Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats

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Abstract

In this study we examined the mechanisms by which *Pomatomus saltatrix* (Pisces: Pomatomidae) larvae and pelagic juveniles are transported from South Atlantic Bight spawning grounds to Middle Atlantic Bight estuarine nursery habitats. Data on larval and pelagic juvenile distributions, estuarine juvenile recruitment, hydrography, wind speed and direction and satellite-derived, sea surface temperature were used to examine potential larval transport mechanisms. On the basis of these analyses, a scenario for northward transport of *P. saltatrix* was developed. Gulf Stream-associated flow moves *P. saltatrix* larvae northeastward from their South Atlantic Bight spawning grounds. Larval transport from the Gulf Stream to the Middle Atlantic Bight shelf edge occurs in warm-core ring streamers, but some more developed individuals may swim across. Finally, *P. saltatrix* pelagic juveniles actively swim across the Middle Atlantic Bight shelf, a behavior initiated when the surface shelf-slope temperature front dissipates in late spring. This scenario predicts that the number of South Atlantic Bight-spawned *P. saltatrix* juveniles entering estuaries (i.e. recruitment) is determined in part by warm-core ring streamer activity. The timing of recruitment, however, is determined almost entirely by the timing of the dissipation of the surface shelf-slope temperature front.

Most marine fish and invertebrate species spawn a large number of small offspring that are transported away from spawning areas by a complex combination of physical and biological processes. Survival of these early life history stages is partly dependent on the outcome of their planktonic transport, as well as on their feeding success and ability to avoid predation. The relative contribution of feeding, predation, and transport in determining planktonic survival and ultimate recruitment to adult populations is actively debated (e.g. Sinclair 1988; Leggett and DeBlois 1994), but is likely to be species-specific. The

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Influence of planktonic transport processes, however, will be greatest in species whose juvenile nursery habitats are spatially distinct from spawning locations, thereby making the continuation of the life cycle dependent on the outcome of larval transport.

An example is the bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae), which spawns along the eastern coast of the U.S. during annual south–north migrations. Although the exact temporal and spatial pattern of *P. saltatrix* spawning remains uncertain, the general patterns of spawning and estuarine recruitment are well described. Spawning occurs in the South Atlantic Bight (SAB; Fig. 1 shows the place names used herein) from March to May and again from September to November (Collins and Stender 1987; Hare and Cowen 1993). Spawning also occurs in the Middle Atlantic Bight (MAB) from May to August (Kendall and Walford 1979; Chiarella and Conover 1990; Hare and Cowen 1993; Smith et al. 1994). Fish spawned in the SAB in spring recruit to MAB estuaries beginning in late May or early June (Nyman and Conover 1988; McBride and Conover 1991). Spring-spawned fish also recruit to SAB estuaries beginning in April, but in much lower numbers than to MAB estuaries (McBride et al. 1993). Fish spawned in the MAB during summer enter MAB estuaries in early August (Nyman and Conover 1988; McBride and Conover 1991). Fall-spawned fish are rare, but apparently recruit to SAB estuaries in late fall (Wenner and Sedberry 1989; McBride et al. 1993).

Because most *P. saltatrix* spawned in the SAB in spring enter estuaries in the MAB, larval transport processes (herein larval transport means the transport of both larval and pelagic juvenile stages) may be critical to both the magnitude and timing of estuarine entrance (i.e. recruitment). Based on the oceanography of the eastern coast of
the U.S., we can break larval transport from the SAB to MAB into three components (Kendall and Walford 1979; Hare and Cowen 1991); Gulf Stream-associated larval transport; movement of larvae from the Gulf Stream to the MAB shelf edge (i.e. across the slope sea); crossing of the MAB shelf by young *P. saltatrix* to their nearshore habitats.

During spring, *P. saltatrix* larvae are distributed on the outer half of the SAB continental shelf (Kendall and Walford 1979; Collins and Stender 1987), where currents are largely driven by the Gulf Stream. On average, flow on the outer SAB shelf is toward the northeast, but local reversals are caused by Gulf Stream meanders and frontal eddies (Lee and Atkinson 1983; Glenn and Ebbesmeyer 1994). South of Cape Hatteras, meanders have wavelengths of 100–250 km, maximum amplitudes of 30 km, and periods of 7–10 d (Olson et al. 1983). Shoreward of the Gulf Stream, winds become increasingly important, and on the inner shelf (<30-m depth), the Gulf Stream has a minimal influence (Lee and Atkinson 1983; Lee et al. 1989). On the basis of these studies, if *P. saltatrix* larvae are in the Gulf Stream, their northward transport rate will exceed 100 cm s⁻¹. If larvae are in outer Carolina shelf water, they will move northward in association with the Gulf Stream at 50–100 cm s⁻¹. Finally, if larvae are in inner Carolina shelf water, their transport will depend largely on wind-driven flow interacting with local bathymetry (see Askari et al. 1989). To clarify the mechanisms by which *P. saltatrix* larvae are transported out of the SAB, it is necessary to determine the distribution of larvae in the different water masses of the SAB: Gulf Stream, outer Carolina shelf, and inner Carolina shelf (see Fig. 1).

Following Gulf Stream-associated transport, larvae must move across the slope sea. Flow in the slope sea is typically to the southwest (Csanady and Hamilton 1988), but several advective, cross-slope larval transport mechanisms exist: wind-driven flow, Gulf Stream meanders, and warm-core rings. Data relating to wind-driven flow in the slope sea are minimal (Csanady and Hamilton 1988), but Gulf Stream meanders and warm-core rings would disrupt wind-driven flow (Csanady and Hamilton 1988), which makes these large-scale features of primary interest. North of Cape Hatteras, Gulf Stream meanders have wavelengths of ~320 km and periods of 7–8 weeks (Halliwell and Mooers 1979). North of Chesapeake Bay, meanders rarely if ever extend across the entire slope sea (Auer 1987). Thus, meanders are probably not integral to the cross-slope transport of *P. saltatrix* larvae.

