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# Dispersal of black sea bass (*Centropristis striata*) larvae on the southeast U.S. continental shelf: results of a coupled vertical larval behavior – 3D circulation model

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## ABSTRACT

In the marine environment, pelagic dispersal is important for determining the distribution and abundance of populations, as well as providing connections among populations. Estimates of larval dispersal from spawning grounds are important to determining temporal and spatial patterns in recruitment that may have significant influences on the dynamics of the population. We present a case study of the dispersal of *Centropristis striata* (black sea bass) larvae on the southeast U.S. continental shelf. We use a coupled larval behavior – 3D circulation model to compare the effects of the timing and location of spawning against that of larval vertical migration on larval dispersal. Using the results of field data on larval vertical distributions, we compare the dispersal of virtual 'larvae' which have ontogenetic changes in vertical behavior with that of particles fixed near the surface and near the bottom. Larvae were released at potential spawning sites four times throughout the spawning season (February through May) for 3 yr (2002–04) and tracked for the assumed larval duration (from 27 to 37 days including the egg stage). Results indicate that adult behavior, in the form of spawning time and location, may be more important than larval vertical behavior in determining larval dispersal on the inner- and mid- continental shelves of this region.

**Key words:** black sea bass, *Centropristis striata*, circulation model, larval behavior, larval dispersal

## INTRODUCTION

Larval dispersal is defined as the spread of larvae from a spawning source to a settlement site (Pineda *et al.*, 2007) and is an important determinant both of the distribution and abundance of marine populations (Nathan, 2001; Cowen *et al.*, 2006). Larval transport, which is one component of larval dispersal (Pineda *et al.*, 2007), results from complex interactions of biological and physical factors including advection, diffusion, and horizontal and vertical behavior (Guichard *et al.*, 2001). For eggs, vertical distribution is largely determined by egg buoyancy and physical mixing (Ådlandsvik *et al.*, 2001). In larvae, buoyancy regulation (and vertical distribution) through swim bladder inflation and deflation begins to develop in the preflexion stages (Govoni and Hoss, 2001). As larvae develop into post-flexion stages, control over vertical position improves (Cowen, 2002) and horizontal behaviors develop (Leis *et al.*, 2006).

The value of site-specific individual-based models incorporating larval transport and behavior has been demonstrated through many studies (see review by Werner *et al.*, 2001). These studies include those examining the dynamics of the early life histories of Georges Bank cod and haddock (Lough and Potter, 1993; Werner *et al.*, 1996, 2000; Lynch *et al.*, 2001) and sea scallops (Tremblay *et al.*, 1994), and others examining the recruitment dynamics of estuarine-dependent fish such as Atlantic menhaden and spot (Hare *et al.*, 1999; Quinlan *et al.*, 1999; Blanton *et al.*, 2003). They use extensions of a basic algorithm to advect large numbers of individual particles and to include specific combinations of both vertical and horizontal dispersion via random flight superposed on the advection (Hannah *et al.*, 1997; Werner *et al.*, 2000). These studies also used various schemes to include the effects of larval behavior on larval transport and dispersal (Werner *et al.*, 1993; Hare *et al.*, 1999).

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As part of ongoing research in support of the development of marine protected areas (MPAs) on the southeast U.S. continental shelf, the purpose of this study is to examine the 3D nature of transport of black sea bass larvae and to develop possible transport pathways from spawning grounds to juvenile nursery habitats in this region. Specifically, this study examines intra-seasonal and inter-annual variability in larval transport from a broad spatial distribution of spawning locations and a variety of possible larval vertical behaviors. Using a coupled larval behavior – 3D circulation model – estimates of larval dispersal from spawning grounds are used in determining temporal and spatial patterns in recruitment that may be important to the dynamics of the population.

## MATERIALS AND METHODS

### *Description of study area*

In the cross-shelf direction, the southeast U.S. continental shelf can be divided into inner-, mid- and outer-shelf regions based on hydrography (Atkinson *et al.*, 1985; Lee *et al.*, 1991), bottom habitat (Struhsaker, 1969; McGovern *et al.*, 1998) and fish assemblages (larval, Marancik *et al.*, 2005; and juvenile, Walsh *et al.*, 2006). Off the coast of Georgia, the central part of the shelf is relatively wide (120 km), while at the northern and southern extremes, the shelf is narrow (10–30 km). Characteristics of the waters differ in each of the cross-shelf regions (Boicourt *et al.*, 1998). The inner-shelf (from the coast to the 20 m isobath) is dominated by river discharge, atmospheric fluxes and tides (Lee *et al.*, 1991). The bottom in this coastal region generally consists of smooth or sandy mud (Struhsaker, 1969; McGovern *et al.*, 1998). The mid-shelf, from roughly the 20 to 45 m isobaths, is driven primarily by wind but is also influenced by tides with frequent contributions from the Gulf Stream (Lee *et al.*, 1991), with bottom habitat consisting primarily of sand (Struhsaker, 1969; McGovern *et al.*, 1998). The outer-shelf is dominated by the Gulf Stream (Lee *et al.*, 1991) with bottom habitat that varies from smooth mud to rocky high relief (Cuellar *et al.*, 1996; McGovern *et al.*, 1998).

### *Models*

Particles were released and tracked in a 3D circulation model with the Lagrangian particle tracking algorithm described in Blanton (1993) and enhanced to account for differences between modeled and observed wind stress on the Georgia shelf (Edwards *et al.*, 2006b). Particles were released at times and locations specified by an adult spawning model (as described below) and advected for assumed larval durations ranging from 20 to 35 days (Table 1, Roberts *et al.*, 1976). During the tracking, the vertical positions of the particles, or the 'larvae', were determined with models of larval fish vertical behavior.

**Table 1.** Summary of the biological parameters for black sea bass used in the model.

| Parameter | Estimate | Main source |
|---|---|---|
| Spawning area | 15–56 m | Sedberry *et al.* (2006) |
| Spawning habitat | Reefs | Lindeman *et al.* (2000) |
| Spawning time | Feb–May (peak March) | Sedberry *et al.* (2006) |
| Larval duration | 20–35 | Roberts *et al.* (1976) |
| Settlement area | <20 m | Able *et al.* (1995),<br>Walsh *et al.* (2006) |
| Settlement habitat | Hard or soft bottom habitat | Able *et al.* (1995),<br>Walsh *et al.* (2006) |

### *3D circulation model and particle tracking*

The 3D circulation model is described in Lynch and Werner (1991) and Lynch *et al.* (1996) and validated for this region by Edwards *et al.* (2006a). The model is a free-surface, 3D finite element time-stepping model of the shallow-water equations with conventional Boussinesq and hydrostatic assumptions. It uses terrain-following vertical coordinates configured to resolve both surface and bottom boundary layers. The model is fully nonlinear and solves prognostically for the evolution of the density field (Lynch *et al.*, 1996; Aretxabaleta *et al.*, 2005).

The advective flow field resulted from wind, tides, and a climatological baroclinic density field (see Edwards *et al.*, 2006a). The wind field was obtained from the National Centers for Environmental Prediction ETA atmospheric model at a 32 km resolution and at 6 h intervals. Surface fluxes were extracted and interpolated onto the grid. For input into the model, the 10 m wind fields were then converted to wind stress as in Large and Pond (1981). Long-term monthly averaged stratification effects and a Gulf Stream were included through the use of climatological density fields (Fig. 1, Blanton *et al.*, 2003) in the particle-tracking algorithm. While there is significant spatial structure in the climatological baroclinic velocity fields on the shelf, the flow is generally northward and is strongest at the shelf-break (i.e., near the Gulf Stream's climatological location).

