

## Flux of larval fish around Cape Hatteras

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### *Abstract*

Convergence of shelf water flows from the Middle and South Atlantic Bights (MAB and SAB) upon Cape Hatteras, North Carolina, presents a potential barrier to the exchange of fish larvae between bights. Impinging water often turns northeastward with the Gulf Stream, and larvae of both cool temperate and warm temperate/subtropical shelf fishes suffer expatriation. Transient oceanographic features exist, however, facilitating shelf retention, cross-bight exchange, and return of expatriated larvae. The impact of these features is mitigated by specific distribution with relation to hydrography, resulting in a selective permeability of this barrier. Dynamic oceanography may result in dynamic recruitment success. We measured the springtime (1996) flux of seven larval fish species assemblages across the confluence by coupling measured water mass/depth specific larval fish concentration with water mass transport values obtained from an extensive moored instrument survey. Strong flows of shallow shelf water from the MAB to the SAB dominated transport of MAB-spawned larvae even for groups with highest concentrations in waters without strong net flows. Most of these larvae passed from the MAB or the open sea into the study region shelf and from there into the SAB. Net flow of SAB water into the convergence retained SAB-affiliated larvae arriving from the south, but nearshore MAB flows transported low numbers from the MAB to the SAB. The importance of this is tied to the unknown point of introduction of these SAB larvae to MAB waters (e.g., well north of the confluence), but northward exchange of SAB-spawned fish was always prevented along the southern MAB shelf.

The flow of shelf water converging upon Cape Hatteras, North Carolina, from the Middle and South Atlantic Bights

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(MAB and SAB) responds to oceanographic and meteorological forcing (Lee and Atkinson 1983; Pietrafesa et al. 1994). Dynamic forcing results in various scenarios of mixing, offshore flow, or penetration of water from one bight into the other (Gawarkiewicz et al. 1992; Flagg et al. 1994; Pietrafesa et al. 1994). Larvae of nearshore fishes transported to the Cape Hatteras Confluence (CHC) should therefore experience variation in their retention, exchange, or export from the bights. Owing to the different origins of the impinging water masses, the convergence corresponds with a major break between cool and warm temperate faunal assemblages (Briggs 1974), the constituency of which may be influenced by the amount of larval exchange between them.

The early life history of most coastal marine fishes consists of a short pelagic egg phase followed by a period of larval development lasting several weeks to months and culminates in a juvenile stage that may include strong swimming capability or settlement and orientation to specific benthic features. That the planktonic period may decouple the year class strength of marine fish populations from spawning stock biomass has been recognized for a long time (e.g., Hjort 1914). Instead, interannual variation in recruitment success may be set by interactive processes such as predation, starvation, and transport during the pelagic early life stage (Sissenwine 1984). Along the eastern U.S. seaboard,

the role of transport in influencing recruitment success is under study for several species. Research has demonstrated, for example, that recruitment success for bluefish (*Pomatomus saltatrix*) is influenced by the flux of larvae from the SAB to the MAB in timing with the occurrence of superior forage there (Nyman and Conover 1988; Juanes et al. 1994). Similar exchange may benefit the recruitment of other species with similar life histories (notably *Sarda sarda*, *Scomber scombrus*, some carangids and bothids), but exchange between the bights may be detrimental to recruitment of species with narrow physiological temperature tolerances. Butterflyfishes (McBride and Able 1998) and crevalle jacks (Hoff 1971) are among species suffering mass hypothermal mortality in the MAB. Conversely, cold water is important to the recruitment or survival of other species, such as winter flounder (Williams 1975). Transport to the warmer SAB shelf is presumably detrimental for these species.

In previous work, we described the fidelity of larvae of various fish species to MAB and SAB originating water masses (Grothues and Cowen 1999). During May of 1996, when the temperature difference between water masses from the MAB and SAB was strong, the distribution of 183 taxa from either bight overlapped little. Notable exceptions were *Peprilus triacanthus*, two flounders, and the synodontids, clupeids, and engraulids; the three families of this group were largely represented by a single species, each identifiable in the late larval stage but without well-developed distinguishing characters in the early stage. Little mixing of species groups was apparent except in collections from nets that actually passed through oceanographic fronts, leading to the conclusion that cross-front exchange was avoided or was fatal to many species. For most species, exchange between the MAB and SAB must have depended heavily upon transport across the confluence zone in distinct water masses, rather than upon exchange between water masses. In addition to exchanging water and larvae between the bights, large oceanographic features displace shelf waters to the open ocean (e.g., Lillibridge et al. 1990). Shelf water loss results in the expatriation of subtropical fishes toward Nova Scotia (Wroblewski and Cheney 1994) and may play an important role in determining the mortality of spring-spawned bluefish (Hare and Cowen 1993).

This paper examines larval exchange across the CHC in recognition of the potential for such exchange to affect recruitment variation. The fluxes of larvae through the MAB/SAB boundary region are calculated for a 37-d period in spring of 1996. We focus on creating a sense of the canonical state of transport at the CHC, i.e., the ground state of physical conditions in which a ground state fish assemblage would be altered by anomalous or episodic events. While we do not try to link these figures with subsequent recruitment here, we do explore the relative contribution of different water masses to the determination of net transport for insight into the pressures acting on early life history.