Warm-core rings are formed by the pinching off of meander crests (Evans et al. 1985). On average, nine of these large anticyclonic eddies (~110 km in diam) are formed each year, and their average lifespan is 4–5 months (Auer 1987). Rings drift to the southwest in the ambient slope sea flow at ~6 cm s⁻¹ and rotate with tangential velocities that average 60 cm s⁻¹ (Zheng et al. 1984). Gulf Stream water is transported across the slope sea when warm-core rings interact with the Gulf Stream, resulting in the formation of warm-core ring streamers (Zheng et al. 1984; Evans et al. 1985) (Fig. 2). For our purposes, warm-core ring streamers will be considered the potential advective cross-slope transport mechanism of *P. saltatrix* larvae. In addition, in species other than *P. saltatrix*,

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**Fig. 1.** Map of the eastern coast of the U.S. noting the various localities and the approximate boundaries of different water masses mentioned in the text.
swimming ability dramatically improves following the transition from larva to juvenile (Hunter 1981; Stobutzki and Bellwood 1994). Thus, it is possible that P. saltatrix pelagic juveniles actively swim across the slope sea.

Similar to the cross-slope component, both active and passive mechanisms exist for the cross-slope transport of young P. saltatrix. Flow in the MAB is primarily alongshelf, toward the southwest (Bumpus 1973; Beardsley et al. 1976). Slope-water intrusions in and below the seasonal thermocline (15–30 m) result in onshore, cross-slope flow (see Flagg et al. 1994 and references therein). However, larval and pelagic juvenile P. saltatrix are surface oriented (Kendall and Naplin 1981; Shima 1989; Sabates and Martin 1993), and thus, slope-water intrusions cannot be responsible for the cross-slope transport of young P. saltatrix. Wind-driven surface flow, which is rotated to the right (in the northern hemisphere) of the wind direction, could advect P. saltatrix larvae across the MAB shelf. Winds out of the northeast, east, or southeast would create onshore flow in the MAB. Finally, horizontal swimming is a possible cross-slope larval transport mechanism for the reasons discussed above.

Our purpose was to examine the roles of the various active and passive larval transport mechanisms outlined above with respect to SAB-spawned P. saltatrix larvae. Each of the three components of the larval transport route was analyzed separately.

Materials and methods

General approaches—The analysis of Gulf Stream-associated larval transport involved a series of ichthyoplankton cruises conducted in the northern SAB and southern MAB. P. saltatrix larval densities were examined in terms of water mass designations. Additionally, larval length distributions were tested for differences between water masses, within cruises, using pairwise Mann-Whitney U-tests (Sokal and Rohlf 1981; Wilkinson 1990).

Mechanisms of cross-slope larval transport were evaluated by calculating Pearson correlation coefficients (Sokal and Rohlf 1981) between recruitment magnitude of spring-spawned P. saltatrix to three MAB estuaries and two physical variables: warm-core ring streamer activity and the average Gulf Stream-shelf break distance. If warm-core ring streamers advect P. saltatrix across the slope sea, recruitment magnitude should be positively correlated with warm-core ring streamer activity. Alternatively, Shima (1989) hypothesized that the closer the Gulf Stream comes to the MAB shelf break south of New England, the greater the recruitment of SAB-spawned P. saltatrix. Although the mechanism was not stipulated, one possible interpretation is that P. saltatrix swims across the slope sea, and as cross-slope distance decreases, the number of individuals that can successfully swim across the slope sea increases.

The potential mechanisms of cross-shelf transport of young P. saltatrix were also evaluated via correlations. If wind-driven flow advects larvae across the shelf, the time of recruitment should be linked to wind events that create onshore surface flow (i.e. winds out of the northeast, east, or southeast). Recruitment time was examined relative to wind speed and direction and also relative to progressive vector diagrams of estimated wind-driven surface transport. Alternatively, if P. saltatrix juveniles swim across the shelf, their time of recruitment should be linked to when they begin swimming. The distribution of pelagic juveniles on the MAB shelf was examined to identify potential causes of the initiation of swimming, and subsequently, correlations between recruitment time and shelf temperature characteristics were calculated.

Cape Hatteras region ichthyoplankton cruises—Four ichthyoplankton cruises were conducted in the Cape Hatteras region from late March to mid-June over the course of 3 yr on board the NOAA Ship Ferrel (Table 1). Larval fish were collected with a 505-μm mesh, opening-closing 1-m² Tucker trawl at three discrete depths (0–5, 5–10, and 10–15 m). The net was positioned at depth with the wire angle and wire out. The tow time for each net was 5 min. A General Oceanics flowmeter was attached to the net bridle, allowing volume filtered to be calculated. All samples were split onboard with a Folsom plankton splitter; half of each sample was preserved in 5% Formalin and the other half in 95% ethanol. Fish larvae were sorted
Table 1. List of ichthyoplankton cruises conducted in the region around Cape Hatteras, North Carolina. Total stations sampled (1), number of Pomatonus saltatrix larvae collected (2), number of stations with P. saltatrix larvae (3), and average density (No. 100 m\(^{-3}\)) of P. saltatrix larvae (4) are shown. Average larval density was calculated by dividing the total number of larvae collected during a cruise by the total volume of water sampled at stations where larvae were collected.

<table>
<thead>
<tr>
<th>Cruise</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>FE-1-89</td>
<td></td>
<td></td>
<td></td>
<td>1.16</td>
</tr>
<tr>
<td>FE-1-90</td>
<td>25–29</td>
<td>31</td>
<td>106</td>
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<td>21</td>
<td>88</td>
<td>8.14</td>
</tr>
<tr>
<td>FE-1-91</td>
<td>22–29</td>
<td>36</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>FE-2-91</td>
<td>11–17</td>
<td>29</td>
<td>704</td>
<td>9</td>
</tr>
</tbody>
</table>

from Formalin halves and identified to the lowest taxonomic level possible.

The total number of P. saltatrix larvae collected at a station (corrected for the initial sample split at sea) and the total volume filtered were used to calculate P. saltatrix larval density. Larval densities were also calculated for each net with the volume of the 10–15-m net taken as 6/16 of the total volume, and the volumes for the 5–10- and 0–5-m nets were taken as 5/16 of the total volume. All P. saltatrix were measured to the nearest 0.1 mm with a computer-enhanced video microscope image.

Temperature and salinity data were collected with an Applied Microsystems CTD (AMS-12) deployed to within 1 m of the bottom or to 75 m, whichever was shallowest. Temperature-salinity (T–S) diagrams were used to identify water masses based on Churchill et al. (1993) and Pietrafesa et al. (1994) (Fig. 3).