Diffusion is simulated through a horizontal turbulent kick in the particle-tracking algorithm. Using a

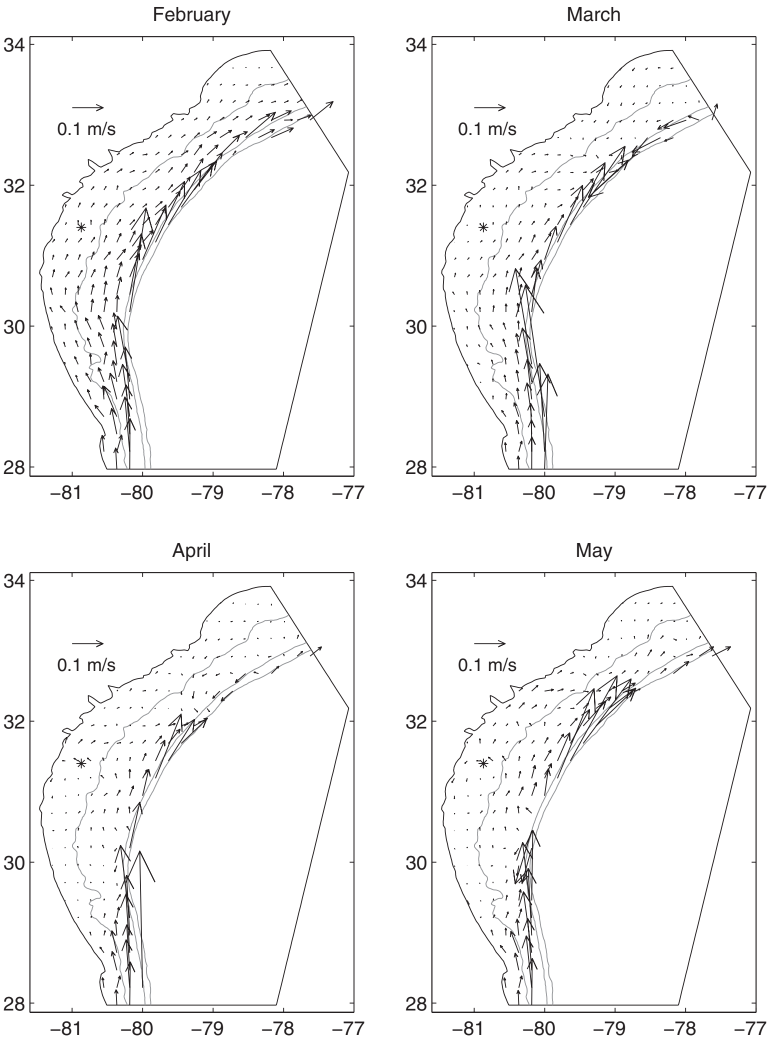


**Figure 1.** Depth-averaged velocity derived from climatological density fields. Grays Reef National Marine Sanctuary is indicated with an asterisk. The 25, 100 and 200 m isobaths are shown. Adapted from Blanton *et al.* (2003).

Gaussian random flight process, displacements are calculated every model time step with model eddy diffusivities ($K_x$ and $K_y$) in the east/west ($x$) and north/south ($y$) directions (Berg, 1993). Eddy diffusivity is used in ocean circulation modeling to describe 'diffusion' due to both sub-grid-scale processes or processes not modeled (omission of physical processes generally requires an increase in the eddy diffusivity specified). This term parameterizes the true advective processes that may be taking place, including frontal instabilities, steering by unresolved topographic features, sea breezes, among others. To select a value for model eddy diffusivity ($K_x$ and $K_y$), we use the relationship between the observed variance ($r^2_{\mathrm{rc}}$), apparent diffusivity ($K_{\mathrm{a}}$), and scale of diffusion ($l$) after 1 month from Okubo (1971) where:

$$\sigma^2_{\mathrm{rc}} = 2 s_{11} s_{22} \tag{1}$$

$$l = 3\sigma_{\mathrm{rc}} \tag{2}$$

$$K_{\mathrm{a}} = 0.0103 l^{1.15} \tag{3}$$

$s_{11}$, $s_{22}$ represent the major and minor axes of the variance ellipse calculated with a principal component analysis (Preisendorfer, 1988) from the positions of the particles after dispersing for 1 month (as calculated in Edwards *et al.*, 2007) . From Okubo's theoretical model, after 1 month, $K_{\mathrm{a}} \approx 10\ \mathrm{m}^2\ \mathrm{s}^{-1}$ and the scale of diffusion ($l$) ≈ 100 km. By computing the particle trajectories with different values for $K_x$ and $K_y$ (=1.0, 10.0 and 50.0 $\mathrm{m}^2\ \mathrm{s}^{-1}$) and comparing the resulting length scales of diffusion with the value of 100 km found in Okubo (1971), we conclude that $K_x = K_y = K_{\mathrm{a}} = 10\ \mathrm{m}^2\ \mathrm{s}^{-1}$ is most appropriate and is used herein.

### *Black sea bass model*

Black sea bass (*Centropristis striata*), a member of the family Serranidae, is a commercially important fishery

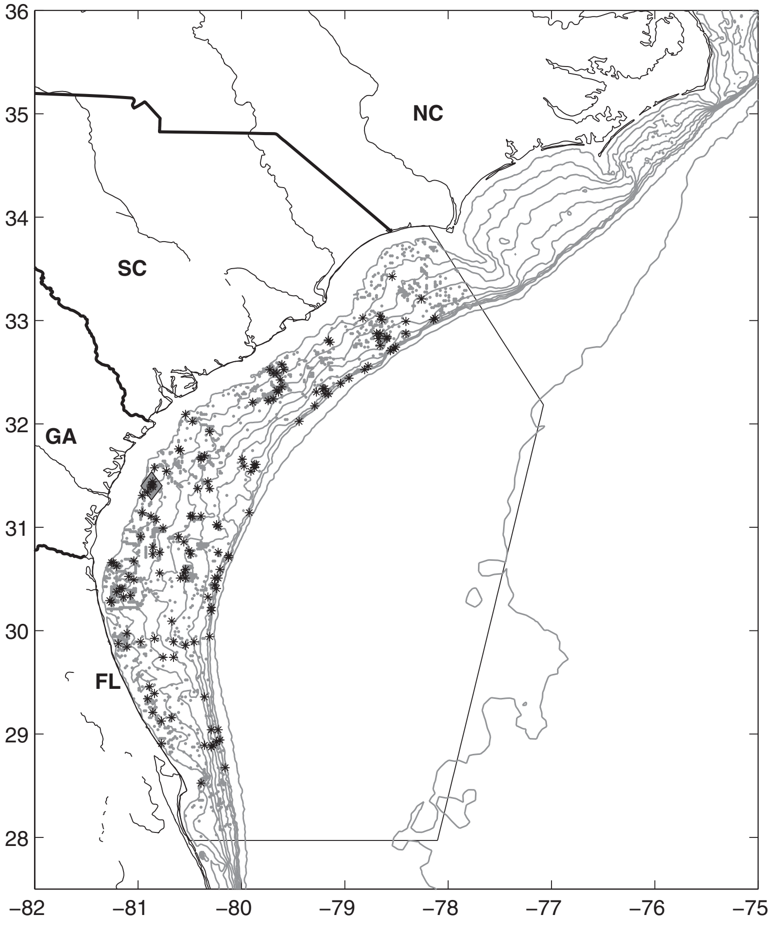


**Figure 2.** The southeast U.S. continental shelf (North Carolina [NC], South Carolina [SC], Georgia [GA], and Florida [FL]) and the model domain used in this study. The location of hard-bottom habitats between the 15 and 56 m isobaths in the domain is shown in gray, selected 'larval' release sites with stars and GRNMS is shown with a diamond. The 15-, 20-, 25-, 30-, 35-, 40-, 45-, 50-, 56-, 100-, and 1000-m isobaths are shown.