## Methods

*Area of interest*—The study area extended from the mouth of Chesapeake Bay at the 36.7°N parallel southward to the

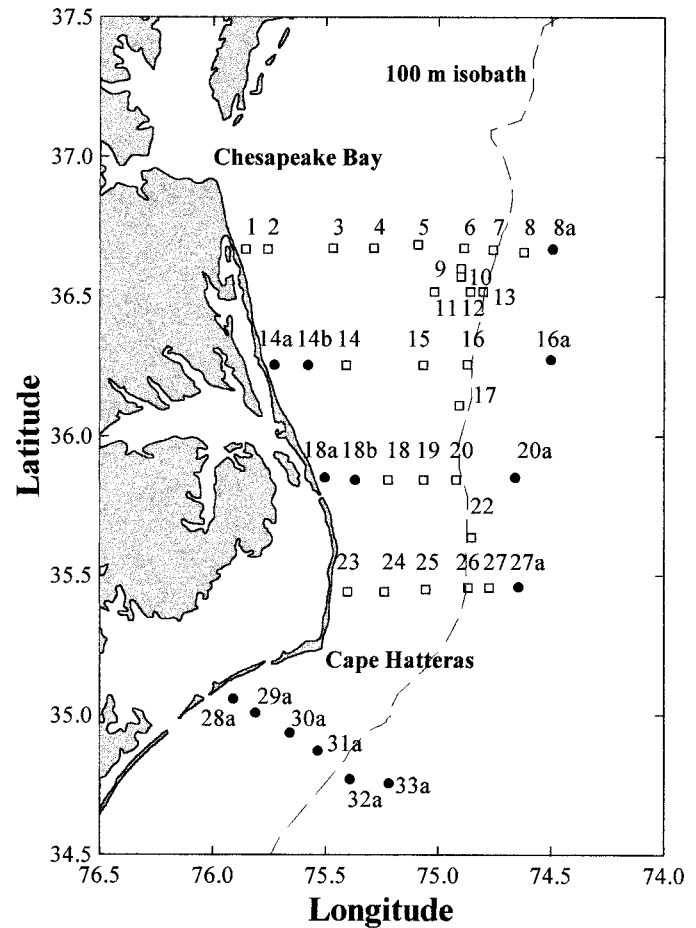


Fig. 1. Study area. The Ocean Margins Project (OMP) oceanographic instrument mooring array is depicted as open squares. All OMP mooring sites coincided spatially with MOCNESS ichthyoplankton sampling sites with the exception of moorings 9–12, where no MOCNESS tows were made. Additional MOCNESS sample sites are depicted as solid circles and are designated with an alphabetic suffix following Grothues and Cowen (1999).

35.5°N parallel just north of Cape Hatteras. The Virginia and North Carolina shorelines (Outer Banks barrier islands) bounded the area to the west and the 76-m isobath shelf break, extending approximately along longitude 74.5°W, to the east (Fig. 1). Boundaries were marked by perimeter moorings from a large array of instruments deployed by the Department of Energy's Ocean Margins Project (OMP) to study shelf carbon flux. It is within this region that the MAB/SAB front fluctuates (Pietrafesa et al. 1985; Churchill and Berger 1998). The Gulf Stream flows near the shelf-slope break in the SAB. The protrusion of Cape Hatteras across the shelf "funnels" shelf waters from both the north and the south off an increasingly steep continental slope to the Gulf Stream within tens of kilometers from shore (Bumpus 1973).

The mooring array established by the OMP from 5 February to 13 May 1996 consisted of 27 instrument moorings. Moorings contained either acoustic Doppler current profilers or multiple current meters packaged with SBE Seacat 16 (Seabird Electronics) conductivity and temperature sensors; SeaPac 2000 (Marsh-McBirney), S4 (InterOcean Systems),

Aanderaa, and BSCM (based on Geodyne101). Current meter packages were moored to achieve a high resolution, observable cubical control volume ( $<15 \text{ km} \times 10 \text{ km}$  half diagonal) with instruments at each mooring at depth intervals of 3 to 20 m (depending on depth) starting 7 m below the surface and continuing as water depth allowed. Over 70 packages were deployed at 26 moorings, although not all were used for this work (Fig. 1).

Owing to the loss of several current meters, the study area perimeter was closed through definition of the following boundaries: northern boundary, designated hereafter as "line A"—shore to mooring 5, then at an angle through mooring 9 to mooring 13; eastern boundary "line C"—mooring 13 to mooring 22; southeast boundary "line B"—mooring 23 to 25, then at an angle northeast to mooring 22 (Fig. 1). Because the current meter at 71 m at mooring 13 stalled several times during the deployment, flow could not be calculated accurately for the deep water in the northeast corner of the study region. The stalls affected flow calculation mostly of slow moving slope water (as seen from temperature and salinity recordings at that mooring and flow measures from adjacent moorings) from 40 m downward and extending to the bottom at mooring 5 on the northern boundary and to the bottom at mooring 16 on the eastern boundary.

Between 13 May and 23 May, the first available cruise dates during and immediately following the retrieval of the OMP moorings, the study area was sampled for ichthyoplankton using a multiple opening closing net and environmental sensing system (MOCNESS). This system fishes eight remotely triggered (open/close) nets ( $1 \text{ m}^2$ ,  $505\text{-}\mu\text{m}$  mesh) and controls frame mounted temperature, conductivity, pressure, tilt, and flow sensors. MOCNESS sample stations were established at the previous sites of the OMP moorings on or within days of their recovery. Several additional stations were sampled to determine the identity and concentration of ichthyoplankton in Carolina Capes water and Gulf Stream before the potential entry of those water masses into the boundary region for a total of 35 MOCNESS sample sites, several of which were sampled twice (Fig. 1). At each station occupation, each net sampled along an oblique 5-min tow within a previously defined depth stratum, as allowed by the total station depth, for a total of 222 samples. The MOCNESS software parsed raw data from the environmental sensors to association with individual nets within a tow as delineated by the net trigger signal. Larval fish were sorted from the net collections in the laboratory and identified to lowest possible taxonomic level; abundance of fish by species was standardized to density (concentration) for each net using a sample volume calculated from the tilt angle and flow meter data (individuals per  $1,000 \text{ m}^3$ ). Details of this sampling, as well as an analysis of larval distribution, are given in a previous paper (Grothues and Cowen 1999). That study characterized the assemblage on either side of, and across, the front separating MAB water masses from SAB waters (including the Gulf Stream). Several groups of species characterized the boundary assemblage, with group membership tied to a close affinity in the principle spawning area of the adults (MAB or SAB). Correlation between the abundance (weighted mean position along a cline) of individuals of a species and environmental variables, especially

temperature and salinity, was strong. Species also turned over or declined in relative abundance with depth and distance offshore. Strong species-environment correlation, coupled with an indication of only weak cross-frontal exchange, allows for confidence in calculating the first-order flux of larvae through the study area as a function of water mass/depth specific flow and larval concentration.