Estuarine recruitment data—Data on the timing and magnitude of spring-spawned P. saltatrix recruitment to MAB estuaries were obtained from three seine surveys (Table 2). Data from Jamaica Bay, New York, for 1984–1992 were provided by K. McKown (B. H. Young et al. unpubl. rep.). Data from Great South Bay, New York, for 1985–1992 were obtained from Nyman (1987), McBride (1989), Juanes (1992), and Buckel et al. (unpubl. data). Annual recruitment of spring-spawned P. saltatrix was calculated by averaging their catch from the first date of collection through 31 July; summer-spawned P. saltatrix begins to enter these same estuaries in early August (McBride and Conover 1991; McBride et al. 1995). Annual recruitment magnitude of spring-spawned P. saltatrix for Narragansett Bay, Rhode Island, was obtained from McBride et al. (1995).

The annual magnitude of SAB-spawned P. saltatrix recruitment to MAB estuaries was calculated from the catch-per-unit-effort (CPUE) data of the three surveys. Because variances in annual catch among surveys were not significantly different (F\(_{\text{max-test}}\) = 2.77, P > 0.10), the standard deviate was calculated as

\[
\hat{\sigma}_{c_j} = \frac{c_j - \bar{c}_j}{\sigma_{c_j}}.
\]

Fig. 3. Temperature-salinity diagrams illustrating the water mass boundaries north (A) and south (B) of Cape Hatteras. Three water masses are recognized north of Cape Hatteras: Gulf Stream (GS), Virginia shelf (VS), and slope sea (SS). Slope sea water was defined as having salinities intermediate between Virginia shelf and Gulf Stream water. Three water masses were also recognized south of Cape Hatteras: Gulf Stream (GS), outer Carolina shelf (OCS) and inner Carolina shelf (ICS). Inner Carolina shelf water was defined as having salinities less than outer Carolina shelf water. South of Cape Hatteras, Gulf Stream water included T–S data that fell within the Gulf Stream envelope, but it may also be outer Carolina shelf water because the two overlap.

\(\hat{\sigma}_{c_j}\) is the standard deviate of the log-transformed spring-spawned P. saltatrix catch for year \(i\) in survey \(j\). \(c_j\) is the log-transformed catch for year \(i\) from survey \(j\), \(\bar{c}_j\) is the average log-transformed catch for survey \(j\), and \(\sigma_{c_j}\) is the SD of the log-transformed catch for survey \(j\). Recruitment strength for each year was then calculated as
Table 2. Annual magnitude and time of South Atlantic Bight-spawned *Pomatomus saltatrix* recruitment to three Middle Atlantic Bight estuaries: Jamaica Bay (JB), Great South Bay (GSB), and Narragansett Bay (NB). For each bay, the average log-transformed number of *P. saltatrix* collected before 1 August is given, as well as the number of seine hauls made between the first collection date of *P. saltatrix* and 31 July. Recruitment index (RI) was calculated as described in the text. Estimated recruitment times (RT) were based on a combination of data from Jamaica Bay and Great South Bay. The difference between first (1) and first strong (2) recruitment is described in the text. The range in these estimates is presented in Fig. 8. The number of sampling dates (3) used in the estimation of recruitment time is shown.

<table>
<thead>
<tr>
<th>Year</th>
<th>JB log CPUE</th>
<th>Hauls</th>
<th>GSB log CPUE</th>
<th>Hauls</th>
<th>NB log CPUE</th>
<th>Hauls</th>
<th>RI</th>
<th>RT 1</th>
<th>RT 2</th>
<th>RT 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>0.55</td>
<td>19</td>
<td>nd</td>
<td>0</td>
<td>nd</td>
<td>0</td>
<td>-1.04</td>
<td>150</td>
<td>150</td>
<td>5</td>
</tr>
<tr>
<td>1985</td>
<td>1.15</td>
<td>4</td>
<td>1.13</td>
<td>46</td>
<td>1.14</td>
<td>16</td>
<td>0.70</td>
<td>143</td>
<td>143</td>
<td>7</td>
</tr>
<tr>
<td>1986</td>
<td>1.16</td>
<td>18</td>
<td>1.19</td>
<td>45</td>
<td>1.12</td>
<td>16</td>
<td>0.86</td>
<td>158</td>
<td>158</td>
<td>10</td>
</tr>
<tr>
<td>1987</td>
<td>2.19</td>
<td>22</td>
<td>0.53</td>
<td>58</td>
<td>1.12</td>
<td>16</td>
<td>0.77</td>
<td>154</td>
<td>163</td>
<td>14</td>
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<tr>
<td>1988</td>
<td>0.48</td>
<td>14</td>
<td>0.63</td>
<td>42</td>
<td>0.65</td>
<td>16</td>
<td>-0.84</td>
<td>155</td>
<td>170</td>
<td>13</td>
</tr>
<tr>
<td>1989</td>
<td>1.21</td>
<td>18</td>
<td>0.46</td>
<td>135</td>
<td>1.02</td>
<td>16</td>
<td>0.08</td>
<td>151</td>
<td>168</td>
<td>15</td>
</tr>
<tr>
<td>1990</td>
<td>0.77</td>
<td>15</td>
<td>0.67</td>
<td>60</td>
<td>0.68</td>
<td>16</td>
<td>-0.77</td>
<td>161</td>
<td>165</td>
<td>13</td>
</tr>
<tr>
<td>1991</td>
<td>0.97</td>
<td>27</td>
<td>nd</td>
<td>0</td>
<td>0.72</td>
<td>16</td>
<td>-0.30</td>
<td>156</td>
<td>163</td>
<td>8</td>
</tr>
<tr>
<td>1992</td>
<td>1.16</td>
<td>17</td>
<td>0.76</td>
<td>61</td>
<td>0.38</td>
<td>16</td>
<td>-0.39</td>
<td>164</td>
<td>166</td>
<td>8</td>
</tr>
</tbody>
</table>

$R_i = \frac{\sum \hat{C}_i}{n_i}$.

$R_i$ is the standardized recruitment index of spring-spawned *P. saltatrix* for year $i$. $\sum \hat{C}_i$ is the summation of standard deviations over all surveys sampling in year $i$, and $n_i$ is the number of surveys sampling in year $i$.