species along the U.S. Atlantic coast from Cape Cod, Massachusetts to Cape Canaveral, Florida and in the Gulf of Mexico (Wenner *et al.*, 1986; McGovern *et al.*, 2002). On the Atlantic coast, genetic studies indicate one population, but two stocks are recognized and managed separately (McGovern *et al.*, 2002), with Cape Hatteras North Carolina representing the division between the two stocks (shown in Fig. 2). The stock south of Cape Hatteras in managed by the South Atlantic Fishery Management Council as part of the Snapper-Grouper complex (South Atlantic Fishery Management Council, 2005). Along with red porgy (*Pagrus pagrus*) and vermilion snapper (*Rhomboplites aurorubens*), black sea bass constitute a substantial portion of the commercial and recreational landings in this region (McGovern *et al.*, 1998). Stock assessments in 1996 and 2003, along with a 2005 update, all concluded that black sea bass was overfished and that overfishing was occurring with landings decreasing from 3 million lb in 1988 to 1.1 million lb in 2002 (South Atlantic Fishery Management Council, 2005).

Black sea bass adults are distributed throughout the southeast U.S. continental shelf from 2 to 130 m but are generally found in depths less than 60 m associated with hard substrates (McGovern *et al.*, 2002). North of Cape Hatteras, as inshore water temperatures decrease in the fall, black sea bass appear to migrate south and offshore (Able *et al.*, 1995 and references therein). However, with the warmer year-round bottom water temperatures south of Cape Hatteras (Blanton *et al.*, 2003), black sea bass are year-round residents on the shelf and do not make a seasonal migration (Mercer, 1989).

### *Black sea bass model: adult spawning*

Spawning occurs on the rocky reefs located in the mid-shelf depths from 15 to 56 m with peak spawning between February and May (Sedberry *et al.*, 2006). Laboratory studies indicate that spawning occurs at night with eggs released near the bottom (D. Berlinski, University of New Hampshire, Durham, NH, USA, personal communication). To examine intra-seasonal and inter-annual variability in black sea bass larval dispersal, we use four spawning times per year (February 1, March 1, April 1, and May 1) in each of 3 yr (2002, 2003, and

2004). In the model, eggs were released at night, 1 m off the bottom.

To select release locations, the shelf was divided into three along-shelf regions by state boundaries (South Carolina, Georgia, and Florida) and eight cross-shelf depth zones (referred to as depth zones 1–8 in order: 15–20, 20–25, 25–30, 30–35, 35–40, 40–45, 45–50, and 50–56 m) for a total of 24 spawning subregions. Based on the relative proportion of hard bottom habitat located within each of these 24 subregions, adult spawning locations were chosen randomly from the suitable habitat within each subregion. A total of 145 release locations were chosen with 100 larvae released at each location, at four spawning times, in each of 3 yr providing a total of 14 500 larvae released in each model run and a total of 60 model runs.

### *Black sea bass model: larval behavior model*

We have modeled behavior at the individual level, thus embedding stochasticity in the population at the lowest level. At the length scales contemplated, the principal behavioral variable is an individual larva's vertical positioning (e.g., as in Werner *et al.*, 1993; Hare *et al.*, 1999). The larval duration of black sea bass is approximately 20 and 35 days post-hatch (Table 2). Here we examine the effects of shorter and longer larval durations and competency periods, where during the competency stage, metamorphosis to the juvenile stage may occur given the right environmental cues (Cowen, 1991).

Larval vertical position was included by assigning larvae to the upper half or lower half of the water column over a diel cycle. These assignments were based on the proportion of vertical distributions of *Centropristis* spp. larvae from Delaware Bay to the Georgia shelf collected during 1999/2000. A 1 m$^2$ Tucker trawl sampled the lower and upper half of the water column at 294 stations during September, November, and March; *Centropristis* spp. larvae were caught at 36 stations primarily during March. Larvae were grouped into pre- and post-flexion stages and time of capture was grouped into day or night. Average proportions of larvae captured in the upper and lower half of the water column were calculated for the two ontogenetic stages and the two time periods. This approach was used because there was a lot of variability in the depth of black sea bass larvae when averaged over time and space.

A suite of behaviors was included to fully explore the possible effects of larval behavior and larval duration on the resulting larval dispersal. Two simple behaviors, fixed depth – near surface (SF) and fixed depth – near bottom (DF), provide an envelope for the possible effects of larval vertical behavior. Five more complex behaviors that include ontogenetic vertical migration and different development times are also modeled (termed behaviors A, B, C, D, and E; see Fig. 3 for a comparison of behaviors and Tables 2 and 3 for a comparison of model parameters). In scenarios A–D, individual larvae determine their depth preference at the start of each day/night cycle within the stage. In contrast, in scenario E, individual larvae have a fixed preference for the upper or lower half of the water column for the entire stage. When a larva enters the pre- or post-flexion stages, it determines whether it will be in the upper or lower half of the water column at night and during the day using the probabilities in Table 4. The larva then moves to these same proportional positions throughout the stage. Scenarios A and C represented faster developing larvae while scenarios B, D, and E represented slower developing larvae – development times are explained in sections below.

### *Black sea bass model: eggs*

All behavior scenarios included the same egg vertical behavior. The egg stage is assumed to last for 2 days (Tucker, 1988; Nelson *et al.*, 2003; Berlinsky *et al.*, 2004). Viable black sea bass eggs are positively buoyant (Nelson *et al.*, 2003). While there are no species-specific estimates of ascent rate for black sea bass eggs, ascent rates are known to vary among species, i.e., *Leiostomus xanthurus*: 0.005 cm s$^{-1}$ (Cambalik *et al.*, 1998), *Brevoortia tyrannus*: 0.23 cm s$^{-1}$ (Cambalik *et al.*, 1998), *Hoplostethus atlanticus*: 0.35 cm s$^{-1}$

**Table 2.** Summary of the behavioral parameters for black sea bass used in the model.

| Stage | Egg | Yolk-sac | Preflexion | Post-flexion | Competency |
|---|---|---|---|---|---|
| Size (mm) | | 2 | 2–6 | 6–10 | >10 |
| Duration (days) | 2 | 3 | 12 or 15 | 5 or 7 | 5 or 10 |
| Behavior | Passive | Passive | Active | Active | Active |
| Buoyancy (cm s$^{-1}$) | 0.2 | 0.3 | 0.0 | 0.0 | 0.0 |
| Vertical swimming (cm s$^{-1}$) | 0.0 | 0.0 | 1.0 | 2.0 | 2.0 |