Of 189 taxa collected, 42 were considered for flux calculations (Table 1). Taxa were chosen for their known use of MAB or SAB shelf habitat as nurseries (*see* Fahay 1983; Able and Fahay 1998; Steves et al. 2000) and their relative abundance in May samples. Taxa with affinities to epipelagic or mesopelagic environments (i.e., myctophids, stomatids, *Ariomma*, etc.) were not considered. It was assumed that the abundance and distribution of larvae with respect to hydrography in these water masses applied to the entire study period. Analysis of unpublished data indicates that, up to a threshold convergence in surface water temperature between the MAB and SAB, the May assemblages of each of these regions remain distinct and stable over the short term (Grothues and Cowen, unpubl. data). Species were condensed into groups of similar water mass affinity by cluster analysis (single linkage amalgamation) using Euclidean distance calculated from sample mean, maximum, and minimum salinity, temperature, and depth of occurrence. Larval fish concentrations for each group were taken as the sum of that from all group members to represent a concentration of larval shelf-dependent fish experiencing a unique flux through the area (Table 1).

## Calculations

Flux was calculated using OMP flow data for 37 d from 1 April to 7 May 1996, and the larval fish concentration/distribution determined from collections of 13–24 May. The following approach was used to calculate a first-order estimate of larval fish flux between the MAB and SAB: (1) define study area boundaries, (2) calculate depth specific water mass specific transport across boundaries, (3) multiply mass transport with values of temperature salinity depth specific larval concentration.

Flow signal was low-pass filtered using a Lanczos cosine taper filter with a 40 h period to remove tide. Low-passed salinity, temperature, and residual velocity components from perimeter mooring instrument packages were fit to boundary surfaces (each line at all instrument depths) by cubic-triangle based interpolation in 2 m deep by 5 km ( $10 \text{ km}$  for line C) grids using MATLAB (The MathWorks). Surface transport ( $<5 \text{ m}$  depth) was not calculated owing to a lack of data. In realizing that species are not uniformly distributed with respect to hydrography, transport of water was calculated on a water mass specific basis. Water mass definitions were based on salinity and temperature and roughly followed the definitions given by Pietrafesa et al. (1985): plume water (outflow from the Chesapeake Bay) was defined as that with salinity  $<32 \text{ psu}$ , MAB shelf water as that between 32 and 34 psu, SAB water as that with salinity  $>34 \text{ psu}$  and temperature  $\geq 18^\circ\text{C}$ , slope water as that with salinity  $>34$ , temperature  $< 18^\circ\text{C}$ . Each water mass was further divided into

Table 1. Aggregate concentration of larval fish groups as used in flux calculations and the weighted mean temperature and salinity of occurrence of group members. Groups were defined at the 75% dissimilarity level cutoff from cluster analysis constructed from an Euclidean distance matrix using a single linkage amalgamation rule. Concentrations are in units of larvae per 1000 m<sup>-3</sup>.

Larval fish group	Water mass	Shallow	Deep	Weighted mean temperature (°C)	Weighted mean salinity (PSU)
Group 1 <i>Lophius americanus</i> , <i>Scomber scombrus</i> , <i>Tautoga onitis</i>	Plume	9.8305	0	14.82	31.29
	MAB	2.3140	0		
	Slope	0	0.2906		
	SAB	0	0		
Group 2 <i>Glyptocephalus cynoglossus</i>	Plume	1.1975	0	12.25	32.05
	MAB	1.0751	0		
	Slope	0	0		
	SAB	0	0		
Group 3 <i>Centropristis spp.</i> , <i>Enchelyopus cimbrius</i> , <i>Limanda ferruginea</i>	Plume	0.9597	0	11.53	32.27
	MAB	6.3054	0.2457		
	Slope	0	0		
	SAB	0	0		
Group 4 Engraulidae	Plume	7.3708	0	19.82	30.86
	MAB	2.3129	0		
	Slope	0	0		
	SAB	6.4811	0.2925		
Group 5 Haemulidae, <i>Paralichthys dentatus</i> , <i>Peprilus triacanthus</i> , Synodontidae	Plume	4.2606	0	17.56	34.15
	MAB	6.3723	0		
	Slope	100.0800	1.4075		
	SAB	17.2033	6.9950		
Group 6 <i>Hippoglossina oblonga</i>	Plume	0.7939	0	15.18	31.44
	MAB	0.0453	0		
	Slope	0	0.5806		
	SAB	0	1.0500		
Group 7 <i>Astroscopus guttatus</i> , <i>Bothus spp.</i> , <i>Caranx spp.</i> , <i>Callionymus pauciradiatus</i> , <i>Citharichthys arcifrons</i> , <i>Citharichthys gymnorhinus</i> , <i>Citharichthys spp.</i> , Clupeidae, <i>Cynoscion nebulosus</i> , <i>Cynoscion regalis</i> , <i>Dactyloscopidae</i> , <i>Decapturus punctatus</i> , <i>Etropus crossotus</i> , <i>Etropius microstomus</i> , <i>Eucinostemus spp.</i> , <i>Ioglossus spp.</i> , <i>Monacanthus hispidus</i> , <i>Pomatomus saltatrix</i> , <i>Rhomboplites aurorubens</i> , <i>Sarda sarda</i> , <i>Scomber japonica</i> , Serraninae, <i>Syacium spp.</i> , Triglididae <i>Xyrichtys novacula</i>	Plume	1.9713	0	22.15	35.67
	MAB	3.9025	0		
	Slope	15.9725	4.6975		
	SAB	120.461	44.9325		

shallow (<40 m) and deep (>40 m). Integration of the product of velocity (m s<sup>-1</sup>), boundary surface area (m<sup>2</sup>), and elapsed time (s) for each boundary face gave the mass transport on a water mass specific basis for each study day. Transport was integrated over all days on a water mass specific/depth specific and total basis. Small errors in the recorded daily flow at any or all of the current meters, or resulting from inaccurate interpolation of velocity (between current meters where  $dv/dx$  or  $dy/dx$  was not adequately approximated by the cubic-triangle based interpolation), resulted in a positive (mass gained) or negative (mass lost) calculated mass balance within the study area. This discrepancy was treated by dividing the mass balance evenly among all grid cells of the perimeter surfaces (line × depth) and recalculating water flux with the correction factor on a daily time step. Subsequently, mass balance was calculated for each water mass individually to examine changes in hydrography.