Recruitment time was estimated for spring-spawned *P. saltatrix* from the temporal record of catches in Jamaica Bay and Great South Bay. Sampling in Jamaica Bay was approximately biweekly; sampling in Great South Bay was approximately weekly. Data from Narragansett Bay were not used because sampling was monthly. Estimated time of first recruitment was taken as the midpoint between the last sampling day with no *P. saltatrix* collected and the first sampling day with *P. saltatrix* collected. In some years, initial recruitment was low (<1 CPUE), and then at some later time, the numbers of *P. saltatrix* increased rapidly. Estimated first strong recruitment was taken as the midpoint between sampling dates that exhibited an increase in catch CPUE.

**Warm-core ring streamers**—Satellite-derived, infrared images of sea-surface temperature (archived at the University of Rhode Island) were used to estimate activity of warm-core ring streamers. Images from 1 April to 31 May 1984–1992 were examined. Warm-core ring streamers were identified as warmer Gulf Stream water wrapped around the western edge of warm-core rings (Fig. 2). If the slope sea was covered by clouds in a given image, the image was not used in the analysis. If a warm-core ring streamer was present in two consecutive images, it was assumed that it was present for all days between images. If a warm-core ring streamer was present in one image but not in the image immediately preceding or following, it was assumed that the streamer was present for half of the days between the two images (see Zheng et al. 1984; Evans et al. 1985) (Table 3).

<table>
<thead>
<tr>
<th>Streamers present</th>
<th>GS-shelf break distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>Days</td>
</tr>
<tr>
<td>1984</td>
<td>0</td>
</tr>
<tr>
<td>1985</td>
<td>53</td>
</tr>
<tr>
<td>1986</td>
<td>36</td>
</tr>
<tr>
<td>1987</td>
<td>56</td>
</tr>
<tr>
<td>1988</td>
<td>7</td>
</tr>
<tr>
<td>1989</td>
<td>12</td>
</tr>
<tr>
<td>1990</td>
<td>0</td>
</tr>
<tr>
<td>1991</td>
<td>20</td>
</tr>
<tr>
<td>1992</td>
<td>0</td>
</tr>
</tbody>
</table>

**Gulf Stream-MAB shelf edge distance**—The distance from the Gulf Stream to MAB shelf break was measured from oceanographic feature analysis charts produced by the Ocean Data Products division of NOAA. Weekly charts from 1 April to 31 May 1984–1992 were used. Charts depict the northern wall of the Gulf Stream based on infrared satellite imagery. The distance due south of Montauk Point from the shelf edge to the Gulf Stream was measured from available charts, and the mean for each year was calculated (Table 3).

**Wind data analyses**—Hourly wind speed and direction data were obtained for Ambrose Light from the National
Oceanic Data Center. Data from March 1 to 30 June for 1985–1992 were analyzed. Wind stress (τ, dyn cm⁻²) was calculated as

$$\tau = \rho_a C_d WS^2.$$  

ρₐ is the density of air (assumed to be 0.0012 g cm⁻³), WS is wind speed (cm s⁻¹), and C_d is the drag coefficient, which is dependent on wind speed (Large and Pond 1981):

$$C_d = 1.14 \times 10^{-3} \quad \text{if } WS > 10 \text{ ms}^{-1};$$

$$C_d = (0.49 + 0.065 WS) \times 10^{-3} \quad \text{if } WS > 10 \text{ ms}^{-1}.$$  

Progressive vector diagrams of the estimated wind-driven surface flow were calculated as follows (Price et al. 1987; Epifanio et al. 1989):

$$V_0 = \tau/\rho_w(Af)^{1/2}.$$  

V₀ equals the estimated current speed at the surface (cm s⁻¹), ρₚ is the density of seawater (assumed to be 1.025 g cm⁻³), A is a kinematic viscosity coefficient (assumed to be 60 cm² s⁻¹), and f is the Coriolis parameter (9.3718 x 10⁻⁵). The value used for kinematic viscosity is relatively low (Price et al. 1987), thereby maximizing the estimated wind-driven surface velocity.

Because of the range in the reported direction of wind-driven surface flow (see Madsen 1977; Price et al. 1987), estimated surface current vectors were calculated for both a 10⁰ and a 45⁰ rotation. The surface speeds (cm s⁻¹) were transformed to hourly displacements (km h⁻¹), which were then used to develop progressive vector diagrams for the 30 d before the last possible day of first strong recruitment. The purpose was to evaluate whether predicted wind-driven flow, calculated to maximize its values would be in the appropriate direction and of the necessary magnitude to advect P. saltatrix across the MAB shelf.

**MAB ichthyoplankton cruises** — Distributions of pelagic juvenile P. saltatrix along the MAB shelf edge were determined during two cruises (1–3 and 10–16 June 1988) on the NOAA Ship Delaware II. This portion of our study represents a reanalysis of data initially presented by Shim (1989). Station locations and sampling methods are fully described by Cowen et al. (1991). Briefly, a 5-m³, 2-mm-mesh neuston net was towed for 10 min at 7.4 km h⁻¹ off the side of the ship. Samples were preserved in 95% ethanol, and all fish were identified to the lowest possible taxonomic level.

A Martek Mark VI multiparameter recorder was deployed at all stations. Temperature, conductivity, and depth measurements were made every meter from the surface to ~70 m, or to within 10 m of the bottom. Cross-shelf salinity, temperature, and density profiles were examined relative to the distributions of pelagic juvenile P. saltatrix.

**Temperature characteristics of the MAB shelf** — Surface temperature data for the MAB shelf were obtained from the NOAA Ship of Opportunity Program (SOOP) (Benway et al. 1993). Data along a 180-km transect (from

<table>
<thead>
<tr>
<th>Year</th>
<th>No. SOOP cruises</th>
<th>Warming rate b</th>
<th>31 Mar temp. a</th>
<th>r²</th>
</tr>
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<tr>
<td>1984</td>
<td>6</td>
<td>0.186</td>
<td>3.781</td>
<td>1.423</td>
</tr>
<tr>
<td>1985</td>
<td>5</td>
<td>0.175</td>
<td>4.880</td>
<td>1.735</td>
</tr>
<tr>
<td>1986</td>
<td>3</td>
<td>0.137</td>
<td>7.970</td>
<td>2.459</td>
</tr>
<tr>
<td>1987</td>
<td>4</td>
<td>0.148</td>
<td>4.263</td>
<td>1.850</td>
</tr>
<tr>
<td>1988</td>
<td>3</td>
<td>0.128</td>
<td>5.272</td>
<td>1.329</td>
</tr>
<tr>
<td>1989</td>
<td>4</td>
<td>0.174</td>
<td>5.077</td>
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</tr>
<tr>
<td>1990</td>
<td>9</td>
<td>0.143</td>
<td>5.852</td>
<td>1.321</td>
</tr>
<tr>
<td>1991</td>
<td>9</td>
<td>0.148</td>
<td>7.075</td>
<td>1.234</td>
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<tr>
<td>1992</td>
<td>3</td>
<td>0.116</td>
<td>5.516</td>
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</tbody>
</table>