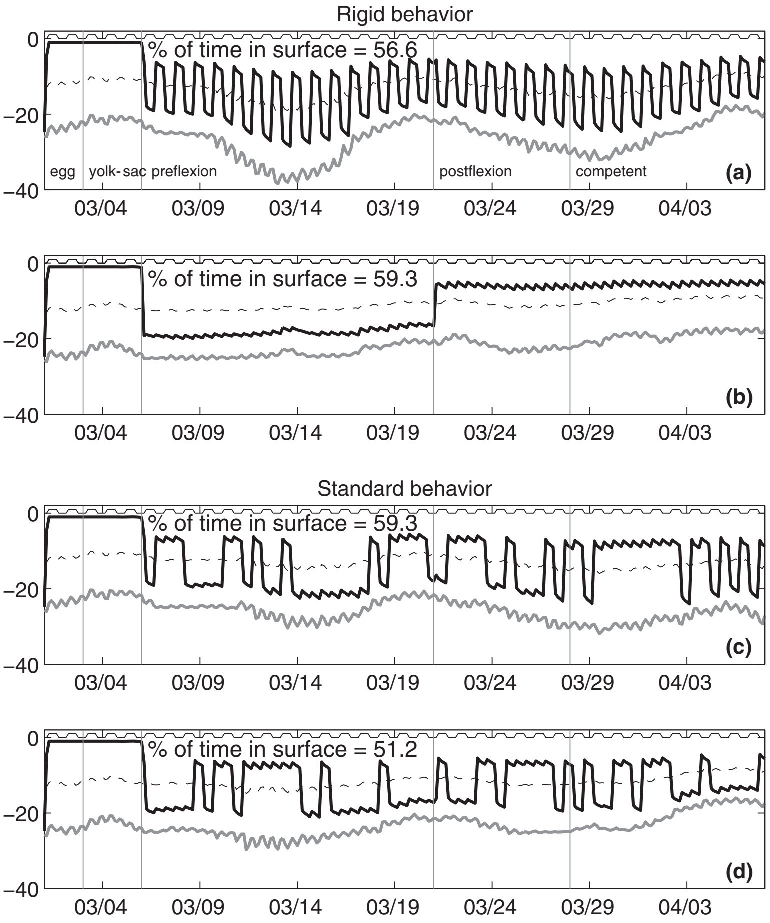


**Figure 3.** Results of Black sea bass larval vertical behavior models for 37 days indicating different behaviors for larvae started at the same location. Thick black lines indicate larval depth. Thick gray line represents the bottom depth at the larva's location and dashed black line indicates the mid-point of the water column. (a, b) Rigid behavior (Table 3, behavior E). (c, d) Standard behavior (Table 3, behavior D): the larva chooses at the beginning of each day/night period where it prefers to be in the water column.

**Table 3.** Summary of the variable stage durations and active behaviors used in the model. Total larval duration column includes the egg and yolk-sac stages.

| | | Post-flex (days) | | Total larval | |
|---|---|---|---|---|---|
| Behavior scenario | Preflex duration (days) | Duration | Competency | Duration (days) | Behavior |
| A | 12 | 5 | 5 | 27 | Standard |
| B | 12 | 5 | 10 | 32 | Standard |
| C | 15 | 7 | 5 | 32 | Standard |
| D | 15 | 7 | 10 | 37 | Standard |
| E | 15 | 7 | 10 | 37 | Rigid |
| SF | 15 | 7 | 10 | 37 | Near-surface, fixed-depth |
| DF | 15 | 7 | 10 | 37 | Near-bottom, fixed-depth |

(Zeldis *et al.*, 1995), and with ambient water environmental conditions (Ådlandsvik *et al.*, 2001). An ascent rate of 0.2 cm s$^{-1}$ was used here.

### *Black sea bass model: yolk-sac stage*

All behavior scenarios included the same yolk-sac stage vertical behavior. Yolk-sac larvae are typically more buoyant than eggs because the chorion, the dense fraction of an egg, is shed at hatching (Ådlandsvik *et al.*, 2001). The buoyancy of preflexion larvae is unknown, but buoyancy regulation through swim-bladder inflation and deflation begins to develop in preflexion stages (Govoni and Hoss, 2001). Thus, preflexion larvae were modeled as neutrally buoyant and yolk-sac larvae were modeled with linearly decreasing buoyancy from 0.3 cm s$^{-1}$ to neutral over

**Table 4.** Probability of preflexion and post-flexion larvae being in different portions of the water column.

| | Preflexion larvae | | Post-flexion larvae | |
|---|---|---|---|---|
| Location in water column | Night | Day | Night | Day |
| Upper 50% | 0.49 | 0.35 | 0.70 | 0.32 |
| Lower 50% | 0.51 | 0.65 | 0.30 | 0.68 |

the 3 day yolk-sac stage (Roberts *et al.*, 1976; Tucker, 1988).

### *Black sea bass model: preflexion stage*

It is in the preflexion stage that the differences in larval behavior reflected in scenarios A–E first become apparent. Stage durations of either 12 days (A, C) or 15 days (B, D, and E) are assumed for the time it takes the larvae to grow to ~6 mm and enter the post-flexion stage (Roberts *et al.*, 1976).

Beginning in this stage, larvae actively control their vertical positions in the water column based on preferences for the upper or lower half of the water column (see Table 4). At sunset, the larva starts to swim to either the middle of the upper or lower water column based on its depth preference. Once its preferred depth is reached, the larva moves passively until sunrise as long as it is in its chosen half of the water column. If the larva moves outside of its preferred half of the water column, it swims, either up or down, to reach the middle of the selected region. At sunrise, the larva starts to swim to the mid-point of its preferred daytime depth. Once this depth is reached, the larva moves passively until sunset as long as it is in its chosen half of the water column.

### *Black sea bass model: post-flexion stage*

The post-flexion stage is assumed to be reached once a larva is either 17 days (A, C) or 20 days (B, D, and E) post spawning (≈6 mm SL). In the model, the length of this stage is either 5 or 7 days and reflects the length of time it takes a larva to grow to ~10 mm (Roberts *et al.*, 1976; Berlinsky *et al.*, 2000; Marancik and Hare, NOAA, Beaufort, NC, unpublished data) and reach competency. The behavior in this stage is similar to that in the preflexion stage except that the larvae are assumed to have a faster vertical swimming rate of 2 cm $s^{-1}$ (or 2–3 body lengths $s^{-1}$ for an 8 mm larva, Miller *et al.*, 1988) and different day/night proportions at depth (Table 4).

### *Black sea bass model: competency stage*

The competency stage is reached once a larva has grown to ≈10 mm. Larvae are then competent to settle for either 5 or 10 days and are assumed to survive if they reach suitable habitat during their competency period. Black sea bass larvae settle in the inner-shelf on either hard- or soft-bottom habitats within the 20 m isobath (Able and Fahay, 1998; Table 1). During their competency period, the larvae are assumed to continue the same behavior as in the post-flexion stage but settle if they reach suitable habitat within this time period. For comparison, for the surface- and deep-fixed behaviors, we have assumed the same competency period to calculate success as for behaviors D and E.

Juvenile black sea bass have been found in both the inner continental shelf and estuarine environments associated with many different benthic habitats: jetties, piers, wrecks, and shell bottom (Mercer, 1989; Able *et al.*, 1995). Therefore, in this study, we have assumed that larvae are successful in finding suitable settlement habitat if they are found within the 20 m isobath (on the inner-shelf) during their competency period.

### *Analysis of model results*

To quantify the effect of the various physical and biological factors contributing to the dispersal patterns, we performed an analysis of variance (ANOVA) using the success rate from each release location from each model run as the response variable to the following factors: year, month, release location and larval behavior. The ANOVA included both the primary factors plus second-order interaction effects. Success rate was defined as the percentage of larvae from a given release location that reached suitable settlement habitat during their competency period. The purpose of the ANOVA was not to test for the significant effect of the various factors, but to quantify the percent of the total variance in larval success explained by each factor (Langsrud, 2000, 2002).

Differences in larval success were compared by year. Within each year, inter-seasonal larval success was compared for each of the modeled behavior scenarios. Release locations were divided into along-shelf (by state: South Carolina, Georgia, and Florida) and cross-shelf zones (by depth: 15–20, 20–25, 25–30, 30–35, 35–40, 40–45, 45–50, and 50–56 m) providing an investigation into differences in larval success by depth zone in the wider and narrower parts of the shelf. Successful arrival locations are also divided into along-shelf zones (by state: South Carolina, Georgia, and Florida) to provide a comparison of retention and dispersal by state.

