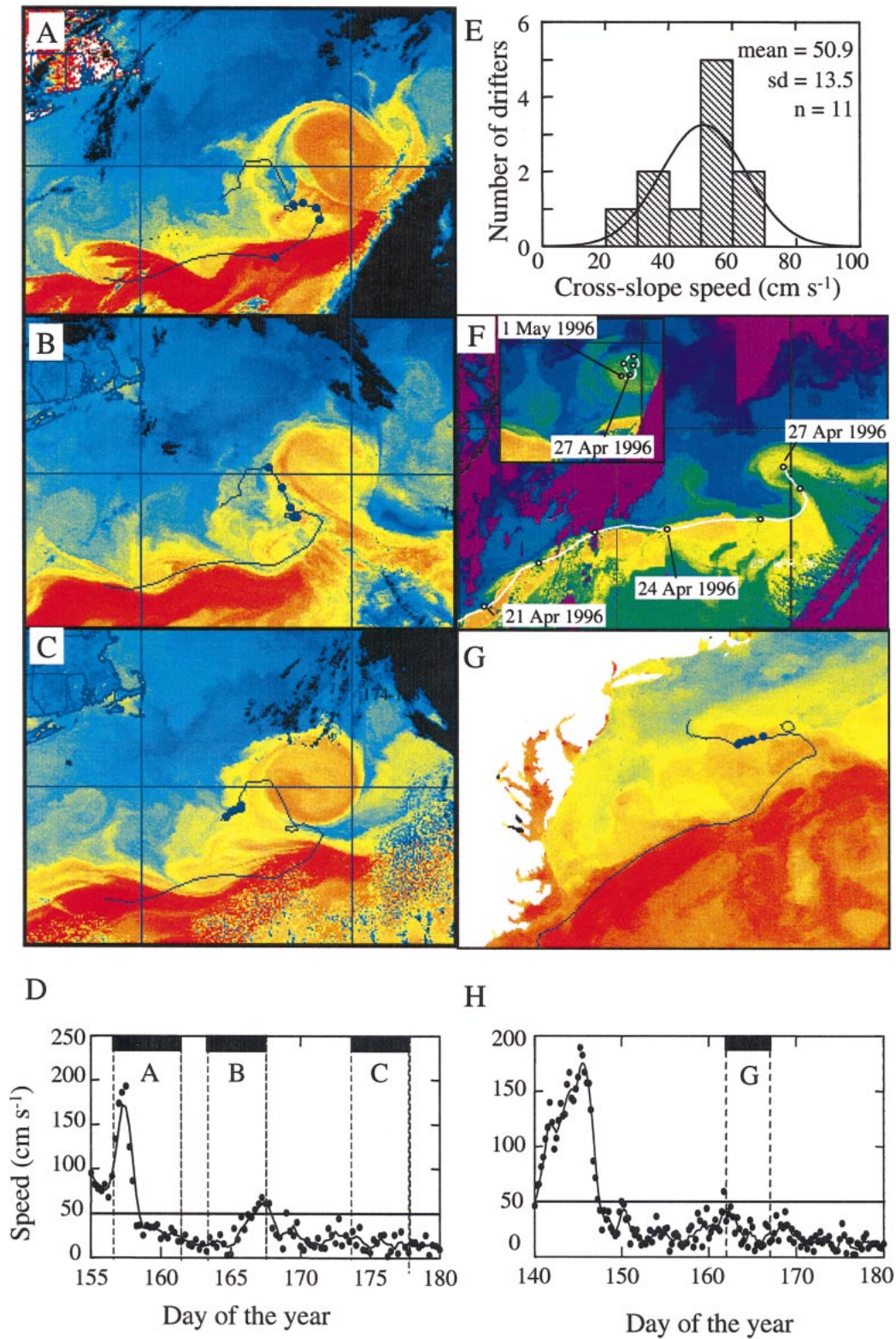
a speed of roughly 200 cm s⁻¹. Between stations M23 and M24, estimated geostrophic velocity at 5 m was 195 cm s⁻¹ (750 m reference depth); between stations M24 and M25, estimated geostrophic velocity at 5 m was 211 cm s⁻¹ (330 m reference depth).