Ambrose Light toward Bermuda) from 1 April to 30 June 1984–1992 were used. A linear regression of temperature on year-day was calculated, and the resulting slope was used as an estimate of the rate of shelf-water warming. Temperature on year-day 90 (31 March) was estimated from the regression equation; lowest shelf temperatures are typically observed in late March or early April (Ketchum and Corwin 1964) (Table 4).

### Results

**Larval distributions in the Cape Hatteras region** — P. saltatrix larvae were collected in the vicinity of Cape Hatteras during three of four cruises (Table 1). In March 1991, sampling was conducted from north of Cape Hatteras to south of Cape Lookout, but no P. saltatrix larvae were collected. In March 1990, P. saltatrix larvae were collected throughout the area sampled and densities were highest along the southern transect (Fig. 4A). P. saltatrix larvae were also collected throughout the sampling area in April 1989 (Fig. 4B). In June 1991, sampling was conducted from Cape Hatteras to Cape May, but P. saltatrix larvae were found only south of Chesapeake Bay (Fig. 4C).

In March 1990, P. saltatrix larvae were collected predominantly in outer Carolina shelf water with T-S characteristics close to Gulf Stream water (Fig. 5A). In April 1989, moderate densities of P. saltatrix larvae were collected in both Gulf Stream and outer Carolina shelf water. Low densities of larvae were found in slope sea water, inner Carolina shelf water, and Virginia shelf water (Fig. 5B). In June 1991, large numbers of P. saltatrix larvae were collected in water fresher than Virginia shelf water, which represents the influence of the Chesapeake Bay plume (Pietrafesa et al. 1994). Lower larval densities were found in Gulf Stream water, and moderate densities were found in water with T-S characteristics intermediate between Gulf Stream and Virginia shelf water (Fig. 5C), which represents either slope sea water or outer Carolina
shelf water moving in association with the Gulf Stream (Churchill et al. 1993).

During March 1990, smaller (<5 mm) *P. saltatrix* larvae were found predominantly in Gulf Stream water, and larger larvae (>5 mm) were restricted to outer Carolina shelf water (Fig. 6); the length distributions from these two water masses were significantly different (Mann-Whitney U-test, \( P < 0.05 \)). Similarly, in April 1989, larger *P. saltatrix* larvae were found in SAB shelf water than in Gulf Stream water (Mann-Whitney U-test, ICS vs. OCS, \( P < 0.05 \); ICS vs. GS, \( P < 0.01 \); OCS vs. GS, \( P < 0.05 \)). *P. saltatrix* larvae collected in the slope sea were not significantly larger than those collected in the Gulf Stream (Mann-Whitney U-test, \( P > 0.05 \)). In June 1991, when sampling was focused north of Cape Hatteras, larval sizes increased from the fresher Virginia shelf water to slope sea (Mann-Whitney U-test, \( P < 0.001 \)) and Gulf Stream water (Fig. 6).

**Warm-core ring streamers, Gulf Stream−shelf edge distance, and recruitment magnitude**—A significant correlation was found between warm-core ring streamer activity and the recruitment index (Fig. 7A, \( r = 0.916, P < 0.01 \)). Recruitment to Jamaica and Narragansett Bays was significantly correlated with activity of warm-core ring

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**Fig. 4.** Distribution of *Pomatomus saltatrix* larvae during three cruises in the Cape Hatteras region. A. March 1990. B. April 1989. C. June 1991. Stations—O: histograms represent *P. saltatrix* larval density. The scales for panels A and B are different than for panel C. Dotted lines represent the 200-m isobath.

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streamers (\( r = 0.724, P < 0.05 \); \( r = 0.876, P < 0.05 \), respectively); recruitment to Great South Bay was not (\( r = 0.557, P > 0.05 \)).

The relationship between Gulf Stream−shelf edge distance and the recruitment index was not significant (Fig. 7B, \( r = -0.091, P > 0.05 \)). Similarly, the correlations between Gulf Stream−shelf edge distance and recruitment to each of the estuaries were not significant (Jamaica Bay, \( r = 0.169, P > 0.05 \); Great South Bay, \( r = -0.508, P > 0.05 \); Narragansett Bay, \( r = 0.126, P > 0.05 \)).

**Wind and recruitment time**—In several years (e.g. 1985, 1986, 1990), wind stresses toward the northeast were strong around the time of recruitment (Fig. 8). In other years (1987, 1988, 1989, 1991) northeastward wind stresses occurred around the time of recruitment but at lower magnitudes (Fig. 8). The difference in magnitude of northeastward wind stress reflects the years during which first recruitment and first strong recruitment occurred simultaneously and separately (Fig. 8).

Progressive vector diagrams indicated that in most years, wind-driven surface flow was not in the appropriate direction nor of sufficient magnitude to transport young *P. saltatrix* across the MAB shelf. In 1992, estimated displacement of surface water for the 30 d before recruit-
ment was from the shelf break to the MAB coast. In the other 7 yr, estimated wind-driven surface transport was along the shelf or offshore; maximum cross-shelf displacement in these years was only half of the shelf width (Fig. 9). However, the effect of northeastward winds just before recruitment can be seen as either northeastward or eastward displacement over the last 10 d of the series (Fig. 9).

Pelagic juvenile distributions in the Middle Atlantic Bight—During the first cruise (1–3 June), 27 pelagic juvenile *P. saltatrix* were captured in the vicinity of the MAB shelf break (Fig. 10). Ten days later (10–16 June), in more extensive sampling, only three pelagic juveniles were collected more to the north and farther inshore (Fig. 10). The estimated day of first recruitment in 1988 was 4 June (range 1–8 June) (Table 2), suggesting that the two cruises bracketed the time during which *P. saltatrix* pelagic juveniles crossed the shelf.

