

# YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

## JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.  
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



# The physics of blue crab larval recruitment in Delaware Bay: A model study

by Charles E. Tilburg<sup>1</sup>, John T. Reager<sup>2</sup> and Michael M. Whitney<sup>3</sup>

## ABSTRACT

Recent studies have shown that the tidal-, wind- and buoyancy-driven surface currents govern the transport of blue crab (*Callinectes sapidus*) larvae within the coastal ocean and estuaries. Here, we develop a model of larval transport within Delaware Bay and the adjoining coastal ocean using a particle advection scheme coupled to a previously validated physical circulation model which includes realistic tidal forcing, bottom bathymetry, wind stress and river discharge. The coupled model is then used to quantify the effects of several mechanisms on larval transport and recruitment in this region and hindcast actual larval settlement for a four-year period.

The model is run for the years 1989–1992 and compared with observations of larval settlement collected in the Broadkill River, a small tributary to Delaware Bay. It is able to reproduce all of the major observed recruitment events in 1990–1992, suggesting that larval recruitment is primarily driven by the physical mechanisms included in the model. Analysis of the modeled particle trajectories and the settlement data reveals that wind stress is the dominant mechanism in the determination of the timing of the settlement events, while horizontal diffusion and mortality determine the magnitude of the events. The model fails to agree with observations in 1989, indicating that small-scale physical events as well as larval behavior not reproduced in the numerical model can be important in larval settlement.

## 1. Introduction

A fundamental question in fisheries oceanography concerns those factors that control the supply of larvae to juvenile nurseries. A greater understanding of these mechanisms is valuable because the supply of larvae is often an important determinant of the size of the adult populations (Roughgarden *et al.*, 1988; Sutherland, 1990). Of particular interest on the U.S. east coast are the dynamics that affect the blue crab (*Callinectes sapidus*), which supports the largest inshore fishery on the Mid-Atlantic Bight. There have been a number of studies that have examined its life cycle and the mechanisms that govern the development, transport, and settlement of its larvae. Recent studies have demonstrated that, although blue crabs spawn near the mouths of estuaries, they spend a significant portion of

1. Department of Marine Sciences, University of Georgia, Athens, Georgia, 30602, U.S.A. *email:* [tilburg@uga.edu](mailto:tilburg@uga.edu)

2. Graduate College of Marine Studies, University of Delaware, Newark, Delaware, 19716, U.S.A.

3. College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, 97331, U.S.A.

their larval stages on the continental shelf. Since blue crab larvae are poor swimmers, they rely on the physical flow field of the region to remove them from the bay and return them at a later time for settlement (Epifanio, 1995). Natunewicz *et al.* (2001) followed larval patches on the shelf near Delaware Bay and found early stage larvae leaving the bay and late stage larvae returning. Modeling studies (e.g. Johnson, 1985; Johnson and Hess, 1990; Garvine *et al.*, 1997) of larvae were able to show that the wind field is the primary mechanism for larval transport. Statistical analyses support these studies. Johnson and Hester (1989) were able to explain 36% of blue crab harvest variation in Chesapeake Bay using low frequency wind patterns. Using observed wind stress and larval settlement data, Jones and Epifanio (1995) have shown that the settlement of blue crabs within Mid-Atlantic Bight estuaries is episodic and the observed frequency of settlement events was significantly greater than expected during downwelling winds.

Epifanio and Garvine (2001) provide a detailed summary of the blue crab life cycle and the physical processes responsible for successful recruitment in the Mid-Atlantic Bight estuaries, and the interested reader is referred to their work and the included references for a more comprehensive description. Here, we briefly summarize their conceptual model (shown schematically in Fig. 1) as applied to Delaware Bay.