Finally, to provide a comparison of the larval dispersal between behavioral scenarios, two-dimensional dispersal kernels, defined as the probability that a larva will settle at a given distance from its release location, were defined for larvae released at Grays Reef National Marine Sanctuary (GRNMS) as in Edwards *et al.* (2007). Positive dispersal direction ($\theta$) reflects dispersal generally to the north of the spawning location, while a negative direction indicates dispersal south of the spawning location. We compare the results of the long-term monthly average dispersal kernels (from Edwards *et al.*, 2007) and those using more realistic, time-varying wind fields presented here.

## RESULTS

### *ANOVA results*

Spawning location was the most significant factor determining the success rate from each of the starting locations (Table 5). Cross-shelf location (release depth) was more important in determining successful settlement compared to along-shelf location (Table 6) implying relatively little along-shelf variability and much greater cross-shelf variability in success rate. In total, the physical and biological factors tested in this model explained almost 80% of the total variance in larval success (Tables 5 and 6).

As the shallowest spawning depth zone (15–20 m) had very high success rates in most of the runs, we also ran the ANOVA excluding this depth zone (Tables 5 and 6). Release location and depth zone still explained most of the variance in successful settlement but the importance of other factors including the interaction terms became apparent. Year and the interaction between year and release location (depth zone) were also important in explaining the variance in larval success rate from each spawning location. On its own, larval behavior explained less than 1% of the variance in success rate, but was more significant in interaction with year and release location.

| Factor | DF | All factors (%) | DF | Excl zone 1 (%) |
|---|---|---|---|---|
| Year | 2 | 1.1 | 2 | 1.9 |
| Month | 3 | 0.4 | 3 | 1.1 |
| Release location | 23 | 70.6 | 20 | 49.8 |
| Larval behavior | 4 | 0.1 | 4 | 0.5 |
| Year × month | 6 | 0.2 | 6 | 0.3 |
| Year × Rel. Loc. | 46 | 1.0 | 40 | 2.3 |
| Year × behavior | 8 | 1.0 | 8 | 1.6 |
| Month × Rel. Loc. | 69 | 1.4 | 60 | 2.4 |
| Month × behavior | 12 | 0.5 | 12 | 0.6 |
| Rel. Loc. × behavior | 92 | 1.0 | 80 | 1.3 |
| Error | 8434 | 22.7 | 6184 | 38.6 |

**Table 5.** Results of ANOVA with response variable = % success from each starting location (with state and depth zones combined). Results are given for larvae spawned in all depth zones and larvae spawned in depth zones 2 through 8 (20–56 m). The percentages represent the amount of variance in the response variable that is explained by each factor. All primary factors and second-order interaction effects are included in this table.

| Factor | DF | All factors (%) | DF | Excl zone 1 (%) |
|---|---|---|---|---|
| Year | 2 | 1.1 | 2 | 1.9 |
| Month | 3 | 0.4 | 3 | 1.1 |
| Release state | 2 | 1.0 | 2 | 0.6 |
| Release depth | 7 | 62.9 | 6 | 44.5 |
| Larval behavior | 4 | 0.1 | 4 | 0.6 |
| Year × month | 6 | 0.2 | 6 | 0.3 |
| Year × state | 4 | 0.2 | 4 | 0.2 |
| Year × depth | 14 | 0.6 | 12 | 1.7 |
| Year × behavior | 8 | 1.1 | 8 | 1.6 |
| Month × state | 6 | 0.2 | 6 | 0.6 |
| Month × depth | 21 | 0.5 | 18 | 1.6 |
| Month × behavior | 12 | 0.5 | 12 | 0.6 |
| State × depth | 14 | 2.7 | 12 | 4.1 |
| State × behavior | 8 | 0.3 | 8 | 0.5 |
| Depth × behavior | 28 | 0.3 | 24 | 0.6 |
| Error | 8560 | 23.8 | 6292 | 40.3 |

**Table 6.** Results of ANOVA with response variable = % success from each starting location (with state and depth zones analyzed separately). Results are given for larvae spawned in all depth zones and larvae spawned in depth zones 2 through 8 (20–56 m). The percentages represent the amount of variance in the response variable that is explained by each factor. All primary factors and second-order interaction effects are included in this table.

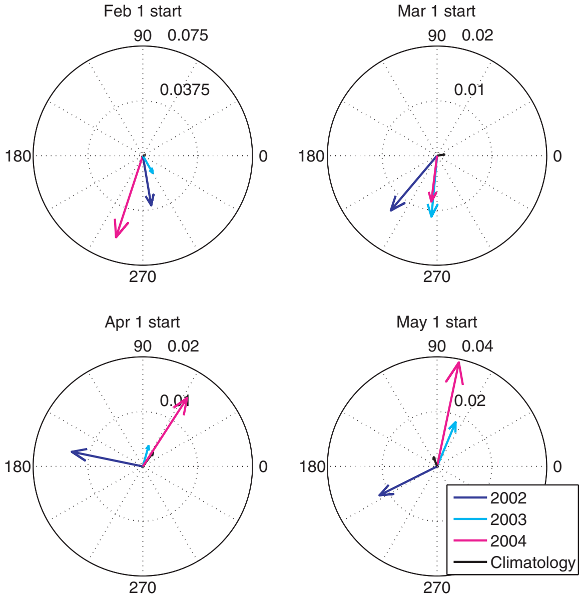
### *Results by year*

In general, larvae spawned in 2002 had a higher success rate than those spawned in 2003, and larvae spawned in 2003 had a higher success rate than those spawned in 2004 (Fig. 4). In all years, a high percentage of larvae spawned in the two regions nearest the coast arrived at suitable settlement habitat, but 2002 had successful larvae from a broader range of spawning depths than the other years (Fig. 4) reflecting the average onshore, or along-shelf to the south, winds during that year (Fig. 5).

Most of the larvae spawned at the locations closest to the coast found suitable habitat during their competency periods in all years. The narrowest cross-shelf range of survivors occurred in 2004 with almost no survivors from spawning deeper than 30 m. While the lowest success rates occurred in May 2002 for larvae spawned in the shallowest depth zone off the coast of SC. However, larvae spawned further offshore during this same time did well, with 30–40% success in larvae spawned between 35 and 40 m depth.

There were inter-annual differences in the success of faster (behaviors A and B) versus slower (behaviors C, D, and E) larvae. In 2002, the faster developing larvae were more successful at reaching suitable settlement regions during their competency period than the slower developing larvae at almost all spawning depths and months (Fig. 4). In 2003, the opposite pattern was observed and the slower growing larvae were more successful than the faster growing larvae; no clear pattern emerged in 2004 (Fig. 4).

**Figure 5.** The average wind stress for February, March, April and May for the climatological wind fields and the individual years 2002–04 at GRNMS. Note the scale differences in the different months. Data for the individual years are from the NDBC buoy at GRNMS. The climatological wind fields are from COADS data at the location of the GRNMS buoy.



The general pattern of transport was clearly related to the winds. In 2002, with generally southward winds, the larvae were advected southward until they reached the southern part of the domain where the climatological Gulf Stream is near the coast and dominates the wind-driven flow. At this point, the larvae were advected to the north and not returned to the inner-shelf.