Transport of larvae was calculated as the product of the net water mass transport and the group aggregate concentration of larvae in a water mass/depth division. Larval fish transport was integrated over all water masses/depths for each line for each of the investigated species groups. This is analogous to multiplying the salinity/depth weighted mean concentration of fishes by the salinity/depth weighted mean velocity through all boundary faces for each of seven fish groups, but the vectors can be examined individually. For each group, the ratio of total fish transported to transport in each line/depth/water mass combination (i.e., transport vector) was calculated as an indication of the relative importance of each transport vector. Passage of larvae from near-shore species eastward through line C was defined as loss export. Larvae from SAB species were exchanged to the MAB if they moved north across the northern boundary, line A. MAB larvae were exchanged with the SAB if they moved

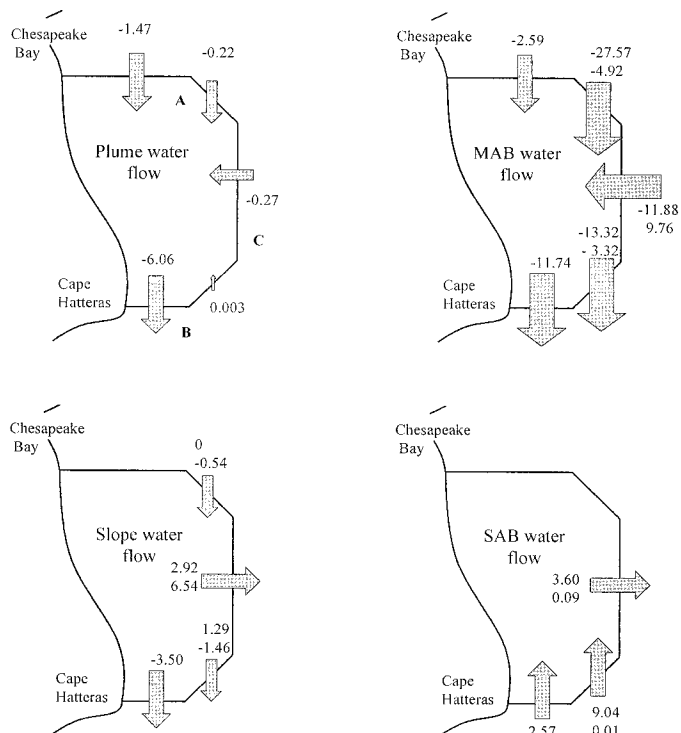


Fig. 2. Mass transport ( $m^3 \times 10^{10}$ ) of plume, MAB, slope, and SAB water for the period from 1 April through 7 May 1996. For line segments in deep water, shallow transport ( $<40$  m depth) is given above deep transport except for plume water, which had no deep flow component. Arrows are scaled to order of magnitude and point in the direction of net flow across each line. Flux values are positive north and east. Study boundaries are designated by A (including northern diagonal), B (including southern diagonal), and C in the first subplot.

south across the southern boundary, line B. Larvae crossing the southern boundary into the study area were also transported into the MAB but were considered separately from transport across line A for the purpose of calculating net gain or loss to the study area.

Data from mooring 26 at the southeast corner of the study area supported only a surface current meter. Although unsuitable for high-resolution calculation of flow, those data were examined to describe the impingement of the Gulf Stream on the shelf just outside of the study boundary. Knowledge of the Gulf Stream's influence is important to drawing conclusions regarding the fate of exported larvae.

## Results

**General flow description**—Plume water entered the study area from the north (MAB) and from the east; three times the influx volume exited the study area into the SAB (Fig. 2, Table 2). MAB water also entered from the north and east, with transport of an order of magnitude greater than plume water (Fig. 2). Eighty-one percent of the incoming MAB water volume left the study area southward into the SAB (Table 2). The relatively small remaining balance represented a larger volume gain to the study area than that lost as plume water.

Table 2. Mass balance into the study area. Values indicate the net volume of each water type gained by the study area during the 37-d study period.

Water mass	$\times 10^{10} m^3$
Plume water	-4.1042
MAB water	8.8121
Slope water	-12.6370
SAB water	7.9200

Slope water entered the study area as a deep flow through the northeastern boundary that exited through the southern boundary as a contiguous flow along the shelf break. A weak offshore flow over a large area resulted in substantial loss of this water to the study area (Fig. 2, Table 2). Water of slope sea temperature and salinity (TS) characteristics also entered north across the southern boundary, probably as the result of mixing at the oscillating MAB/SAB front. SAB water entered the study area from the south; 31% of the influx volume exited through the eastern boundary such that this water accumulated in the study area (Fig. 2, Table 2). No SAB water crossed the northern boundary of the study area into the MAB.

Flow of all water at all crossed lines varied greatly with coefficients of variation from detided flow always exceeding one and ranging as high as 15.3 (Table 3). For plume and MAB water, this belied oscillation in a direction suggestive of upwelling and relaxation. (Inspection of National Ocean Service buoy wind data from the Chesapeake Bay mouth supports this interpretation.) Water of slope sea temperature and salinity also oscillated near the surface across the outer part of the southern boundary; otherwise, variability in slope water transport was mostly in the strength of southward flow. SAB water flow varied more at depth than near the surface owing to a strong jet that periodically formed along the shelf edge in the southeastern part of the study area.

**Larval fish flux**—Larvae from group 1 were most closely tied to plume water; however, because of the relatively low flow of this water type, MAB water was the most important transport vector through all lines. MAB water accounted for roughly 75% of the total transport for this group (Fig. 3). Onshore transport in MAB water offset offshore transport in slope water across the eastern line as well. Consequently,

Table 3. Coefficient of variation (CV) for daily detided mass transport through the eight boundary faces. NA (Not applicable) indicates a mean of zero in the denominator (i.e., water mass did not flow through that line segment).