During mid-summer, gravid female crabs migrate to the mouth of Delaware Bay and spawn during ebb tide, releasing larvae that rise to the surface. These larvae remain within the upper 1–2 meters of the water column, exit the bay due to a combination of tidal currents and buoyancy-driven flow, and proceed downshelf (where we define downshelf as the direction of coastally trapped wave propagation) with the buoyancy-driven flow (indicated by arrow 1 in Fig. 1). The offshore and upshelf surface transport associated with upwelling events tends to arrest the downshelf movement of the larvae and transport them back upshelf toward the bay (arrow 2 in Fig. 1). During this time on the shelf, the larvae mature through seven zoea stages followed by a single megalopa stage. In the coastal ocean, zoeal development typically requires 3–4 weeks, while the megalopa stage lasts 1–2 weeks (Epifanio and Garvine, 2001). Downwelling events and the associated onshore surface flow can transport megalopae back into the bay (arrow 3 in Fig. 1). Once the megalopae return to the mouth of the bay, they perform a series of vertical migrations that coincide with flood tides and migrate up the bay to their nursery habitat (Epifanio *et al.*, 1984; Forward *et al.*, 2003). The metamorphosis of megalopae into juvenile crabs is dependent on the successful transport of the megalopae from the continental shelf to the benthic nursery within Delaware Bay.

Garvine *et al.* (1997) developed a mathematical means to test this conceptual model and examine the relative effects of river discharge and alongshelf winds on larval recruitment. Using an extensive set of observations gathered from current meters within the Delaware Coastal Current and on the continental shelf, they were able to construct an empirical model of transport within discrete zones based on correlations between shelf currents and the forcing functions of river discharge and wind stress. Their model neglected the effects