Analysis of cross-shelf temperature distributions demonstrated that the shelf-slope surface temperature front dissipated between the two cruises. In early June, the shelf-slope temperature front was about 130 km offshore and extended from 70 m to the surface (Fig. 11A). Pelagic *P. saltatrix* juveniles were collected offshore of the front in warmer slope sea water (Fig. 11A). In mid-June, along a similar cross-shelf transect, the shelf-slope temperature front was ~130 km offshore but did not extend to the surface; surface temperatures were nearly isothermal across the entire shelf and into the slope sea (Fig. 11B). No pelagic *P. saltatrix* juveniles were collected along this transect (Fig. 11B).

Recruitment timing and shelf temperatures—The timing of *P. saltatrix* estuarine recruitment was significantly correlated with the rate of warming on the MAB shelf but not with 31 March temperature (Fig. 12). Pearson correlation coefficients between 31 March temperature and recruitment time were 0.461 ($P > 0.05$) for first recruitment and 0.213 ($P > 0.05$) for first strong recruitment (Figs. 12A,C). Pearson correlation coefficients between shelf warming rate and recruitment time were $-0.824$ ($P < 0.01$) for first recruitment and $-0.626$ ($P < 0.05$) for first strong recruitment (Figs. 12B,D).

Discussion

Transport of *P. saltatrix* larvae from SAB spawning grounds to MAB estuarine nursery habitats is complex and involves a variety of mechanisms and water masses. Previous ichthyoplankton studies have found that during spring, *P. saltatrix* larvae are primarily distributed on the outer SAB shelf (Kendall and Walford 1979; Collins and Stender 1987). Our results support these findings and
show that south of Cape Hatteras, most larvae are distributed in outer Carolina shelf and Gulf Stream water (Fig. 5). These water masses typically move northeastward at velocities of 50–100 cm s\(^{-1}\) (Lee and Atkinson 1983; Glenn and Ebbesmeyer 1994), indicating that \(P.\) \(s\)altatrix larvae move out of the SAB in association with these flows.

Analysis of length frequencies suggest that some spring-spawned \(P.\) \(s\)altatrix larvae are retained within the SAB. Larger larvae were found in inner Carolina shelf water, implying onshore transport (Fig. 6) (see also Collins and Stender 1987). McBride et al. (1993) found that spring-spawned \(P.\) \(s\)altatrix larvae recruit to SAB estuaries but in much lower numbers than to MAB estuaries. This recruitment pattern is consistent with the larval data; some SAB-spawned \(P.\) \(s\)altatrix are retained in the SAB and recruit to SAB estuaries, but most larvae are exported from the SAB and recruit to MAB estuaries.

The possibility of larval retention in the SAB is pertinent to the fate of \(P.\) \(s\)altatrix larvae spawned in fall. During September and November, \(P.\) \(s\)altatrix larvae are distributed on the outer SAB shelf (Collins and Stender 1987). Presumably, most of these larvae are advected out of the SAB in association with the Gulf Stream, which is similar to the fate of larvae spawned in the SAB in spring. In fall, however, it is unlikely that exported larvae could survive north of Cape Hatteras because temperatures are too low (5–10°C, Ketchum and Corwin 1964). The only chance for survival of fall-spawned larvae is retention in the SAB. Several studies have found evidence of fall-spawned \(P.\) \(s\)altatrix juveniles in SAB estuaries (Wenner and Sedberry 1989, McBride et al. 1993), which is compatible with the idea of limited retention of larvae in the SAB.

Following Gulf Stream-associated northward transport, \(P.\) \(s\)altatrix larvae must cross the slope sea. A strong relationship was found between warm-core ring streamer activity and SAB-spawned \(P.\) \(s\)altatrix recruitment to MAB estuaries (Fig. 7A), indicating that streamers are an important cross-slope transport mechanism. Cross-slope transport of other SAB-spawned larvae (e.g. \(B\)othus sp., \(X\)yrich\(t\)ys \(n\)ov\(a\)c\(u\)l\(a\)) has also been linked to warm-core ring streamers (Hare and Cowen 1991; Cowen et al. 1993). However, in years with no streamer activity (1984, 1990, 1992), \(P.\) \(s\)altatrix still recruited to MAB estuaries, implying that other cross-slope transport mechanisms (e.g. wind-driven flow, Gulf Stream meanders, horizontal swimming) supply low numbers of \(P.\) \(s\)altatrix to the shelf edge.

Shima (1989) proposed that the Gulf Stream’s path north of Cape Hatteras may enhance SAB-spawned \(P.\) \(s\)altatrix recruitment through decreasing the cross-slope distance that larvae must transverse. The nonsignificant correlations between Gulf Stream–shelf edge distance and SAB-spawned \(P.\) \(s\)altatrix recruitment that we found (Fig. 7B) do not support this hypothesis. In addition, Bane et al. (1988) found that southwestward current velocity along the MAB shelf break was negatively correlated with the distance from the shelf break to the Gulf Stream front; as the distance between the Gulf Stream and MAB shelf decreased, southwestward current velocities along the shelf break increased. Thus, \(P.\) \(s\)altatrix estuarine recruitment may be inhibited when the Gulf Stream is close to the shelf edge, because stronger southwestward flows would
Fig. 7. A. Index of annual recruitment of South Atlantic Bight-spawned Pomatomus saltatrix to Middle Atlantic Bight estuaries and annual estimates of warm-core ring streamer activity, 1 April to 31 May 1984–1992. B. As panel A, but of annual average distance from the Gulf Stream to the shelf edge.

ad vect larvae away from northern MAB estuaries. The study of Bane et al. (1988) was based on current meters deployed along the shelf edge at \( \sim 200 \) m, and thus, the effect of the distance to the Gulf Stream on surface flow along the MAB shelf break remains uncertain. Clearly, a more thorough understanding of the physical oceanography of the slope sea is needed to clarify the cross-slope transport mechanisms utilized by young P. saltatrix.