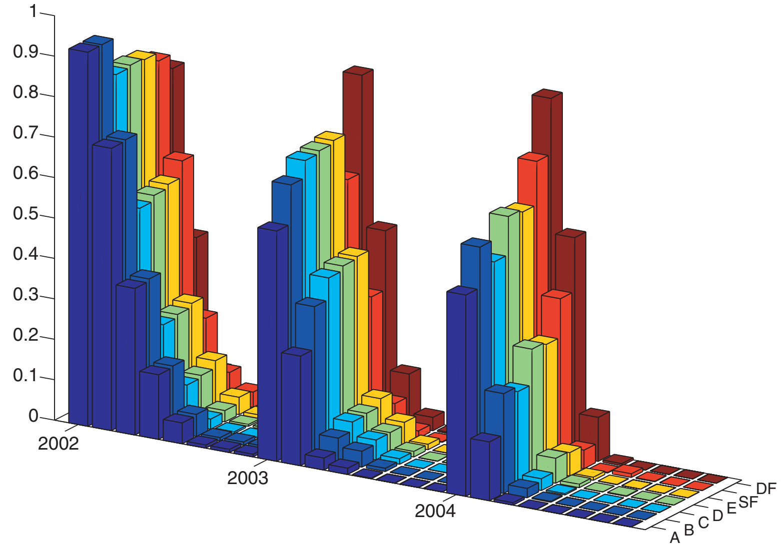


**Figure 4.** Results for each year. Bar height represents the fraction of successful larvae in each starting region (cross-shelf spawning zone) for each behavior scenario (from Table 3: A, B, C, D, E, SF, and DF). Cross-shelf spawning zones = 15–20, 20–25, 25–30, 30–35, 35–40, 40–45, 45–50, and 50–56 m.

*Results by region*

While year and month explained only a small percentage of the variation in larval success (Tables 5 and 6), the regional statistics only indicate that the larvae reached suitable settlement habitat within the 20 m isobath during their competency periods. These statistics do not tell us where, in the along-shelf direction, the larvae settled. Off the South Carolina coast, spawning in 2002 was the most successful with larvae from even some of the offshore spawning locations reaching suitable habitat (Fig. 6). In contrast, May 2003 had successful larvae from more cross-shelf spawning locations off the Georgia coast. For larvae spawned on May 1, 2002 and arriving at suitable habitat on the South Carolina coast, most originated at South Carolina spawning locations (Fig. 7) whereas larvae spawned on May 1, 2004 and arriving at suitable habitat on the South Carolina coast generally originated from spawning sites in Georgia.

In a comparison of successful larvae arriving at suitable habitat in each of South Carolina, Georgia and Florida (Fig. 8 and Table 7), it is apparent that each state has some degree of retention from spawning locations within the state along with dispersal between the states. Larvae finding suitable habitat in Georgia came from the broadest range of spawning locations (Fig. 8b). While the model resulted in very little exchange of larvae between South Carolina and Florida (Fig. 8a,c and Table 7), spawning in Georgia resulted in larval recruitment to all three states and around 10% of the larvae spawned in northern Florida successfully settled in Georgia. However, the low success rates for larvae spawned off the South Carolina coast may be misleading as many of these larvae exited the model domain to the north but may have reached suitable habitat on the North Carolina coast.

*Behavioral effects*

The effects of behavior on larval success rates were greatest in interaction with other factors such as year and spawning location (Tables 5 and 6). On its own, vertical behavior was not important in explaining differences in success rates between the model runs. Although both inter-annual and intra-seasonal patterns in larval transport were identified, there were no clear patterns in behavioral effects: at different times and locations, all behaviors were successful. There were also no clear patterns in success based on time spent in either the top or bottom half of the water column.

To show the effect of behavior on larval track, Fig. 9 presents the tracks of the same larva (same starting location and time) with the different behaviors (details of the vertical behaviors C, D, and E are provided in Fig. 3). In this example, only larvae with behaviors E and the deep fixed-depth were successful in finding suitable habitat during their competency period. The diel vertical migrations in E seem to have resulted in greater cross-shelf movement of the larvae bringing the larvae out to almost 40 m depth and back to within the 20 m isobath to settle.

*Dispersal kernels at Grays Reef National Marine Sanctuary*

Larval dispersal, as measured by the mean distance ($d$) and direction ($\theta$), from spawning at GRNMS shows strong inter-annual and intra-seasonal patterns (Table 8). In general, the dispersal in the individual years was greater than in climatology models (for durations of both 30 and 45 days, Edwards *et al.*, 2007) with 2004 having the largest mean dispersal distances. March has the shortest dispersal distances for the climatology and all of the individual years and all three behaviors. Larval dispersal from the climatology circulation fields was along- or on-shelf to the north for most of the spawning months and behaviors tested here. In contrast, there was more variation in the dispersal direction from individual years but it was generally along-shelf, either to the north or south, reflecting the stronger along-shelf winds and resulting circulation. The dispersal kernels were generally rotated in the along-shore direction

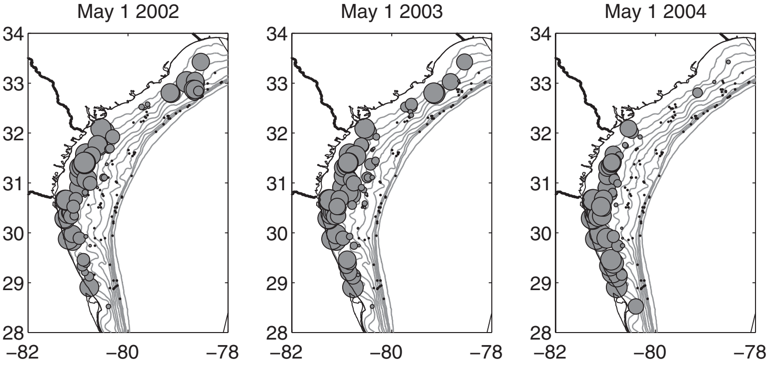


**Figure 6.** A comparison of the larval success for behavior E spawning on May 1, 2002, 2003, and 2004. The size of the circle represents the relative success from each spawning location (larger circles = higher success rate). The black dots mark spawning locations with no successful larvae in this model scenario.

(data not shown) because of the dominance of the alongshore flow. As all model runs for each month included the same long-term average baroclinic velocity field (Blanton *et al.*, 2003), the main differences in the dispersal, as presented herein, were due to differences in the wind-driven circulation on the shelf.

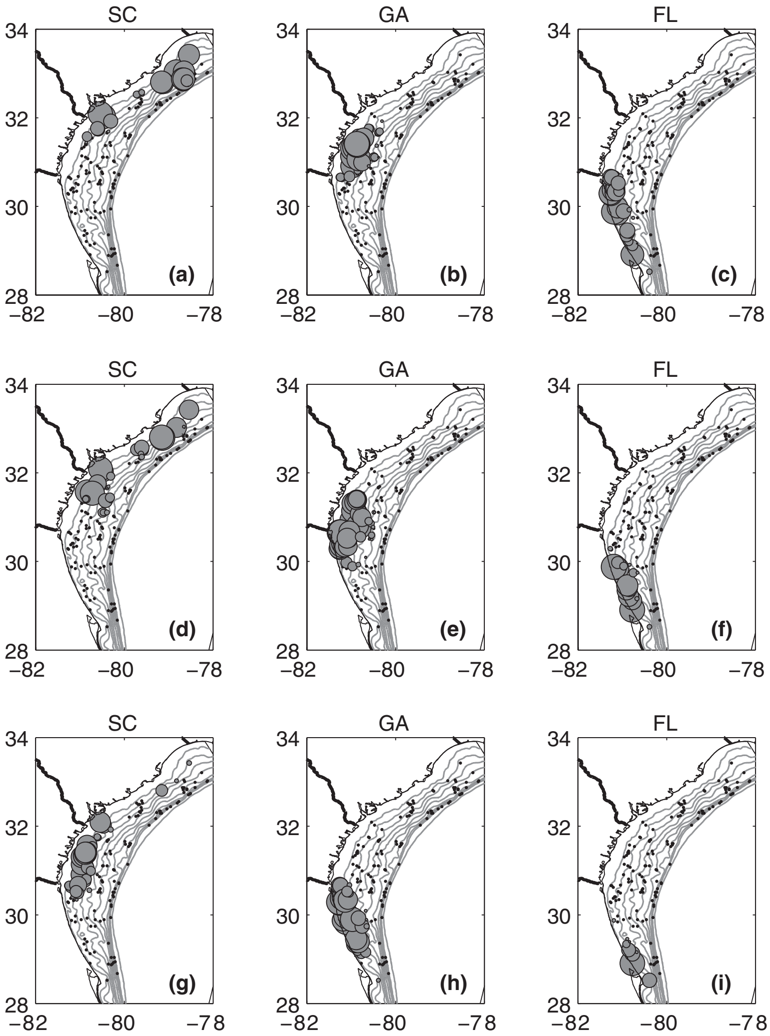


**Figure 7.** A comparison of the larval success for behavior E spawning on May 1, 2002, 2003, and 2004 by ending state. The size of the circle represents the relative success from each spawning location (larger circles = higher success rate). Each subplot represents the starting locations resulting in successful arrival at a different state. (a–c) 2002; (d–f) 2003; (g–i) 2004.