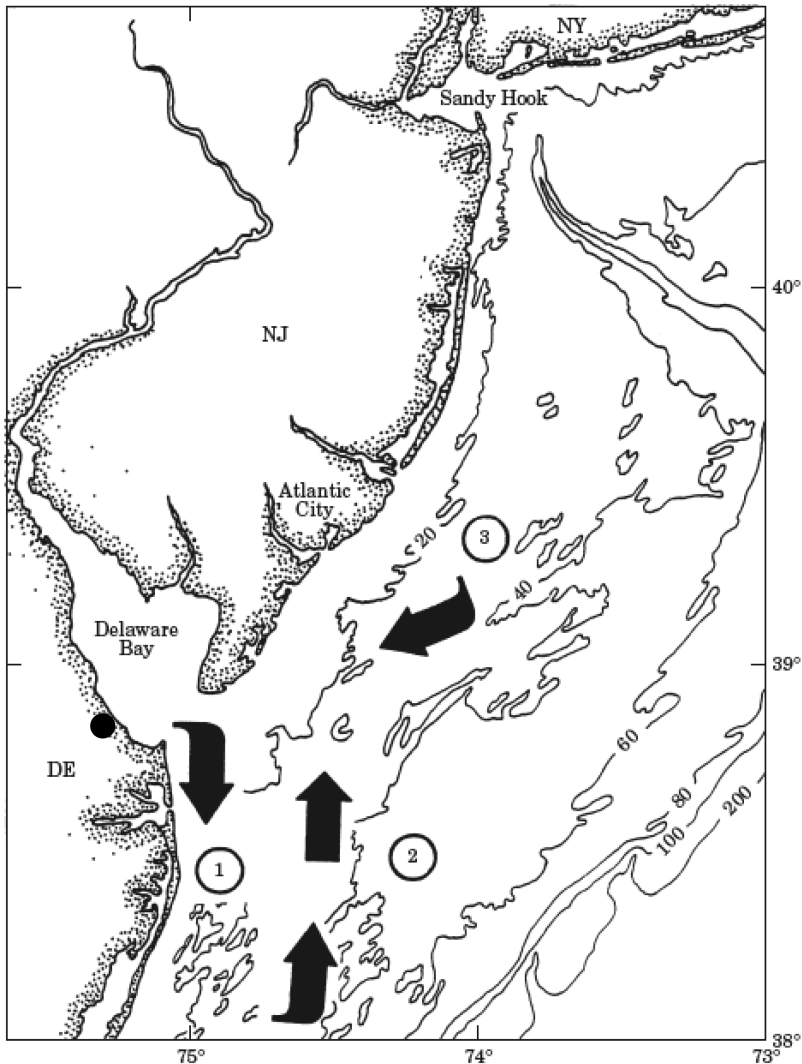


Figure 1. Map of Delaware Bay region illustrating the conceptual model of Epifanio and Garvine (2001) for transport of blue crab larvae and eventual settlement into Delaware Bay. Their model states that the successful recruitment of larvae consists of three parts: (1) transport with buoyancy-driven flow out of Delaware Bay and down the shelf, (2) offshore and upshelf transport associated with upwelling winds, and (3) return to the bay due to onshore transport associated with downwelling winds. The black circle indicates the location of the mouth of the Broadkill River in which settlement observations were made.

of tides and alongshelf variations of the wind-driven current. The model domain was a planar shelf and did not include Delaware Bay. Instead, the buoyancy-driven flow originating at the head of Delaware Bay was specified as a boundary condition on the

coastline. A particle advection scheme was used to follow the trajectories of particles that were instantaneously placed into the flow field (or spawned) near the source of the buoyancy-driven flow. These larvae were placed into the flow field once a day for the duration of the simulation (120 days). Simulated larvae were considered settled if they returned to their spawning site any time after 22 days, which roughly corresponded to the observed duration of the seven zoea stages. Comparison of modeled larval settlement with observations of settlement in the Broadkill River for the years 1989–1992 (Jones and Epifanio, 1995) revealed that the initial settlement events of the model coincided with observations for the years 1989 and 1990. However, there was little agreement between the model and observations for the years 1991 and 1992. Garvine *et al.* (1997) attributed this mismatch to a difference in the modeled and actual spawning of blue crabs, which is not well understood due to a lack of fine-scale information concerning the timing and location of egg hatching. They concluded that the agreement between the model and observations for the years 1989 and 1990 suggested that the recruitment of larvae depended on the flow field on the continental shelf and that physical mechanisms could result in the variations in blue crab larval settlement rates observed in Delaware Bay.

With the development of a realistic physical circulation model whose domain encompasses Delaware Bay and the adjoining coastal ocean (Mele, 2002; Whitney and Garvine, 2005), we are able to build on the preliminary modeling investigations of Garvine *et al.* (1997) and more closely examine those dynamics responsible for blue crab recruitment. The circulation model is a validated primitive equation finite-difference model that includes tidal variations, wind-forcing, and vertical structure of the velocity fields. The model domain includes Delaware Bay, a portion of the Delaware River, and the adjoining coastal region. Coupled with a particle advection scheme, the model provides an ideal tool to examine those mechanisms first investigated by Jones and Epifanio (1995) and Garvine *et al.* (1997), which can transport larvae out of Delaware Bay, onto the coastal shelf and back into the bay.

Previous analyses of the physical mechanisms governing larval recruitment (e.g. Johnson *et al.*, 1984; Jones and Epifanio, 1995) have been complicated by the episodic nature of the settlement and the spawning of larvae. The combination of physical factors that can be measured (i.e. currents) and biological factors that cannot (i.e. timing of spawning events) have made rigorous analysis of the relative effects of the different mechanisms responsible for larval settlement problematic. The use of a deterministic model whose larval spawning is specified allows us to examine the physical mechanisms responsible for larval recruitment without the complications associated with unknown spawning rates. In this paper, we investigate the processes responsible for blue crab larval recruitment in three steps: (1) compare our numerical model to the observations and evaluate its effectiveness in predicting observed settlement, (2) examine the separate effects of several mechanisms on larval recruitment, and finally (3) evaluate the conceptual model of Epifanio and Garvine (2001) and make needed modifications. The numerical model and the advection scheme are described in Section 2. The results of the comparison

of the model with observations are discussed in Section 3, while the summary and conclusions are contained in Section 4.