Drifter tracks supported the geostrophic estimate of SEUSCS water speed along the edge of the Gulf Stream but indicated that the path of this water can be complex. Most drifters entrained from the SEUSCS into the Gulf Stream remained in the Gulf Stream frontal region after passing Cape Hatteras (Fig. 6A). The speed of all drifters exceeded 100 cm s⁻¹ at some point downstream of 75°W (Fig. 6B), and several traveled in excess of 200 cm s⁻¹. However, few of the drifters maintained rapid downstream transport for extended periods of time; many drifters either slowed in the Gulf Stream or left and then reentered the Gulf Stream current (Fig. 6C–F). Detrainment of drifters from the main Gulf Stream current occurred to both sides of the Gulf Stream (e.g., into the slope region between the Gulf Stream and the NEUSCS edge, and into the Sargasso Sea) and typically occurred near the crest of a meander. Similar detrainment and entrainment of deeper RAFOS drifters has been described by Bower and Rossby (1989). As a result of the detrainment from and subsequent re-entrainment into the main Gulf Stream current, the average speed between 75 and 71°W was 101.1 cm s⁻¹ (Fig. 7).

Cross-slope movement of water from the Gulf Stream edge to the NEUSCS edge—Evidence of WCR-associated transport of water from the edge of the Gulf Stream to the shelf edge of the NEUSCS is frequently seen in satellite-derived SST images (Joyce et al. 1984; Evans et al. 1985). Images from June to August 1988 provide relevant examples of WCR streamers (Fig. 3), covering the period during which *P. saltatrix* and *X. novacula* larvae were captured near Hudson Canyon (Shima 1989; Hare and Cowen 1991, 1996). These SST images show a series of rings moving southwestward through the NEUSCS slope region, each with a band of entrained Gulf Stream water.

Drifter tracks from the EPA-DWDS study show evidence of cross-slope transport in WCR streamers. Upon release over the NEUSCS upper slope, most of the 58 drifters moved to the southwest. All were eventually entrained into the Gulf Stream. Once in the Gulf Stream, these drifters moved northeastward at the edge of the Gulf Stream, similar to the drifters released in the SEUSCS (Fig. 2B). Eleven of the EPA-DWDS drifters were incorporated into WCR streamers west of 65°W, some directly from the Gulf Stream

Fig. 8. (A–C) Track of an EPA-DWDS drifter released off the shelf of the NEUSCS. The drifter initially moved to the southwest before becoming incorporated into the flows associated with the Gulf Stream in the vicinity of Cape Hatteras (not shown). The drifter traveled east-northeastward with the Gulf Stream but was then detrained in association with a Gulf Stream meander. Within 4 d, the drifter was entrained into the cross-slope circulation of a WCR streamer. After crossing the Slope Sea, the drifter exited the WCR streamer and moved westward parallel to the NEUSCS edge. In panels A, B, and C, red indicates warmer water and blue indicates cooler water. The black line shows the entire track. Black circles show daily positions concomitant with the 5-d composite image. (D) Speed time series derived from the drifter track shown in panels A–C. The period corresponding to panels A–C are indicated by black bars. (E) Distribution of cross-slope speed associated with the WCR streamer for the ensemble of 11 EPA-DWDS drifters. (F) The track of a drifter released off of South Florida in January 1998. Once north of Cape Hatteras, the drifter moved northeastward with the Gulf Stream. The drifter was then



incorporated into the interior of a WCR upon formation, where it remained for 30 d. Note the difference in the fate of this drifter relative to those that are transported across the slope in association with WCR streamers (Fig. 8A–C). Temporal series of track times are coincident with the underlying satellite SST images. Circles indicate locations at 24-h intervals. Red indicates warmer water and blue indicates cooler water. (G) Track of a FRED drifter released in the northern SEUSCS in May 1987. The drifter moved across the slope region to the NEUSCS edge in association with a Gulf Stream discharge. The black line shows the entire track. Black circles show daily positions concomitant with the 5-d composite image. (H) Speed time series of FRED drifter shown in panel G. Period corresponding to panel G is indicated by a black bar.