**Figure 8.** A comparison of the larval success for all active behaviors (A–E) for all spawning periods by along-shelf ending location. The size of the circle represents the relative success from each spawning location (larger circles = higher success rate). Each subplot represents the starting locations resulting in successful arrival at a different state. (a) SC; (b) GA; (c) FL. The black dots show the locations of spawning sites with no successful larvae finding suitable habitat.

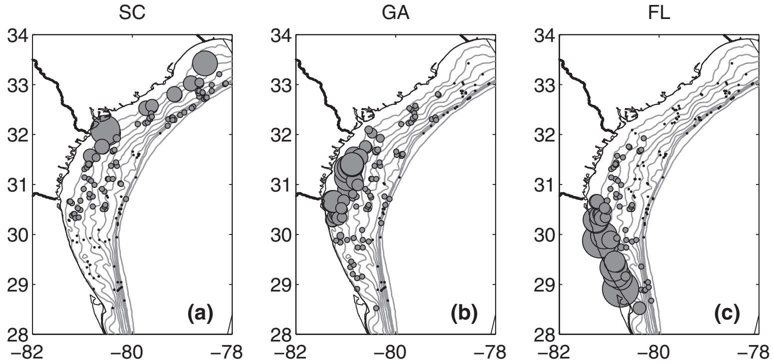


**Table 7.** Mean and standard deviation of larval success by release state and arrival state for all spawning times and active behaviors (A–E).

| | Along-shelf release location | | | | | |
|---|---|---|---|---|---|---|
| | Mean success | | | SD success | | |
| Arrival location | SC | GA | FL | SC | GA | FL |
| SC | 13.5 | 6.5 | 0.3 | 8.9 | 7.1 | 1.2 |
| GA | 1.5 | 22.0 | 10.4 | 3.3 | 14.8 | 9.9 |
| FL | 0.0 | 0.6 | 23.0 | 0.0 | 1.7 | 11.2 |
| Lost | 85.0 | 70.9 | 66.2 | | | |

Values are expressed in percentage.

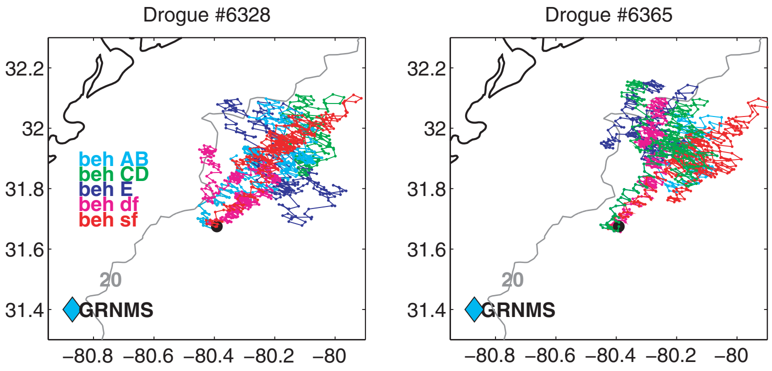


**Figure 9.** A comparison of the larval pathways for the larvae in Fig. 3 for each of the different behavior scenarios (see Table 3). The starting location is shown with a black circle and the location of GRNMS and the 20 m isobath are shown for reference. The larva's locations are plotted every 3 h. Larva 6328 was successful with behaviors E and df (left) while larva 6365 was successful with behaviors D, E and df (right).

**Table 8.** Mean distance and direction dispersed ($d$ and $\theta$) for particles released in at GRNMS for each of three behaviors: fixed depth near the surface, fixed-depth near the bottom, and active behavior reflecting either behavior E or mid-depth passive [Clim 30 days and Clim 45 days from Edwards *et al.* (2007)].

| | | Surface fixed | | Bottom fixed | | Active | |
|---|---|---|---|---|---|---|---|
| Month | Year | $d$ (km) | $\theta$ (deg from E) | $d$ (km) | $\theta$ (deg from E) | $d$ (km) | $\theta$ (deg from E) |
| Feb | Clim 30 | 23 | 70 | 27 | 98 | 27 | 88 |
| | Clim 45 | 35 | 62 | 37 | 92 | 37 | 81 |
| | 2002 | 65 | −100 | 32 | −110 | 48 | −81 |
| | 2003 | 62 | 46 | 50 | 79 | 70 | 51 |
| | 2004 | 103 | −99 | 54 | −110 | 92 | −95 |
| Mar | Clim 30 | 5 | 18 | 13 | 125 | 11 | 123 |
| | Clim 45 | 8 | 35 | 18 | 118 | 16 | 117 |
| | 2002 | 29 | −117 | 15 | −72 | 32 | −78 |
| | 2003 | 28 | 18 | 15 | 98 | 30 | 9 |
| | 2004 | 33 | 55 | 40 | 106 | 31 | 57 |
| Apr | Clim 30 | 20 | 95 | 33 | 110 | 27 | 103 |
| | Clim 45 | 26 | 73 | 35 | 102 | 32 | 85 |
| | 2002 | 48 | 73 | 33 | 76 | 41 | 56 |
| | 2003 | 90 | 35 | 47 | 71 | 79 | 30 |
| | 2004 | 135 | 48 | 98 | 66 | 107 | 50 |
| May | Clim 30 | 7 | −162 | 22 | 125 | 17 | 147 |
| | Clim 45 | 8 | −177 | 26 | 115 | 17 | 142 |
| | 2002 | 49 | 80 | 38 | 83 | 50 | 66 |
| | 2003 | 71 | 50 | 54 | 67 | 71 | 50 |
| | 2004 | 254 | 46 | 167 | 54 | 201 | 43 |

## DISCUSSION

The Lagrangian biological–physical model used in this study provided significant insight into the transport of black sea bass larvae from spawning grounds to juvenile habitats on the inner-shelf of the southeast U.S. continental shelf. This modeling study highlighted the complicated interactions between the physics and biology in transporting larvae. While it is generally assumed that larval vertical migration results in different advective pathways experienced by larvae and, therefore, in different larval dispersal patterns, the results of the ANOVA indicate that adult spawning behavior, not larval vertical behavior, was a major determinant of larval success in this region. This analysis generally supported the results found in Edwards *et al.* (2007) using the climatological circulation fields. On its own, larval behavior explained very little of the variance in larval success rates, but did explain more of the variance in combination with both year and release location. This implied that the success of the different behaviors is variable over time and space, and highlights the importance of using realistic circulation fields for a variety of years and seasons to get an accurate picture of larval transport and success along with the resulting population connectivity.