## 2. Model and methods

The physical circulation model used in this investigation is ECOM3d, a primitive equation finite-difference model in sigma (terrain following) coordinates based on the model developed by Blumberg and Mellor (1987). This model and a similar model, the Princeton Ocean Model, have been used extensively to study transport on coastal shelves (e.g. Kourafalou *et al.*, 1996a,b; Austin and Lentz, 2002; Whitney and Garvine, 2005). The model used here is an extension of that described by Whitney and Garvine (2005), who validated the model with a series of observations of currents and hydrographic surveys during the spring of 1993. Consequently, the model is only briefly described here and the interested reader is referred to Whitney and Garvine (2005) for a more comprehensive description.

The coastline and model bathymetry are based on data provided by the NOAA National Geophysical Data Center. The model domain is shown in Figure 2a. The offshore boundary is located along the 100 m isobath and its free surface is fixed to the tides by specifying the amplitude and phase of the semi-diurnal M2 tidal constituent derived from an inverse tidal model incorporating TOPEX/Poseidon altimetry data (Egbert *et al.*, 1994). The across-shelf boundaries at the up- and downshelf locations are combination clamped/radiation boundaries that are specifically developed to realistically treat tidal, wind, and buoyancy forcing (Whitney, 2003). Flow at the bottom boundary is governed by a quadratic drag law. Vertical mixing is handled by the Mellor-Yamada level 2.5 turbulence closure scheme, while horizontal eddy viscosities and diffusivities are treated by the Smagorinsky scheme (Smagorinsky, 1963). Since ECOM3d is a sigma-level model, the vertical resolution is proportional to water depth. This simulation contains 15 sigma levels whose spacing is much closer near the surface and the bottom boundaries to better resolve the surface and bottom Ekman layers. The horizontal grid size for the simulation varies from 0.75 km within Delaware Bay to 3 km on the shelf. However near the boundaries grid sizes increase to 8 km. The model uses a split time step of 9.2 s for the barotropic mode and 92 s for the baroclinic mode.

The model is forced with winds obtained from hourly surface meteorological observations at the Atlantic City International Airport collected by the Northeast Regional Climate Center. Freshwater discharge is specified by river flow obtained from the United States Geological Survey daily river discharge records at Trenton, NJ.

To create trajectories of the simulated larvae, we use a particle advection algorithm that tracks several thousand particles released into the model flow field. Since the swimming speeds of the larvae are much less than the advective velocities within the bay and on the shelf, the larvae are modeled as passive particles. This approach is common in the