Line	Plume	MAB	Slope	SAB
A	8.59	15.13	NA	NA
A2 shallow	4.27	1.02	NA	NA
A2 deep	NA	1.27	2.23	NA
B	2.54	2.44	2.62	9.75
B2 shallow	6.08	2.78	7.77	2.09
B2 deep	NA	1.37	1.43	7.24
C shallow	8.38	3.52	2.80	3.38
C deep	NA	1.29	2.34	6.08

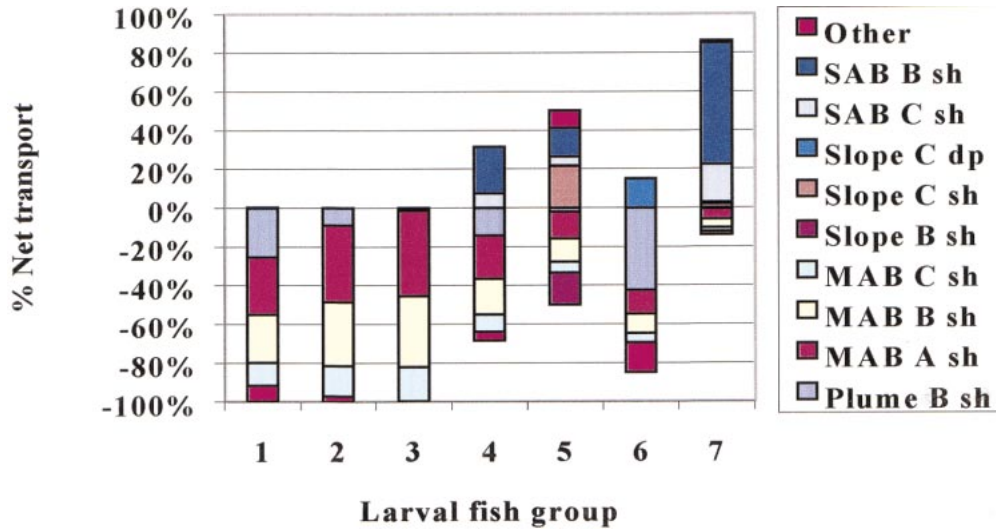


Fig. 3. Relative importance of flow/boundary combinations in determining net transport of larvae through the study area as a fraction of the total transport for each group. See text for definitions of plume, MAB, slope, and SAB water. Line codes are A = line A, B = line B, C = line C, sh = shallow, dp = deep. Positive values denote transport vectors north (into the MAB) or offshore depending on the line indicated. Despite differences in distribution among water masses, southward flow of MAB water dominated the net transport of most MAB affiliated groups because other water masses carrying these larvae had little net flow in comparison.

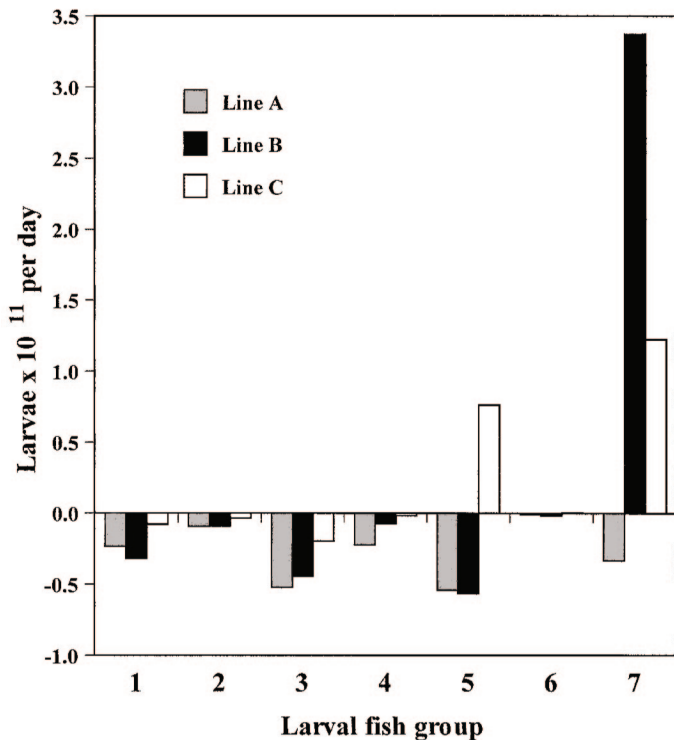


Fig. 4. Mean daily transport of seven fish larvae groups through the northern (A), southern (B), and eastern (C) study area boundary lines. Transport is positive north through lines A and B and positive east through line C. Standard error is given in Table 4, rather than as bars, to maintain legibility of the smaller mean values.

group 1 larvae experienced net transport from the MAB and from offshore into the SAB (Fig. 4). Species making up this group were not abundant except in plume water; total transport of larval fishes was relatively low. Higher flow of MAB water also dominated exchange of group 2 (witch flounder, *Glyptocephalus cynoglossus*) despite similar concentrations in plume and MAB water (Fig. 3 and Table 1). A relatively low transport of witch flounder through all lines (Fig. 4) reflected a low total concentration of this monospecies group. Predominantly MAB taxa also made up group 3, with a concentration in MAB water sixfold that in plume water. Larvae from this group were also carried from the MAB into the SAB in similar quantity but accumulated in the study area owing to additional influx from offshore (Figs. 3, 4).

Group 4 larvae (anchovies) were abundant in plume, MAB, and SAB water. Opposing MAB and SAB water flows nearly canceled transport through the southern boundary line (Fig. 4). A higher concentration in plume water did little to increase the role of this flow relative to that of MAB water (Fig. 3). Anchovy larvae passed south into the SAB in both plume and MAB water. With a high concentration in SAB water, anchovy larvae also entered the study area from the SAB but did not cross into the MAB, being lost to sea instead. Loss across the shelf in SAB water, however, was not sufficient to offset gain across the shelf in MAB water.