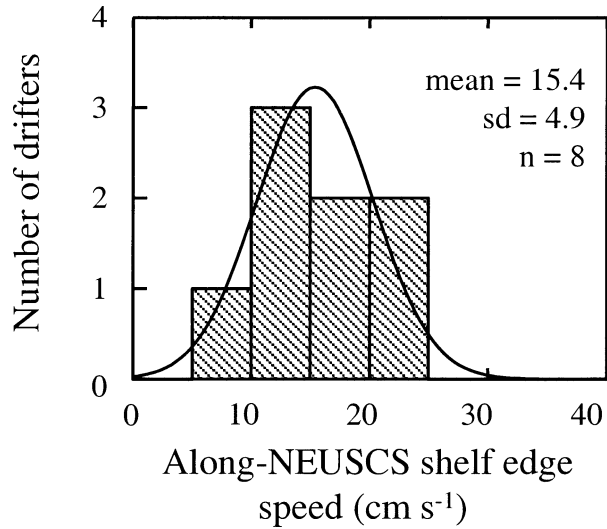


Fig. 9. Distribution of along-NEUSCS speeds for EPA-DWDS drifters that crossed the slope region in association with WCR streamers and were ejected from WCR circulation in the vicinity of the NEUSCS edge.

front and others after detrainment from the Gulf Stream in association with a Gulf Stream meander (Fig. 8A,B). Following entrainment into a WCR streamer, transport across the Slope Sea was direct, with an average speed of 50.9 cm s⁻¹ (Fig. 8D,E).

Cross-slope transport of water in WCR streamers was distinct from the circulation of the ring itself. An example was provided by a drifter released off of the Florida Keys that traveled along the northern edge of the Gulf Stream during April 1998 (Fig. 8F). This drifter moved into a meander crest as a WCR formed and remained in the anticyclonic circulation of the ring for at least 30 d. Such transport would trap larval fish in the ring until either the ring decayed or larvae developed the ability to actively move out of the ring.

One drifter was ejected from the Gulf Stream near the crest of a meander and moved across the Slope Sea to the NEUSCS edge within a filament of discharged Gulf Stream water (Fig. 8G). While in the filament, the drifter's cross-slope speed was slower (~25 cm s⁻¹) than typical cross-slope speeds within WCR streamers (~50 cm s⁻¹) (Fig. 8D,

Table 2. Summary of specific transport distances used for each transport segment for parameterization of the probability model. Transport distances were determined by tracing the proposed transport route (Fig. 1) on satellite-derived SST images and extracting distances (Fig. 3). Mortality values used in the model are also provided. Mortality rates were determined from abundance-at-age data (Ricker 1975).

Transport model segment	Segment No.	Transport distance (km)		
		Jun 88	Jul 88	Aug 88
Gulf Stream	2	668	553	455
Cross-slope	3	280	313	285
Along-NEUSCS	4	172	0	0
Mortality rate (α)		0.11	0.12	0.12

H). This observation indicates that although the probability of cross-slope transport in a Gulf Stream discharge decreases from Cape Hatteras northward (Churchill and Cornillon 1991b), such transport can occur north of Delaware Bay.

Expulsion of water from a WCR at the NEUSCS edge—Drifter tracks indicate that the probability of water in a WCR streamer being ejected from the ring into the shelf edge region is high. Eight of the 11 EPA-DWDS drifters left the WCR circulation near the NEUSCS edge and moved west-southwestward (Fig. 8C). The remaining three drifters continued around the WCR and were eventually re-entrained into the Gulf Stream current. Once along the NEUSCS edge, all eight drifters initially moved to the west-southwest with an average speed of 15.4 cm s⁻¹ (Fig. 9).

Probability model—The probability model used distances determined from SST imagery (Fig. 3, Table 2), mortality rates calculated from abundance at age (Table 2), and speeds determined from drifter statistics (Table 3). One potential concern with the model was the small number of observations used to determine the speed components. However, the values reported here agree with observations from a number of studies that used a variety of techniques (Table 4). Thus, we have confidence in the values used here.