The final component of P. saltatrix transport from SAB spawning grounds to MAB nearshore habitats is movement across the MAB shelf. Two potential mechanisms were evaluated: wind-driven flow and active horizontal swimming. Analyses of wind stress indicated that recruitment time may be linked to the occurrence of winds blowing out of the southwest (Fig. 8). Progressive vector diagrams showed that these winds would create either along shelf (toward the northeast) or offshore (toward the east-southeast) surface flow (Fig. 9). These calculations do not reflect the actual flow on the MAB shelf, which is predominantly to the southwest. The progressive vector diagrams do, however, provide an indication of the magnitude of cross-shelf transport at the surface that could be explained by wind stress. On the basis of these calculations, wind-driven surface flow does not appear capable of advecting P. saltatrix across the shelf. The potential relationship between southwest wind events and P. saltatrix recruitment deserves further examination. On the MAB shelf, southwest winds result in a slowing or reversal of the average southwestward flow (Epifanio et al. 1989; Flagg et al. 1994), which may facilitate the cross-shelf transport of young P. saltatrix.

The analysis of pelagic juvenile distributions, estuarine

Fig. 8. Estimated hourly wind stress at Ambrose Light, 1985–1992. The oceanographic convention is used (i.e. southwest winds create wind vectors pointing toward the northeast). Estimated time of first recruitment is shown as shaded bars; estimated time of first strong recruitment is shown as open bars. The middle of a bar is the time of recruitment and the extent of a bar is the range of the estimate. Where no open bars are present, the two estimates of recruitment time were equal.
recruitment time, and shelf temperature characteristics supports the hypothesis that *P. saltatrix* pelagic juveniles begin swimming across the shelf when the surface shelf-slope temperature front dissipates in late spring-early summer. Several studies (Kendall and Walford 1979; Smith et al. 1994; this study Fig. 5) have identified a minimum temperature for the occurrence of *P. saltatrix* larvae (15–18°C) and pelagic juveniles (13–15°C). Thus, pelagic juveniles would not cross onto the MAB shelf until the surface shelf-slope temperature front breaks down. This conclusion is supported by the distributions of pelagic juveniles (Figs. 10, 11) and the analysis of recruitment time relative to shelf warming rates (Fig. 12B,D).

Directed swimming by pelagic juvenile fish has rarely been invoked as a horizontal transport mechanism (but see Cowen et al. 1991; Werner et al. 1993). The distance across the MAB shelf is 100–130 km. From the 1988 data presented above, *P. saltatrix* pelagic juveniles apparently crossed the shelf in 3–18 d, which equates to sustained cross-shelf swimming speeds of 6–50 cm s⁻¹ or, given the size of pelagic juveniles collected offshore (35 mm, Shima 1989), 1.7–14.3 body lengths s⁻¹. These estimated speeds
Mechanisms of larval transport

Fig. 10. Station locations and distributions of pelagic juvenile Pomatomus saltatrix for two cruises conducted in the central Middle Atlantic Bight (1-3 and 10-16 June).

are in line with recent work on the swimming capabilities of larval and pelagic juvenile coral reef fish (Stobutzki and Bellwood 1994; Stobutzki pers. comm.).

In addition to being physically able to swim across the shelf, P. saltatrix pelagic juveniles would need to have a mechanism for orienting their swimming behavior (e.g. celestial navigation, magnetic navigation, temperature-mediated movements, salinity-mediated movements, and rheotaxis, see McCleave et al. 1984). Leis et al. (1996) found that late-stage larvae of a variety of coral reef fish exhibited directional horizontal swimming away from reefs; the mechanism, however, was equivocal. In light of these recent studies, active horizontal swimming behavior can no longer be dismissed; it clearly plays an important role in the transport of the early life history stages of fish. Future work needs to examine the ontogenetic development of active swimming behavior and must identify the mechanisms of orientation used by fish larvae and pelagic juveniles.

Based on our results, we propose a mechanistic scenario for the transport of SAB-spawned P. saltatrix to nearshore habitats in the MAB. This proposed scenario should be viewed as a working hypothesis, the various components of which require further testing. From March through at least May, P. saltatrix spawns on the outer SAB shelf where the flow is primarily influenced by the Gulf Stream. Gulf Stream-associated transport results in the export of most P. saltatrix larvae out of the SAB. Transport of larvae across the slope sea is largely dependent on warm-core ring streamers. Other advective mechanisms (e.g. wind-driven flow, Gulf Stream meanders, and discharges) may contribute to cross-slope transport of larvae and some, more developed individuals (e.g. pelagic juveniles) may swim across the slope sea. P. saltatrix larvae and pelagic juveniles then accumulate on the slope sea side of the surface shelf-slope temperature front. This front acts as a thermal barrier, but once the surface expression dissipates, P. saltatrix pelagic juveniles begin to swim across the shelf to nearshore juvenile habitats. Wind-driven flow may be involved in the cross-shelf transport of P. saltatrix but not as the primary mechanism (Fig. 13).

This proposed scenario of P. saltatrix transport from SAB spawning grounds to MAB estuaries is supported by quasi-Lagrangian, satellite-tracked surface drifters. Drifters released in the SAB exhibited north-eastward transport in association with the Gulf Stream (Glenn and Ebbesmeyer 1994). Transport of drifters across the slope sea occurs primarily in association with warm-core rings (Dragos et al. 1996). There is some evidence, however, for cross-slope transport associated with discharges of Gulf Stream water as described by Churchill and Cornillon (1991a, b). Finally, drifter data show that there is
very little surface exchange between the slope sea and MAB shelf, supporting the conclusion that the cross-shelf transport of *P. saltatrix* is not a result of passive, wind-driven advection (Dragos et al. 1996).

Important questions remain relating to the transfer of *P. saltatrix* larvae between the various components of northward transport. One example is that while the basic mechanisms of SAB shelf-water entrainment have been identified (e.g. Glenn and Ebbesmeyer 1994), the influence of these entrainment processes on larval transport is only beginning to be investigated (Govoni 1993; Govoni and Pietrafesa 1994). The fate of SAB shelf water along the edge of the Gulf Stream north of Cape Hatteras may also be important. Lillibridge et al. (1990) found that subsurface MAB shelf water is entrained by and then subducted along Gulf Stream-associated flows. The behavior of surface SAB shelf water is an open question, but one with important consequences for the export of *P. saltatrix* larvae out of the SAB. Additionally, the nature of warm-core ring streamer formation is not clear. Streamers have been investigated by remote sensing (Zheng et al. 1984; Evans et al. 1985) and physical models (Nof 1988), but there have been no detailed physical or biological studies of these features. Finally, there is the question of how *P. saltatrix* larvae and pelagic juveniles move out of warm-core ring streamers at the shelf edge. Drifters that are entrained in streamers also leave these features at the MAB shelf edge (Dragos et al. 1996), but the mechanism is unknown.