The insensitivity of the results to variability induced by larval vertical behavior and inter-annual and intra-seasonal differences in the circulation field on the shelf led to the conclusion that spawning 'inshore' provides a robust retentive habitat. The results of this study showed that those larvae spawned on the shallower portions of the shelf, within depths of 15–20 and 20–25 m, had a much higher success rate than larvae spawned further offshore. Larval success from the mid-shelf spawning locations was more variable within each spawning season and among the 3 years included in this study. In turn, this led to the question of whether the retentive aspect of the physics was properly captured in the model. Other recent work (Edwards *et al.*, 2006a, 2007; Hare and Walsh, 2007) has shown that the inner- and mid-shelf off the coast of Georgia might be highly retentive on time scales relevant to larval transport. Edwards *et al.* (2006a) examined Lagrangian circulation on this shelf through a comparison of observed and modeled drifter tracks throughout 2000 and 2001. Of the 15 drifters released at GRNMS, thirteen of them remained on the shelf for 60 days – well over the estimated black sea bass larval durations – suggesting that the inner-shelf is indeed strongly retentive.

### *Physical model*

The importance of wind in the circulation on the inner- and mid-shelf (Lee *et al.*, 1991) becomes apparent when comparing the larval transport and success under different wind regimes. Larvae spawned in 2002, with its southward or onshore average winds, had a higher predicted success rate in finding suitable habitat (the inner-shelf) than did larvae transported under generally northward or offshore wind conditions. In the cross-shelf direction, the onshore Ekman transport with southward winds contributed to the success rate for larvae spawned in deeper water. The offshore Ekman transport, during northward winds, is apparent in the reduced success of larvae during these times, especially for those spawned in the deeper regions of the shelf.

As with any modeling study, it is important to recognize both the model assumptions and limitations. The importance of the Gulf Stream in the circulation on the southeast U.S. continental shelf is well known (Lee and Atkinson, 1983; Atkinson *et al.*, 1985; Bane and Dewar, 1988; Lee *et al.*, 1989). The Gulf Stream also influences productivity on the shelf (Lee *et al.*, 1991) and larval transport along the east coast (Govoni, 1993; Epifanio and Garvine, 2001; Hare *et al.*, 2002; Hare and Walsh, 2007). With the recent development of a regional climatology (Blanton *et al.*, 2003), we have been able to include a long-term monthly average Gulf Stream and baroclinic circulation on the shelf providing general circulation patterns but not short-term variability. Other recent efforts (Aretxabaleta, 2005) explore the nesting of our regional model in the HYCOM basin-scale circulation model (HYbrid Coordinate Ocean Model, Bleck, 1998, 2002) to provide a realistic time-varying baroclinic velocity field on the shelf including the Gulf Stream. Other possible enhancements to the 3D circulation model are discussed in Edwards *et al.* (2006a).

### *Biological model*

The black sea bass model for spawning was simplified into monthly spawning events to provide an overall look at possible intra-seasonal and inter-annual differences in the resulting larval dispersal. Actual spawning is estimated to occur approximately every 2.7 days or 34 times during the period of peak spawning (McGovern *et al.*, 2002). With the largely wind-driven circulation on the inner- and mid-shelves (Lee *et al.*, 1991), the dispersal of larvae could be affected by spawning times between those tested here. There is also evidence of a smaller spawning in the fall months, which could result in very different larval transport and has not been considered here.

The main component of our larval behavior model incorporates ontogenetic changes in vertical behavior. In general, vertical behavior and distributions of larvae are affected by many factors (Heath *et al.*, 1988; Sclafani *et al.*, 1993; Leis, 2004), which largely determine the physical and biological conditions in which the larvae live. Our estimates of larval vertical migration were based on the proportion of larvae of different sizes found in net tows at different depths. One limitation of using the net tows is that this method only provides information about the distribution of larval populations and not the movement of individuals (Pearre, 1979). However, direct observations of individual larval migration are time-consuming and labor-intensive and only possible in the daylight (Leis, 2004). In this study, we have looked at a range of behaviors for individual larvae, including both fixed-depth and vertically migrating larvae. However, we have not specifically accounted for such factors as larval condition or larval selectivity based on changing hydrographic conditions. While a better understanding of the larval cues for vertical migration would allow for a more complete larval behavior model, our results provide for a comparison of larval dispersal for larvae distributed throughout the water column. Based on these results, larval behavior appears to be of secondary importance for larvae spawned at reefs in less than 25 m water depth but may be more important for larvae spawned further offshore.

The horizontal swimming capabilities of the larval black sea bass are unknown and no attempt has been made to include any horizontal swimming. However, horizontal swimming may be an important part of larval transport (Werner *et al.*, 1993; Hare and Cowen, 1996; Stobutzki and Bellwood, 1997; Leis *et al.*, 2006) and the possibility of directed swimming and its influence on larval dispersal needs to be considered on a species by species basis. Along with directed horizontal swimming capabilities, many larval fish show schooling behavior, which may influence their dispersal versus passive diffusion. In this study, we have used a random flight model for horizontal larval dispersion with a constant diffusivity based on the results of dye-release experiments in the ocean showing increased diffusivity over time (Okubo, 1971). In contrast, in a study of herring larvae in British Columbia, McGurk (1989) showed that the scale-corrected diffusivity of the larvae decreased with increasing larval age due to their schooling behavior.

### *The big picture*

In this study, larval vertical distributions interacted with vertical shear in horizontal currents to influence the spatial outcome of larval transport. The effects of vertical distribution on horizontal distribution were small relative to other factors, predominantly spawning location and time. Larval vertical distributions can also interact with time and space varying vertical distributions of prey and predators to affect feeding success and predation mortality (Neilson and Perry, 1990). Further, vertical differences in turbidity or small-scale turbulence can influence predator–prey interactions (e.g., Utne-Palm, 2004). Thus, larval vertical distributions can influence larval mortality through interactions between feeding, growth and predation rate (Anderson, 1988; Meekan and Fortier, 1996; Hare and Cowen, 1997), resulting in time and space-varying patterns in larval mortality. Although not explicitly included, the modeling approach used here assumes constant mortality over space. Given the importance of mortality in shaping larval distributions (Cowen *et al.*, 2000), variable mortality over space or time would have a large influence on success rate. The inability to include realistic mortality fields over time and space remains a major limitation in modeling larval dispersal (*sensu* Pineda *et al.*, 2007).

Most of the analysis highlights the similarities and differences in success rates (arrival within the 20 m isobath during the larval competency phase), while Table 8 highlights the intra-seasonal and inter-annual differences in dispersal for larvae spawned at GRNMS and provides a comparison with larval dispersal based on the climatological flow fields (Edwards *et al.*, 2007). In general, it may be more appropriate to use climatological flow fields where the long-term mean is greater than the variance in the individual years, which is not the case in this study region (Fig. 5, Werner *et al.*, 1999). However, species where individuals spawn over multiple years may, in essence, experience the climatology with regard to their total reproductive output, but this is weighted to later years as fecundity increases with size and age.

In a fishery-independent study measuring catch per unit effort, the Marine Resources Monitoring Assessment and Prediction program found evidence of overfishing of black sea bass (McGovern *et al.*, 1998). In addition, Sedberry *et al.* (1998) found that fishing pressure was heavier on those reefs closest to shore (on the inner-shelf including GRNMS) and that the size and number of the black sea bass caught in traps increased with increasing depth and distance offshore. Such patterns of overfishing may lead to recruitment overfishing causing lower egg production and an increased chance of recruitment failure (Plan Development Team, 1990). The results of this study, indicating the importance of the shallower spawning sites to recruitment along with the observed patterns of overfishing, provide support for the development of MPAs on the inner- and mid-shelf in this region. A network of MPAs could be designed and used to protect spawning sites and enhance recruitment in a system with large intra-seasonal and inter-annual variability in transport and connectivity. In order to design such a network, the distribution of spawning needs to be defined in more detail – this could be achieved through an egg survey, which would provide spawning distribution within 2 days.

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