Distributions of observed larval ages closely matched larval age distributions derived from the probability model (Fig. 10). Means of observed larval ages were within 4 d of mean modeled ages, and standard deviations of observed and modeled ages were within 3.5 d (Fig. 10). Patterns in observed larval age distributions between sampling times were also replicated in the modeled transit time distributions. Maximum modeled and observed ages were of *P. saltatrix* caught in June 1988 (Fig. 10). The older modeled ages of this scenario resulted from the length of the along-NEUSCS component (Fig. 3, Table 2). Minimum modeled and measured ages were for *X. novacula* caught in August 1988 (Fig. 10). The young modeled ages resulted from shorter Gulf Stream and cross-shelf distances and from the absence of an along-NEUSCS segment (Fig. 3, Table 2).

Larval mortality was an important component of the model (Fig. 11). At the lowest mortality ($\alpha = 0.05$), the means and standard deviations of the modeled ages exceeded the means and standard deviations of observed larval ages (Fig. 11, top row). As larval mortality increased, the mean and standard deviation of model ages decreased. Model results were generally consistent with observations over a range of larval mortality from 0.1 to 0.3 (Fig. 11), which agrees with the mortality rates estimated in this study (Table 2) and with mortality rates reported in the literature (Peterson and Wroblewski 1984; Morse 1989).

Sensitivity analyses also demonstrated that the best fit between modeled and observed larval ages occurred at model distance and speed values within 25% of calculated values (Tables 2, 3). Standard deviations in speed had little effect on modeled distributions (Fig. 11, second row). For transport distances and mean speeds, changes of ± 50 , 75, and 100% resulted in modeled larval ages that were different than observed larval ages (Fig. 11, third and fourth rows); a large number of observed ages fell within the lower and upper 5%

Table 3. Summary of general transport speed values used for each transport segment for parameterization of the probability model. Transport speed values were derived from drifter tracks analyzed in combination with SST images. Segment numbers refer to Fig. 1. SEUSCS residence time is the residence time of a drifter on the SEUSCS. Along-NEUSCS speed is the speed along the NEUSCS shelf/slope frontal region.

Transport model segment	Segment Number	Mean	SD	Sample size	Source
SEUSCS residence time	1	8.5 d	6.4	12	Fig. 4
Gulf Stream speed	2	101.1 cm s ⁻¹	49.9	13	Fig. 7
Cross-slope speed	3	50.9 cm s ⁻¹	13.5	11	Fig. 8
Along-NEUSCS speed	4	15.4 cm s ⁻¹	4.9	8	Fig. 9

tails of the modeled distributions. Greater transport speeds and lesser transport distances had less of an effect on the modeled age distribution of *X. novacula* larvae in July and August 1988, likely because larvae cannot be transported to the NEUSCS edge much faster.

One potential concern with the model is that the transport distances are for one point in time; yet, as larvae move over the route, transport distances change. If we accept the distances from June 1988 (July 1988) to represent the maximum change that could have occurred in transport distances for larvae that were collected in July 1988 (August 1988), the sensitivity analysis indicates that modeled ages would not be greatly affected by changing route length because distance varied by less than 25% between months (Table 2; Fig. 11, bottom row).

Discussion

Drifter tracks and hydrographic data provide direct physical evidence of the proposed route by which larvae spawned in the northern SEUSCS are entrained into the Gulf Stream, transported to the northeast, regularly incorporated in WCR streamers, transported across the slope region and released along the NEUSCS edge. All drifters released in the northern SEUSCS were entrained into Gulf Stream flows and were carried rapidly to the northeast along the edge of the Gulf Stream. Hydrographic data confirmed the presence and speed of SEUSCS water along the edge of the Gulf Stream north

of Cape Hatteras. Similar observations of SEUSCS water along the western Gulf Stream front north of Cape Hatteras have been reported recently (Grothues and Cowen 1999; Hare et al. 2001). Drifters were incorporated in WCR streamers from the edge of the Gulf Stream and then released from ring circulation in the vicinity of the NEUSCS edge.

All three observed larval age distributions fell within modeled larval age distributions, which were based on drifter-derived transport speed distributions and SST image-derived transport distances. Sensitivity analyses found that small changes in model parameters changed the modeled distributions to more closely match observed distributions. The coincidence of actual and modeled ages supports the assertion that the larvae collected on the NEUSCS edge traversed the proposed route, and that the statistics of transport speed over the route's segments, derived from multiple years of drifter track data, are relatively stationary (not changing widely over time).