Flow of all water masses affected group 5 fishes, which had the widest distribution (Fig. 3). This was the only group for which slope water transport played an important role. Group 5 larvae were concentrated 2–3 orders of magnitude higher in slope water than that in other water masses. Near-shore southward slope water flow (“slope B sh” in Fig. 3) accounted for more of the flow south from the study area

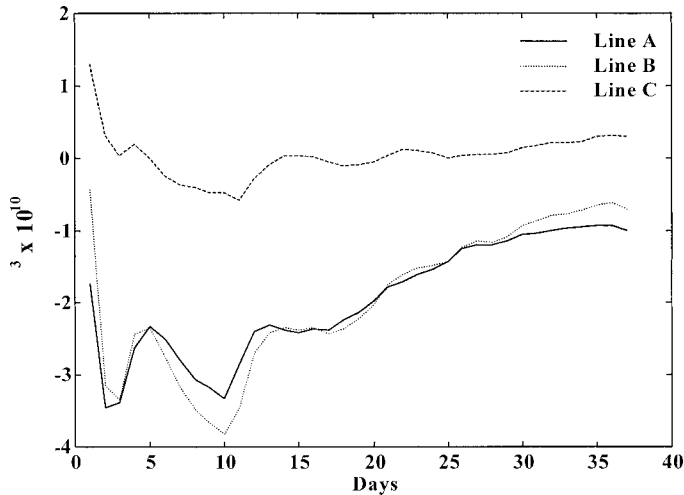


Fig. 5. Progressive mean water mass transport (summed over all masses) at line C with increasing days from 1 April. Export is positive eastward. The addition of daily measurements does not dampen fluctuations in the mean, demonstrating the dependence of fish recruitment on spawning timing at the event scale for species with short larval duration.

into the SAB than did MAB or plume water. Gain to the nearshore study area from across the shelf in MAB water did not offset loss across the shelf in SAB and slope water combined. Net flux was out to sea (Fig. 4).

Group 6 larvae (fourspot flounder, *Hippoglossina oblonga*), with a shallow distribution in plume and MAB water and a deep distribution in SAB and slope water, exhibited a pattern of net exchange similar to that of group 5, although by different vectors (Fig. 3). Lower concentration yielded smaller absolute values of transport than for group 5 (Fig. 4). Off-shelf flow of deep slope water accounted for over 10% of the total transport (Fig. 3). Fourspot flounder larvae experienced a net loss from the study area to both the SAB and to sea, despite inflow through the northern boundary in MAB water.

Slope and SAB water held the highest concentration of group 7 larvae. Plume, MAB, and slope water transported group 7 larvae across the northern boundary (Fig. 3), and despite low individual taxa concentrations the aggregate of so many members yielded a net transport across this boundary similar to that for the more exclusively MAB groups. SAB and slope water flows accounted for about 75% of the total transport. High SAB water flow, containing a high aggregate concentration of this speciose group, transported nearly  $1.4 \times 10^{13}$  larvae northward into the study area across line B (Fig. 4). Nearly 25% of larvae entering the study area from the SAB were transported back out of the area across the shelf break in both SAB and slope water flow. Larvae crossing especially the southern part of line C eastward in SAB water are subject to rapid advection in the Gulf Stream, which repeatedly impinged on the study area periphery with northeast velocities of up to  $1 \text{ m s}^{-1}$  (Fig. 5).

High variability in the daily mean transport of all groups (Table 4) resulted from the oscillation of all water masses. The period and pattern of oscillation relative to the duration of the planktonic life phase and adult spawning duration in

Table 4. Standard error of the mean daily transport of fish larvae from seven groups, as shown in Fig. 4.

Group	Standard error $\times 10^{11}$		
	Line A	Line B	Line C
1	0.1187	0.1299	0.0458
2	0.0370	0.0382	0.0203
3	0.1861	0.1862	0.1181
4	0.1053	0.1713	0.0510
5	0.2045	0.9747	0.3991
6	0.0057	0.0066	0.0024
7	0.1218	2.1685	0.6813

the area is critical in determining to what extent episodic oceanographic events influence ultimate transport fate (Epifanio and Garvine 2001). We plotted the progressive mean of the sum water flux at all lines over the 37 d, a period similar to the planktonic duration of many common fishes (Fig. 6). Addition of successive days did not dampen fluctuations in the mean transport at any line until about 28 d were included in the calculation. The plots slope even then; a longer planktonic duration will effect the mean and a negative turn at the end of plots of progressive mean for both lines indicates a strong change, either an important episodic event or the signal of a longer frequency cycle. Planktonic life stage periods shorter than 28 d would certainly affect the transport fate of larvae at all boundaries. As demonstrated above, the flow of specific water masses making up these total flows changes the effective transport frequency dampening on a species-specific basis.

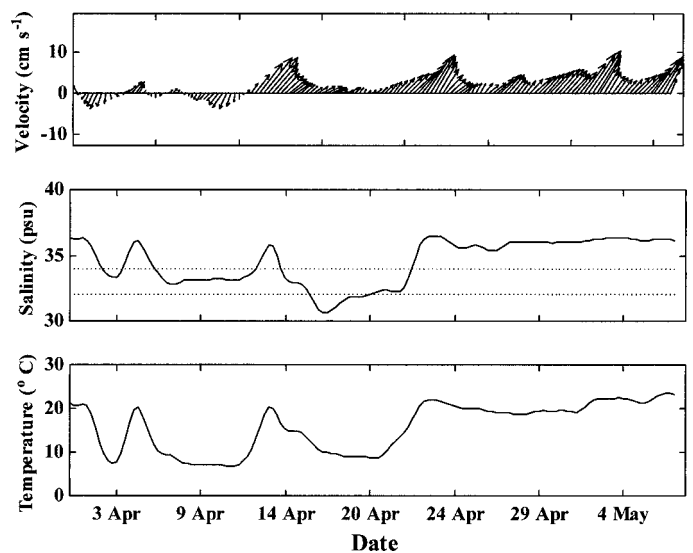


Fig. 6. Current velocity, salinity, and temperature as recorded by near surface (7 m) Seapac current meter at mooring 26. Dashed lines through the salinity plot indicate the upper and lower limits of Middle Atlantic Bight water as defined for this study. High velocities (up to  $1 \text{ m s}^{-1}$  NE) correspond with SAB water salinity signature ( $>34 \text{ psu}$ ) and demonstrate presence of the Gulf Stream front near the mooring during much of the study period.