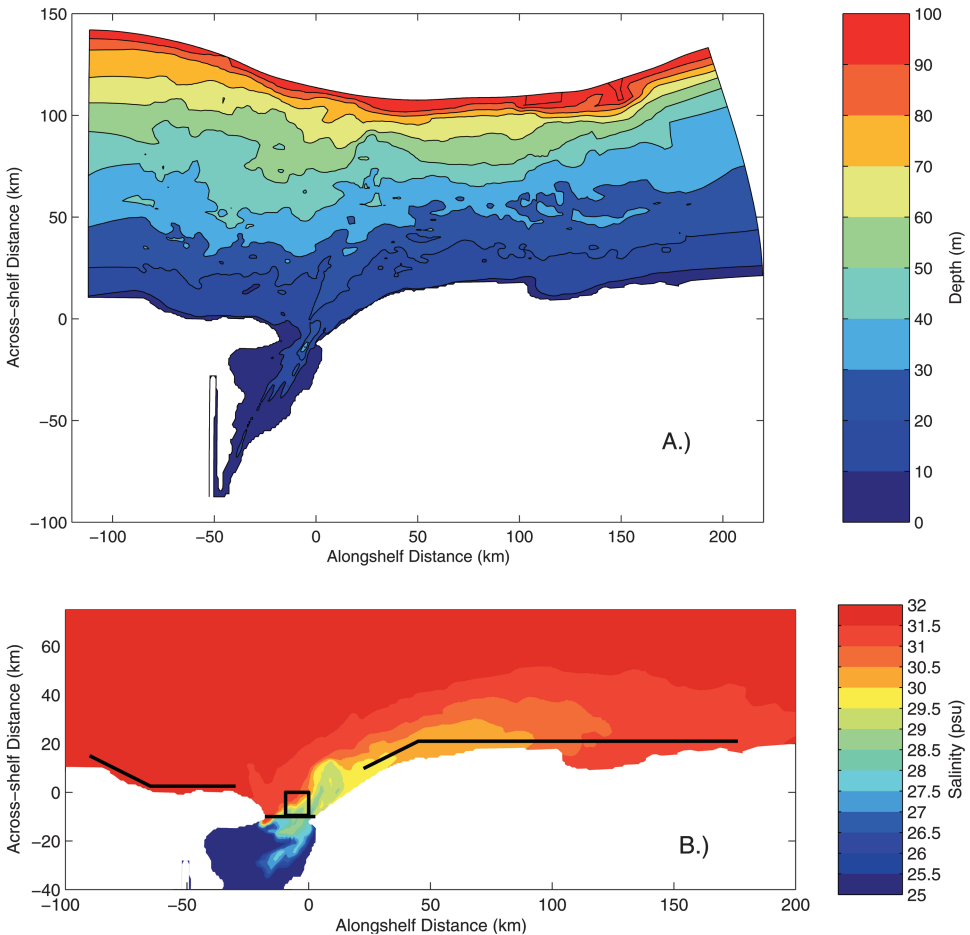


Figure 2. (a) Domain of the circulation model illustrating bottom bathymetry (m). (b) Close-up view of the model sea-surface salinity (psu) near the mouth of Delaware Bay. The black square represents the region in which the larvae are released during spawning. The horizontal black line at  $Y = -10$  km represents the division between Delaware Bay and the coastal ocean. The black lines along approximately the 10 m isobath represent the regions in which larvae are released during up- and downshelf spawning simulations.

examination of individual larvae trajectories (e.g. Johnson and Hess, 1990; Garvine *et al.*, 1997; Hannah *et al.*, 1998) or of convergence and divergence within estuaries (e.g. Hood *et al.*, 1999).

Successful recruitment of larvae to Delaware Bay involves three processes: (1) spawning near the mouth of the bay, (2) passive advection by the physical flow field, and (3) settlement in the bay once the larvae reaches the megalopal stage. The three processes as simulated in the coupled model are discussed below.



*Spawning:* Gravid females migrate to the mouth of Delaware Bay and release their eggs during high slack tide (e.g. Epifanio and Garvine, 2001). Under light wind conditions, the buoyancy-driven flow exits Delaware Bay and turns to the right due to the Coriolis effect. A snapshot of the simulated sea-surface salinity (Fig. 2b) shows the region of low-salinity water confined to the coast that generates the buoyancy-driven flow. Larval spawning is simulated in the model as an instantaneous placement of 121 particles uniformly spaced in a  $10 \text{ km} \times 10 \text{ km}$  square near the mouth of Delaware Bay in the vicinity of this buoyancy-driven coastal flow (black square in Fig. 2b) that exit the bay on the ensuing ebb tide. Additional simulations to examine the effects of larval spawning up- and downshelf of the bay are also performed by placement of particles along the 10 m isobath up and downshelf of the bay (black lines in Fig. 2b). The first group of spawned larvae is placed in the flow field during high slack tide of year-day 190 (July 10). Each new group is placed in the flow field on subsequent high tides for the duration of the simulation (115 days).