The probability of SEUSCS-spawned larvae moving over the proposed route is largely dependent on WCR-Gulf Stream interactions. All drifters released in the northern SEUSCS were entrained into Gulf Stream flows. Approximately 75% of drifters moving in WCR streamers were released from streamers along the NEUSCS edge and traveled southwestward along the shelf edge. Entrainment into a WCR streamer is the most variable step. Although none of the drifters released in the northern SEUSCS were incorporated into WCR streamers, only two passed WCRs. One

Table 4. Speed estimates for the various components of the proposed transport route as reported in other studies. The agreement between velocities derived in this study (Table 3) and those of other studies provide confidence in the speed estimates used in the probability model. Additionally, Nof (1988) indicated that propagation rate around a WCR in a streamer equals one-half of the particle speed along the upstream front of the Gulf Stream. Based on the Gulf Stream speeds shown in this table, cross-slope velocities in WCR streamers would be 20–75 cm s⁻¹, which agrees with the speed derived from drifter tracks (Fig. 8E). ADCP is Acoustic Doppler Current Profiler.

Transport model segment	Segment No.	Estimated speed (cm s ⁻¹)	Method (depth of measurement, m)	Source
Gulf Stream	2	40–150	PEGASUS (0)	Halkin and Rossby 1985
	2	100–130	ADCP (50)	Hummon and Rossby 1998
	2	40–130	ADCP (60)	Pierce and Joyce 1988
	2	30–150	ADCP (100)	Joyce et al. 1990
Cross-slope	3	51.1 (SD = 26.7)	SST (0)	Zheng et al. 1984
	3	40–80	ADCP (50)	Hummon and Rossby 1998
Along-NEUSCS	4	16.4 (SD = 7.8)	Drifters	Lozier and Gawarkiewicz 2001
	4	10.2 (SD = 8.1)	Current meter (10)	Aikman et al. 1988
	4	12.4 (SD = 10.6)	Current meter (10)	Beardsley et al. 1985