## Discussion

At Cape Hatteras, distribution of fish larvae with relationship to hydrography will affect the probability of three transport contingencies: retention in the natal bight, export to the adjacent bight, or export to the open ocean. Subsequently, specific physiological tolerances will impact individual survival and thereby population size and range of affected species (Neill et al. 1994). The interaction of transport and physiology has been explored in a simpler system of on/offshore Eckman transport in the Pacific (Bailey 1981), and transport of haddock larvae to unusual but favorable nursery grounds has been implicated for an extraordinarily strong recruitment year in the MAB (Polacheck et al. 1992). Rice et al. (1999) used hind-cast techniques to model the transport/temperature interaction for Atlantic menhaden recruitment across the CHC, but entirely empirical flux studies linking transport and recruitment through the area are lacking. Bluefish larvae, like adults, are apparently capable of withstanding some temperature differences in crossing the MAB slope and shelf from the Gulf Stream, and their recruitment in the northern MAB is tied to the frequency of warm core ring streamers that transport them across the slope (Hare and Cowen 1996). However, the quantification of progeny loss from the Chesapeake Bight in conjunction with flows at the CHC and the quantification of such a loss on subsequent recruitment remains in question (Hare and Cowen 1993). Prior to arriving at the ability to connect exchange and recruitment for individual species, it is instructive to examine the general patterns of transport in the area, as has been accomplished for the Georges Bank. A broad focus at this point builds our understanding of fish early life history in general and of how transport sorts MAB and SAB larval assemblages in particular. This work exemplifies the potential for episodic events to greatly influence the size of the larval pool and describes a canonical regime for spring of 1996, the effect of which must be mitigated by specific life history. The complexity of oceanography at Cape Hatteras and of fish biology demands several caveats of our results; these are addressed together with some insights below.

Among the most notable findings was that exchange at the CHC was strongly skewed toward that of MAB species moving into the SAB, as opposed to the complement, and that MAB fish were retained nearshore. Pietrafesa et al. (1994) already modified the view that most MAB water was consistently pulled to sea at the edge of the Gulf Stream, estimating that transport of MAB water into the SAB regularly reached 0.1 Sv. Churchill and Berger (1998) demonstrated that MAB water lost to the Gulf Stream came selectively from a narrow band toward the eastern edge of the southern MAB. However, net southward transport of plume and MAB water combined (0.1 Sv during the current study period) was on the low side of the 0.1–0.8 Sv estimated for southward MAB flow by numerous workers including Beardsley and Boicourt (1981), Lillibridge et al. (1990), Mountain (1991), and Churchill and Berger (1998). Larval retention resulted from a net gain of MAB water to the area, clearly that cannot be indefinite. The volume of MAB shelf water in the study area increases and decreases peristaltically

(Churchill and Berger 1998). The peristaltic frequency is interesting because, as demonstrated in the current study, the period may approach that of larval duration for many species, and the timing and duration of spawning in relation to it must influence transport fate. If such spawning occurred to the benefit of a species, it would be analogous to a “match” in the classic “match/mismatch” hypothesis of Cushing (1975), in which recruitment variability is driven by the timing of reproduction relative to that of cyclic favorable conditions at spawning grounds (although in this case the “match” is with favorable transport rather than production). Changing the calculation time window by several days might have increased or reversed net transport several fold. The potential effect of a change in the calculation window has two implications. The first is that the success of exchange, expatriation, or recruitment can vary greatly owing to oceanographic events on the scale of larval fish competency periods (the time period during which a larva is ready to settle and/or metamorphose). The second is that we can expect interannual variability even under similar flow conditions because the reference frame for larvae is reset yearly by the onset of spawning or the arrival of migrating spawning adults (*see* Colton et al. 1979; Musick et al. 1989; Hare and Cowen 1993).

We were not able to measure MAB water loss attached to Gulf Stream flow, a mechanism that may well have occurred east or northeast of the study area. Therefore, there may be a strong, unaccounted flux of MAB-associated larvae to the open ocean, but certainly many MAB-associated meroplankton are transported into the SAB and even shoreward in subsurface upwelling-driven flows. Further, despite the fact that SAB water impinges on the MAB (Churchill and Cornillon 1991; Gawarkiewicz et al. 1992), transport at the CHC may not be an important, or direct, route for the large-scale introduction of SAB-spawned larvae to the MAB. Rather, springtime SAB-spawned planktonic larvae arriving at the CHC must rely on a circuitous route involving intrusions or warm core ring streamers to the north after first being expatriated from the continental shelf (e.g., Hare and Cowen 1991, 1996). Even mixing into MAB water across the front within the study area bounds would have resulted in net movement back into the SAB during our study.

Another notable finding was that the strong affiliation of fish larvae with certain hydrographic features may belie the importance of other features (less affiliated) to species' abundance and distribution. During our study, for example, the relative distribution of MAB larvae among water masses ultimately had little bearing on the importance of transport vectors for these species through the CHC. Strong flows of shallow shelf water from the MAB to the SAB dominated transport even for groups with relatively high concentrations in plume or slope waters, which did not have strong net flows or volumes. Most larvae from all three MAB affiliated groups (1–3), the broadly affiliated Engraulidae (4), and the MAB/SAB transition group (5) passed from the MAB onto the study region shelf and from there into the SAB in varying ratios of their impingement. Differences in distribution did have a noticeable effect on the retention or export of MAB-spawned larvae off the shelf. Larvae from two groups passed offshore, while those of four groups crossed onto the



shelf from the open sea. Affiliation with SAB water by larvae of the remaining group also resulted in net transport into the convergence zone despite substantial export offshore, but most of this owed to transport from the SAB, rather than from the MAB.