*Advection:* The trajectories of individual larvae are determined by using a simple fourth-order runge kutta method to integrate the following equation:

$$\frac{\partial \mathbf{x}}{\partial t} = \mathbf{U} + \mathbf{u}$$

where  $\mathbf{U}$  is the horizontal velocity of the circulation model at 0.5 m below the surface and  $\mathbf{u}$  represents a diffusion term that simulates the random motion of the particle due to small-scale events not resolved by the model flow field and is expressed as

$$\mathbf{u} = \mathbf{U} \times G[0, 1]/B$$

where  $G[0, 1]$  is a Gaussian distribution with zero mean and unit variance and  $B$  is a constant that modifies the variance.

*Settlement:* Since mature megalopae are able to migrate vertically within the water column and use the tidal flow to enter estuaries (Forward *et al.*, 2003), we assume that the successful recruitment of an individual larva requires the presence of the larva at the mouth or within Delaware Bay after it has matured into the megalopal stage, where the bay is defined as that part of the model domain where  $Y < -10 \text{ km}$  (black line in Fig. 2b). This simple model neglects the effects of salinity, temperature, or turbidity variations on settlement due to our lack of *a priori* knowledge of crab behavior.

Within the present model, there are three scenarios that can prevent successful recruitment:

- 1) *The larvae are transported away from the bay and do not return.* The return of larvae is predicated on a series of upwelling and downwelling events. Previous studies (Garvine *et al.*, 1997) have shown that most larvae fail to return due to unfavorable advection by wind and buoyancy-driven transport.



- 2) *Larvae are no longer viable when they return to the bay.* While the time of viability for individual larvae may vary considerably, our model assumes that all larvae are viable from 22 days (the minimum observed time for maturation to megalopa) to 40 days (the maximum age of megalopae, which allows for approximately 4 weeks for the seven zoea stages and two weeks for the megalopa stage). Variations of  $\pm 2$  days for the minimum (22 days) or maximum (40 days) viable age have little qualitative effect on the model performance.
- 3) *The larvae are consumed by predators.* The largest source of mortality in the coastal ocean and estuaries is likely loss to predators (Houde, 1989). The effects of predation are applied to the larvae by randomly removing particles from each spawned group so that the group's population,  $N$ , follows

$$N = N_o e^{-ct}$$

where  $N_o$  is the population at spawning,  $t$  is the time from spawning and  $c$  is the mortality rate, which can range from 0 (no mortality) to  $0.5 \text{ day}^{-1}$  (high mortality).

The physical circulation model, ECOM3d, is run for the time period 1988–1995. The surface flow field for the years 1989–1992 is then used as input for the particle advection scheme. A number of simulations are performed to examine the effects of mortality, diffusion, and the interannual variability of transport on total larval settlement. The simulation used for the primary comparison with observations neglects the effects of mortality and applies a diffusion specified by  $B = 1$ . A series of simulations in which the diffusion and mortality are systematically varied are also performed to examine the effects of increased mixing and predation on total larval settlement.

### 3. Results and discussion

#### a. Model-data comparison

Comparison of modeled larval settlement with observations (Fig. 3) reveals that the coupled model agrees quite well with observations for three of the four years. All significant (i.e. greater than 4 standard deviations) settlement events apparent in the observations (dashed line) are reproduced by the model (solid line) for the years 1990–1992; however, major modeled and observed settlements in 1989 show little if any agreement. The observed settlement in 1989 is dominated by one major event, which is not present in the model output. The following three years show much better agreement. The timing of all observed major settlement events in 1990–1992 coincides with peaks in the model, although the model is not able to capture small-scale fluctuations in settlement events (such as the structure in settlement during yeardays 290–302 in 1990) or smaller (i.e. less than 3 standard deviations) settlement events. The smaller settlement events at yearday 261 in 1990 and yeardays 214, 230, and 275 in 1992 are not well represented in the numerical model. The large-scale agreement between the model and observations is