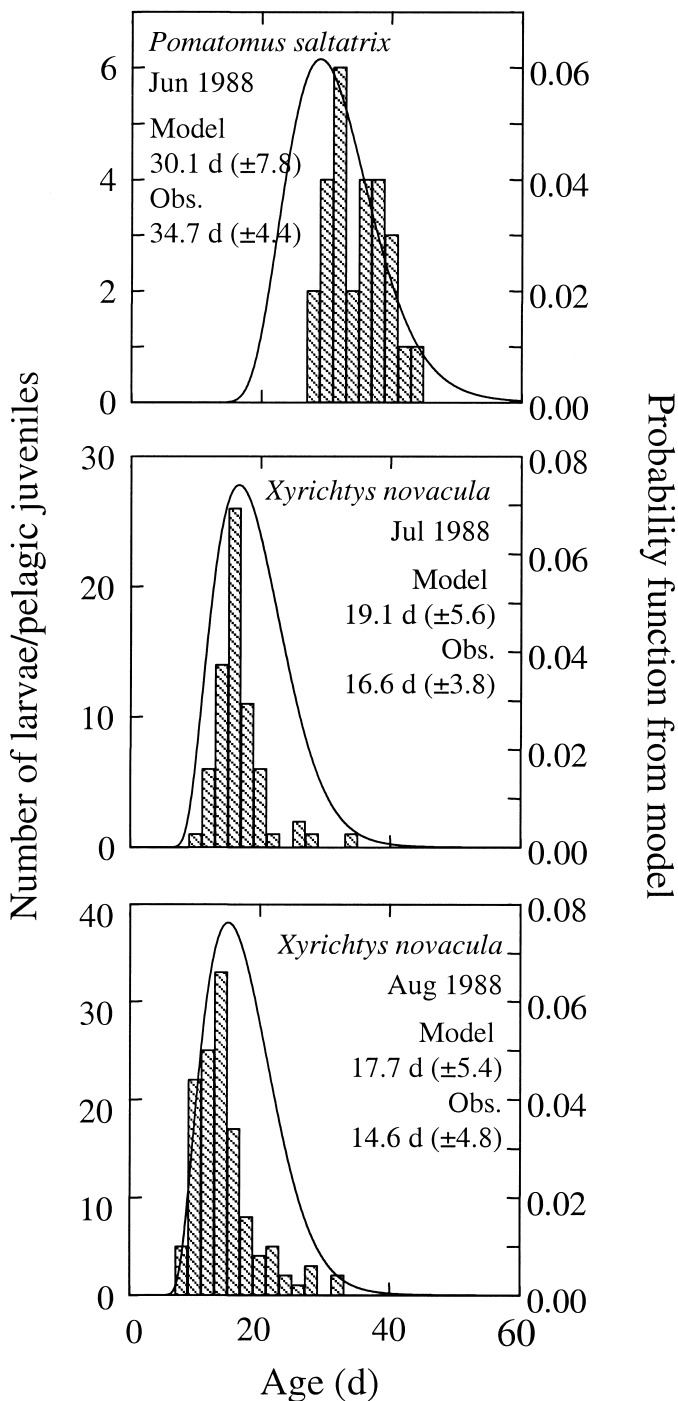


Fig. 10. The results of a probability model (line) compared to observed larval ages (histogram). Modeled and observed mean and standard deviation are provided. In all cases, the model results are very similar to observed ages, supporting the hypothesis that the larvae were transported from the SEUSCS to the NEUSCS edge via the transport route proposed by Hare and Cowen (1991, 1996) and Cowen et al. (1993) (Fig. 1).

interpretation is that the proposed transport route does not occur. An alternative interpretation is that incorporation into WCR streamers occurs at some probability <1 , and is fundamentally dependent on the presence of a WCR. This latter interpretation is supported by the tracks of the EPA-DWDS drifters. These drifters moved northeastward in the Gulf Stream similar to the drifters released in the northern SEUSCS. During the period of the EPA-DWDS study, WCRs were prevalent (Berger et al. 1996) and 11 of 58 drifters were incorporated into WCR streamers west of 65°W , indicating an approximate 20% probability of incorporation into a WCR. These data indicate that entrainment from the Gulf Stream into WCRs depends, first, on the presence of a WCR and, second, on the location of a water parcel (or drifter) relative to the spatial structure of the WCR–Gulf Stream interaction (Hummon and Rossby 1998).

Because entrainment into a WCR streamer is the most variable component of the proposed transport route, the supply of larvae from the SEUSCS to the NEUSCS edge is largely controlled by entrainment into a WCR streamer. This conclusion is consistent with the strong correlation between WCR streamer activity and recruitment of SEUSCS-spawned *P. saltatrix* to NEUSCS estuarine nursery habitats (Hare and Cowen 1996), and the correspondence between the location of WCRs and the occurrence of SEUSCS-spawned larvae along the NEUSCS edge north of Delaware Bay (Hare and Cowen 1991; Cowen et al. 1993). Larval supply of a wide variety of warm-temperate species to juvenile habitats north of Cape Hatteras might be controlled by the cross-slope transport in WCR streamers (Atlantic menhaden, *Brevoortia tyrannus*; American eel, *Anguilla rostrata*; conger eel, *Conger oceanicus*; crevalle jack, *Caranx hippos*; *C. ocellatus*; white mullet, *Mugil cephalus*; striped mullet, *Mugil curema*; butterflyfish, *Peprius triacanthus*). Because WCRs are a universal element of western boundary current systems (Olson 2001), the described transport route could be an important source of larval supply to more poleward continental shelves throughout the world's oceans.

Discharges of water from Gulf Stream meanders also appear to be an important mechanism of larval movement from the Gulf Stream into the slope region of the NEUSCS (Hare et al. 2001), but the likelihood of transport to the NEUSCS edge via this mechanism decreases northward from Cape Hatteras (Churchill and Cornillon 1991b). Discharges of Gulf Stream water might explain the recruitment of SEUSCS-spawned bluefish to NEUSCS estuaries in years of low WCR streamer activity (Hare and Cowen 1996). One drifter in this study provided an example of cross-slope transport in discharged Gulf Stream water. If slower cross-slope transport were indicative of all discharges of Gulf Stream water, then fish arriving at the NEUSCS edge via Gulf Stream water discharges would be older (slower speed) and fewer in number (more cumulative mortality) than those carried across the slope in WCR streamers.