Although there was no net transport into the MAB via any water mass, a small number of SAB-affiliated larvae will have periodically entered the MAB in variable MAB and plume water flows. The potential importance of MAB water transport to SAB species is suspect because it is tied to the unknown introduction region of SAB larvae into MAB water. The magnitude of successful cross-front flux, on a zonally variable basis, becomes an important variable in describing the importance of these flows to species not spawned in them and remains a topic for further examination. If SAB larvae were mixed into MAB water in or north of the study area, then transport in MAB water resulted in movement back to the SAB as calculated here. If, on the other hand, adults would have spawned into MAB water that had flooded the SAB shelf south of Cape Hatteras, then subsequent retreat of some of this water would have resulted in net northward, not southward, transport. This mode of transport would occur inside of the zone of expatriation demonstrated for SAB fish in SAB water and would be a more direct means of access to the MAB shelf than transport in the Gulf Stream followed by cross-slope transport in warm core ring streamers. A similar mechanism is implicated (without implied benefit) in the occurrence of slope fish larvae in shelf water off Spain (Sabatés and Olivar 1996). We cannot, however, suppose that SAB fishes spawn while colder MAB water is flooding the SAB shelf. Until this topic is investigated further, the indication is that the flow regime inhibits northward progress of even those SAB-spawned larvae introduced to MAB waters north of the study area.

Two error sources, unknown surface flow and periodic stalling of the 75-m flow meter at mooring 13, lead to underestimation of transport within the study area. Transport above 5 m depth, in particular, could have been disproportionately high to that of lower strata, and inclusion could have revealed a stronger role for plume water, which is stratified above MAB water. The center of distribution for all MAB species during this study was deeper than the 5-m surface layer. Still, transport in the surface layer must be important, especially as it can be quickly accelerated by wind in strongly stratified conditions. Larvae may react to strong stratification as well, with consequence to their wind-driven transport.

We did not calculate water mass mixing, or, therefore, the loss or production of specific water mass volumes by mixing. Mixing at the MAB/SAB front would have, and probably did, produced slope water. Slope water had the largest mass balance deficiency, and it was out of the study area. Slope water sampled during the ichthyoplankton survey may have also resulted from mixing (Grothues and Cowen 1999), and the larval fish concentration values used in calculating flux may yet represent concentration in newly formed slope water. That must indicate, however, a flux of larvae between the water masses. Larvae are not necessarily mixed conservatively (Govoni 1993; Cowen et al. 1993); other possible responses include increased concentration in the constituent

water masses owing to mixing avoidance or loss to the constituent water masses without gain to the new water owing to mortality. All scenarios lead to error in the calculations presented here. For example, slope water transport was relatively important to the flux of group 5 and *Hippoglossina oblonga*, and the result of mixing on transport deserves focused study. Cowen et al. (1993) begin to address slope sea assemblage dynamics, but on a seasonal rather than single larval lifetime period. Additional study should focus on and follow water directly at the MAB/SAB front.

In relation to the transport calculated here, discussion of larval fish transport fate assumed a uniform larval duration over the study period. As with mixing, mortality and population growth result in a difference between the larval fish constituency of entering and exiting water masses, but estimates of these parameters could not be obtained from the 1996 cruise. It is also possible that the fish population of a water mass changed over the course of transport. In that case, the use of larval concentrations defined from water masses after the fact results in the error of multiplying a resultant concentration by the events that influenced it. In the absence of observations indicating substantial mixing of larvae, however, we believe that the movement of water within the area (and oscillating over the presumed natal grounds) did little to change within-water mass density from the generalized aggregated used here; rather, it relocated fish. This topic also warrants further study.

The consequence of expatriation from shelf spawning grounds may be beneficial or fatal depending on the life history of species or even cohorts (Hare and Cowen 1991, 1993; Juanes et al. 1994; McBride and Able 1998). We might therefore expect similarity in the ecology of similarly transported species. The association of larvae with hydrography did not reflect similar adult ecology, and propagule placement by adults is probably decoupled from transport fate near the CHC. For example, group 1 contained larvae of a reef oriented invertebrate feeder (tautog), a vagile piscivore (Atlantic mackerel), and a soft bottom oriented ambush omnivore (goosefish). Temperature, forage base, and bottom structure at the ultimate transport destination could affect these species in profoundly different ways. However, specific life histories may demand similar environments for the larval stages. The distribution of these species in relationship to one another may be different on the broad shelf to the north of the study area, but the funneling effect off Cape Hatteras may cause a convergence in their distribution. If water mass association of larvae is adaptive to beneficial transport, it is probably in response to more stable pressures occurring over the larger range of the species, or it may interact with traits such as larval period duration.

The described flux conditions could contribute to the loss of a spring-spawned bluefish cohort and individuals of other species from New York Bight populations as hypothesized by Hare and Cowen (1993), albeit by a different, but not mutually exclusive, mechanism. The shelf and plume water transport calculated here might represent that for the rest of May, when bluefish had presumably begun spawning in the area (Kendall and Walford 1979; Chiarella and Conover 1990; Hare and Cowen 1993). Hare and Cowen (1993) did not estimate the mass transport necessary to advect an entire

cohort from the shelf, regardless of the sink destination. However, the wide range in monthly average water mass transport (up to eight times higher as suggested in other years by other workers), coupled with the effect on larval fish flux demonstrated here, implies that transport can strongly influence variability in recruitment at Cape Hatteras. The effect of similar conditions has, in fact, been demonstrated to affect large-scale recruitment patterns at similar points where boundary currents converge (see Cowen 1985; Caputi et al. 1996). The distribution of fish larvae with depth is known to affect retention and export, and behavior affecting distribution is probably selected for on the basis of mechanisms common over a species range (Norcross and Shaw 1984; Boehlert and Mundy 1988; Govoni and Pietrafesa 1994). It is not likely, therefore, that many species can respond evolutionarily to such a highly variable flow regime, at the edge of their range, in such a way as to prevent episodic expatriation. Instead, evolution in a few species may mitigate this effect by selection of traits that promote recolonization of some of the expatriated larvae. The first annual cohort of bluefish recruitment to the New York Bight could be an expression of just that (Hare and Cowen 1993, 1996).

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