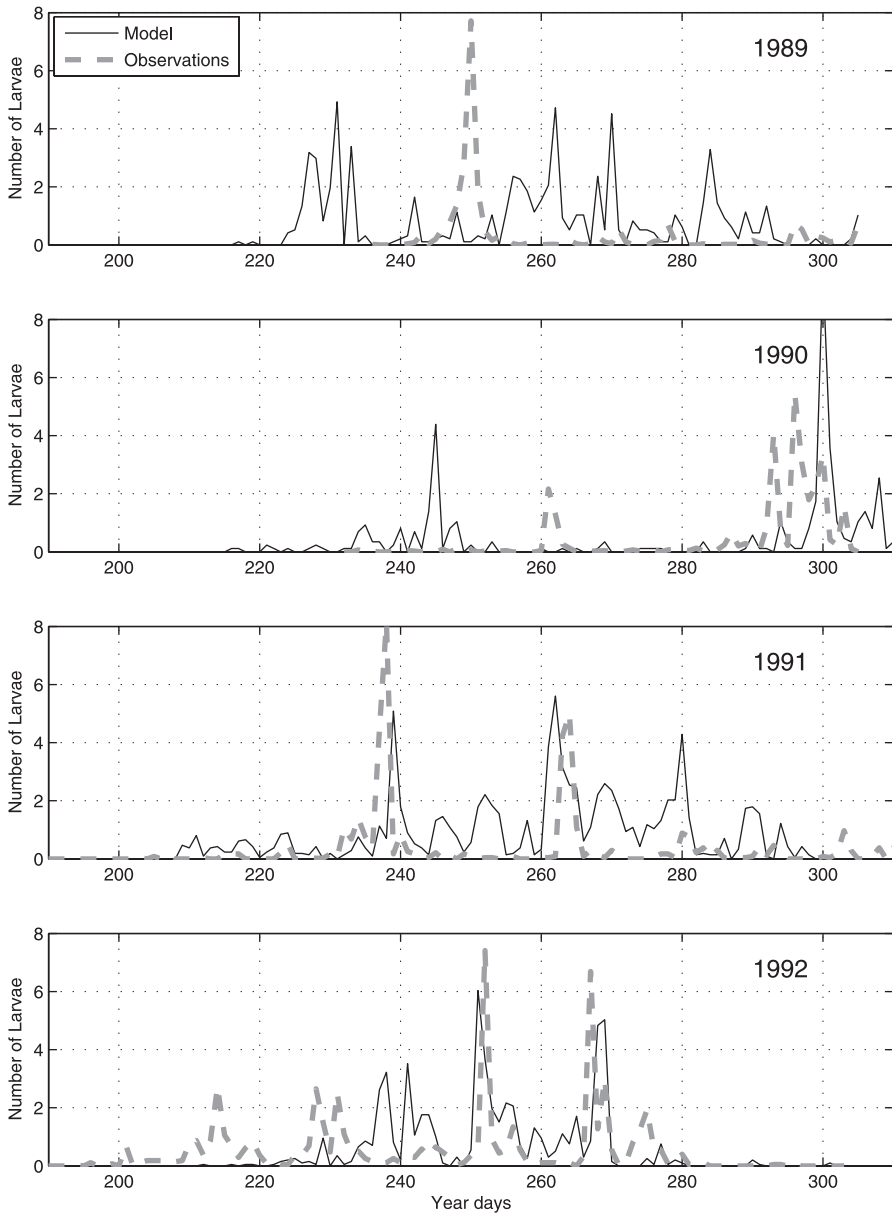


Figure 3. Modeled (solid line) and observed (dashed line) blue crab settled larvae for the years 1989–1992. Observed settlement data were obtained from daily measurements in the Broadkill River. Both modeled and observed settlement data have been nondimensionalized by dividing all values by their standard deviation. A settlement event consists of daily settlement that is greater than 2 standard deviations.