The short resident times of drifters released in the northern SEUSCS indicate that a majority of larvae spawned in this region might be lost to the Gulf Stream. Drift bottle studies (Barans and Roumillat 1976) and modeling studies (Checkley et al. 1999; Hare et al. 1999) indicate that the residence time of surface water in the northern SEUSCS is short and

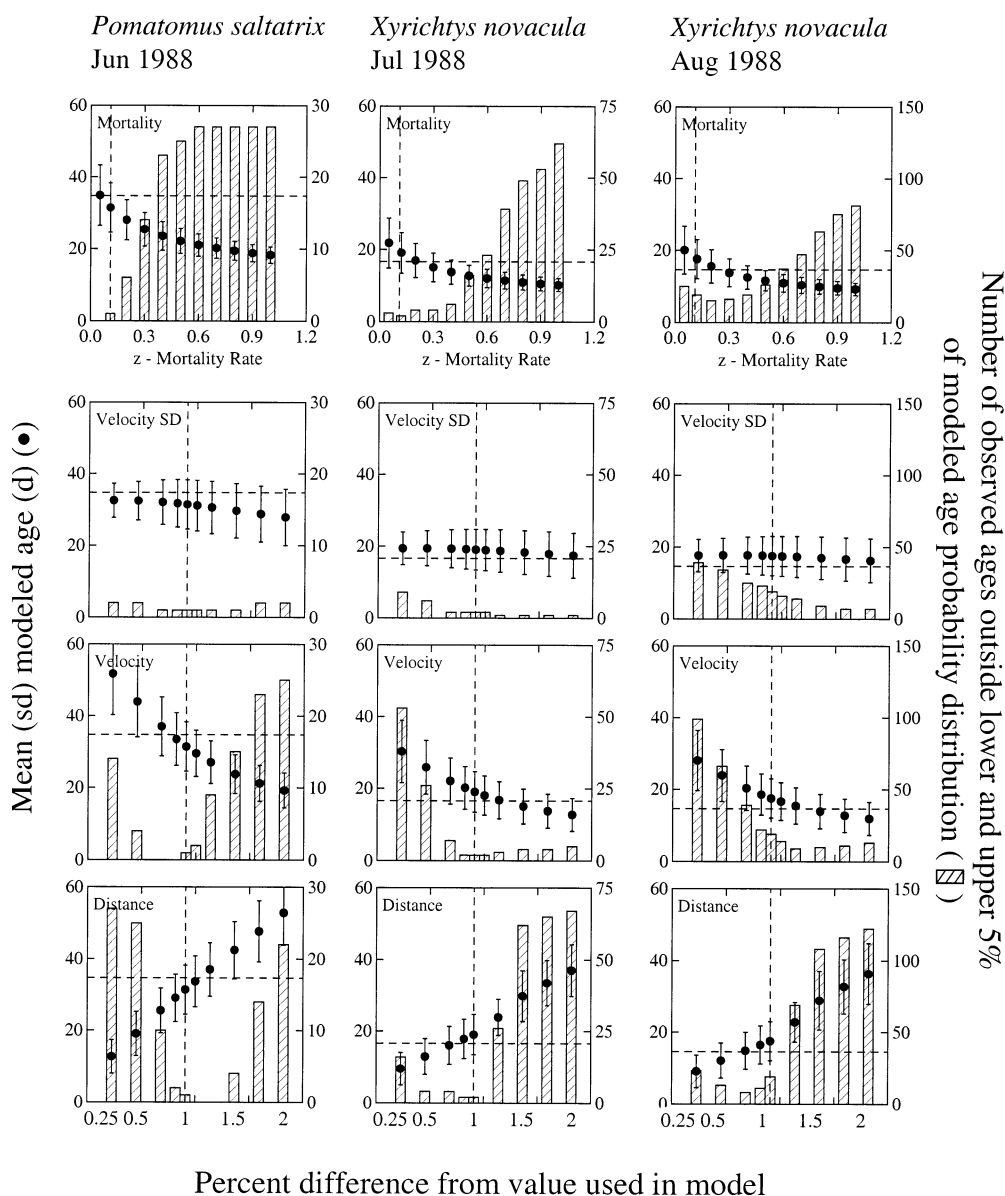


Fig. 11. The sensitivity of model results to variations in larval mortality (z) (first row), standard deviation of transport speed (second row), mean transport speed (third row), and transport distance (fourth row). Columns are the results for the three different time periods modeled: June 1988, July 1988, and August 1988. The observed mean is indicated by a horizontal dotted line for comparison to the model results. Values used in the model (Fig. 10) are indicated by vertical dotted lines. The model mean (\pm SD) from the sensitivity analyses are shown by black circles. The number of observed ages falling within the 5% upper and lower tails of the modeled distributions are shown as the histograms.