The fate of *P. saltatrix* larvae spawned in the southern MAB is another important issue. Data from June 1991 (Figs. 4C, 7C) indicated that larvae were transported off the MAB shelf into the slope sea, a conclusion also reached by Norcross et al. (1974). Previously, we have proposed that *P. saltatrix* larvae spawned in the southern MAB are in the slope sea at the time they normally enter estuaries and thus, their probability of estuarine recruitment is lower than fish spawned in either the SAB or the northern MAB (Hare and Cowen 1993). A problem with this hypothesis is why *P. saltatrix* larvae spawned in the southern MAB do not cross the slope sea, and *P. saltatrix* larvae spawned in the SAB do. Differential larval transport may result from differences in the fate of SAB and MAB shelf water incorporated into Gulf Stream flows. Another possibility is that the loss of these fish is a consequence of the developmental timing of horizontal swimming behavior in relation to the extent of their downstream transport. Both these hypotheses need to be addressed.

One drawback of this proposed scenario is that it is based on correlations. For example, a significant correlation was found between the activity of warm-core ring streamers and recruitment of SAB-spawned *P. saltatrix*, with high recruitment and streamer activity co-occurring in 1985, 1986, and 1987 (Fig. 7A). It is possible, however, that declines in adult abundance (NEFSC 1994, 1995) were responsible for decreasing recruitment during the time series examined, as opposed to the activity of warm-core ring streamers. This hypothesis is not supported by the data; the correlation coefficient between the estimates of spawning stock biomass (NEFSC 1994, 1995) and our recruitment index of SAB-spawned *P. saltatrix* is not significant ($r = 0.372$, $P > 0.10$). Thus, although the correlations in this study do not demonstrate causation, they do allow a detailed transport scenario to be proposed (Fig. 13).

Another drawback to our study is that it includes relatively small sample sizes collected over a large spatial and temporal domain. Larval cruises were conducted in different months and years and in three of the four cruises <110 larvae were collected (Table 1). In addition, the analysis of pelagic juvenile distribution along the MAB shelf-slope front is based on two successive cruises that collected only 30 pelagic juvenile *P. saltatrix* (Fig. 10). Acknowledging these limitations, our study has allowed the development of a mechanistic transport scenario that is consistent with previous studies of larval *P. saltatrix* distributions, available physical oceanographic studies, and other larval transport studies. Process-oriented work should now be conducted to test the various aspects of our proposed scenario.

One approach to test our transport scenario is to collect ichthyoplankton along the proposed transport route with
concomitant collection of hydrographic data and Eulerian and Lagrangian current data. These data would allow direct determination of the transport speed and direction of *P. saltatrix* larvae. Alternatively, each step of the proposed transport route could be investigated separately.

For example, a study of the physical structure of the shelf-slope front in relation to the distribution of young *P. saltatrix* could be coupled with laboratory studies of swimming ability and orientation mechanisms. Such process-oriented work would lead to a coupled biological-physical model of larval transport, which could be used to predict future recruitment of spring-spawned *P. saltatrix*.

Similarities exist in the larval transport scenario proposed here and that described for other species in the SAB-MAB system. For example *Bothus* spp. and *X. novacula* larvae are apparently transported northeastward in association with the Gulf Stream and across the slope sea in warm-core ring streamers (Hare and Cowen 1991; Cowen et al. 1993). The Gulf Stream and warm-core ring streamers may also be responsible for the northward transport of other species that reproduce south of Cape Hatteras but recruit to juvenile habitats in the MAB (e.g. *Anguilla rostrata*, *Conger oceanicus*, *Pepelius triacanthus*). Additionally, pelagic juveniles of other species (e.g. *Urophycis tenuis*, *Mugil curema*) co-occur with *P. saltatrix* at the MAB shelf break in late spring and these species also use nearshore estuarine nursery habitats. Active horizontal swimming may be the mechanism by which these species cross the MAB shelf. A biological-physical model of *P. saltatrix* larval transport, based on future process-oriented studies, would assist in the study of the larval transport of species that exhibit similarities with *P. saltatrix*.

Concomitant with parallels in larval transport are examples where other species are transported differently than *P. saltatrix* larvae. Larvae emigrated from the SAB (e.g. *Bothus* spp., *X. novacula*) apparently cross the MAB shelf via slope-water intrusions and ontogenetic and diel changes in vertical position (Hare and Cowen 1991; Cowen et al. 1993). Cowen et al. (1991) found that *Gasterosteus aculatus* moved offshore, across the MAB shelf, during the time when *P. saltatrix* moved inshore (Figs. 10, 11). Active horizontal swimming was proposed but, on the basis of the progressive vector diagrams (Fig. 9), wind-driven surface flow could also have been involved.
By studying commonalities and differences, a system level biological-physical model of larval transport could be developed. Such a model could be used to examine the recruitment dynamics of the various species in the system and could be integrated with models relating to larval feeding and predation to provide an overall understanding of the population dynamics of species completing their life cycle in shelf and oceanic environments of the South and Middle Atlantic Bights.

References


COLLINS, M. R., AND B. W. STENDER. 1987. Larval king mack-

Fig. 13. Schematic of proposed transport scenario by which Pomatonius saltatrix larvae and pelagic juveniles are transported from South Atlantic Bight (SAB) spawning grounds to Middle Atlantic Bight (MAB) estuarine nursery habitats. 1. Larvae are spawned on the outer shelf of the SAB from March through at least May. 2. Some larvae may be retained within the SAB and recruit to estuaries therein. 3. Most larvae are transported northward, out of the SAB, in association with the Gulf Stream. 4. Some, more developed individuals (i.e. pelagic juveniles) may swim across the slope sea. 5. Most individuals are transported across the slope sea in warm-core ring streamers (see Fig. 2). 6. Larvae and pelagic juveniles accumulate at the surface shelf-slope temperature front. 7. Pelagic juveniles actively swim across the MAB shelf, a behavior that begins when the surface shelf-slope temperature front dissipates in late spring-early summer.


WILKINSON, L. 1990. SYSTAT: The system for statistics. SYSTAT Inc.


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