decreases with distance from shore. Blanton and Pietrafesa (1978) estimated a complete flushing time of Onslow Bay of 60 d, with bottom waters moving in and surface waters leaving. Govoni and Spach (1999) and Grothues and Cowen (1999) estimated large fluxes of larvae off the SEUSCS. Future work should attempt to quantify loss relative to recruitment of species that spawn on the SEUSCS and depend on SEUSCS nursery habitats.

Drifter tracks also support the idea that the transport of larvae onto the NEUSCS *at the surface* is rare. Gawarkiewicz et al. (1996) noted high-salinity slope water above the pycnocline on the outer shelf (between 80- and 100-m iso-

baths) and identified the potential forcing mechanisms as wind and WCRs. No drifters examined here and only a few of the total EPA-DWDS drifter set crossed the 100-m isobath (Berger et al. 1996; Dragos et al. 1996). Yet, many fish larvae cross from the slope onto the NEUSCS, which indicates that the physical mechanisms of cross-frontal exchange predominantly operate below 10 to 15 m. Cowen et al. (1993) proposed that on-shelf movement of some species occurred via an ontogenetic deepening of larval vertical distributions coupled with slope water intrusions along the summertime NEUSCS thermocline (Flagg et al. 1994). For species that cross onto the NEUSCS at the surface (e.g., bluefish, *P. sal-*

tatrix; white hake, *Urophycis tenuis*), Hare and Cowen (1996) and Hare et al. (2001) proposed active horizontal swimming as the mechanism. Drifter tracks indirectly support both mechanisms of cross-shelf transport by demonstrating that passive, surface slope water to NEUSCS transport is rare, but does occur (see Gawarkiewicz et al. 1996).

Larval mortality played an important role in the predicted transport times, influencing both the mean and standard deviation of predicted ages. Generally, larval mortality values from 0.1 to 0.3 resulted in predicted transport times (and standard deviations) that most closely matched observed ages, and these values are similar to observed larval mortality rates (Morse 1989). Inclusion of larval mortality is clearly important in estimating connectivity between local populations (*sensu* Cowen et al. 2000).

In a recent review, Epifanio and Garvine (2001) discussed the importance of local wind and buoyancy forcing in the transport of larval fish and invertebrates along the eastern coast of the United States. This present study and others (Hare and Cowen 1991, 1996; Cowen et al. 1993; Lee et al. 1994; Stegmann and Yoder 1996; Govoni and Spach 1999) indicate that processes related to the region's western boundary current are also involved in larval transport, particularly on the outer shelf and where the shelf is narrow. A difficulty facing the advancement of larval transport studies in this region, however, is a coupled understanding of the role of locally and remotely forced processes in affecting larval transport.

The approach developed here allows hypotheses regarding larval fish transport to be tested. If observed larval ages appeared at very low probabilities in the modeled age distribution, then transport along the proposed route could be deemed unlikely. Although there are valid criticisms of using Lagrangian measurements to follow larval fish (e.g., slippage of drifter owing to wind, drifter tracking fixed depth versus larval fish moving vertically), the large-scale view of larval transport, both subjective and objective, provides valuable insights into larval transport processes. A number of studies have used Lagrangian measurements, both actual and modeled, to examine the mechanisms and outcomes of larval transport (e.g., Pepin and Helbig 1997; Hare et al. 1999; Cowen et al. 2000). Similarly, probabilistic approaches have provided insights into the population-level consequences of larval transport (Levin 1983; Schultz and Cowen 1994). As these techniques continue to develop and are coupled with field observations of larval fish distribution and abundance, the ability to test hypotheses regarding larval transport mechanisms will increase, thereby furthering our understanding of the importance of larval transport in the ecology of marine populations.

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