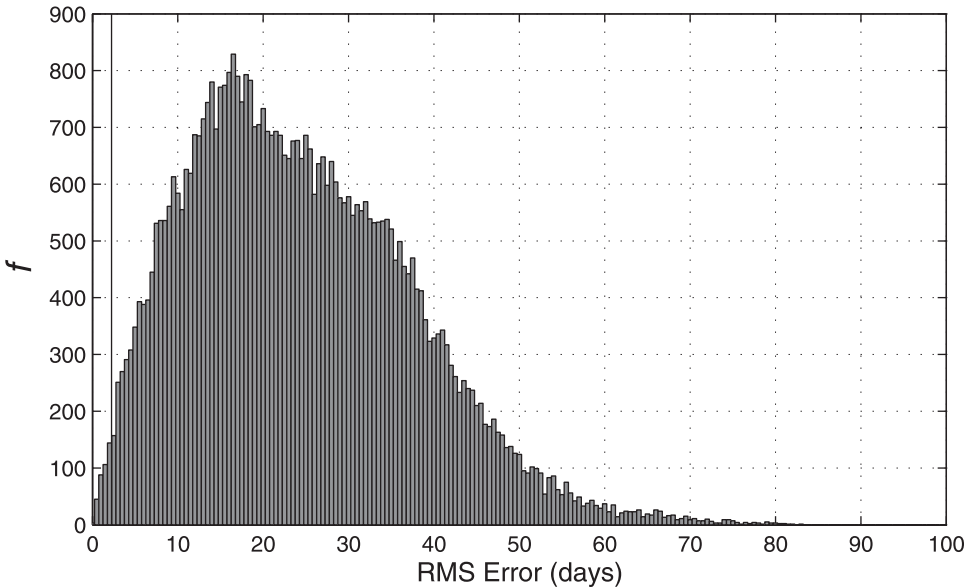


Figure 4. Histogram indicating the frequency distribution of RMS errors (days) obtained from 50,000 synthetic settlement data for the year 1991. The vertical line represents the RMS error of the numerical model for 1991.

significantly different from that of Garvine *et al.* (1997), which matched only the initial observed settlement events, and suggests that better representation of shelf dynamics as well as the inclusion of the transport within Delaware Bay is necessary for accurate simulation of the flow field on the shelf and larval recruitment within the bay.

Although most observed settlement events are reproduced in the model, there are a number of modeled events that are not apparent in the observations (Fig. 3). As was noted by Garvine *et al.* (1997), these spurious events should be expected since no effort was made to match the magnitude and timing of the actual spawning events, which are known to be episodic in other species of crabs (e.g., DeVries *et al.*, 1983; Morgan, 1987; Morgan and Christy, 1995). To provide a quantitative measure of model skill that accounts for these additional events and determine the level of significance of agreement between the model and observations, we use a simple randomization test, which compares root mean square (RMS) error of the model with distributions from a large number of synthetic data sets. The synthetic data sets are constructed by randomly choosing two or three separate days between yeardays 200 and 310 and designating these as settlement events. The number of random settlement events (2 or 3) is determined by the number of events present in the model output for each year. Examination of Figure 3 indicates that there are 3, 2, 3, and 2 significant modeled settlement events for the years 1989, 1990, 1991, and 1992, respectively. Once a large number (i.e. 50,000) of data sets have been created for each year, a frequency distribution of the RMS error can be constructed (see Fig. 4 for a sample

distribution). Comparison of the model RMS error with the distribution for each year provides an estimate of the significance of the model skill. A model RMS error that is less than 95% of the synthetic RMS errors for a particular year indicates that the model skill outperforms random chance at a significance of 95%. Comparison of the model output RMS errors with the RMS error distributions reveals that the model RMS error is less than 51.9%, 86.0%, 99.2%, and 99.8% of the synthetic RMS errors for the years 1989, 1990, 1991, and 1992 respectively. As expected, this quantitative measure of model skill confirms the poor performance of the model for 1989. A random selection of three settlement events is as accurate as the numerical model approximately half of the time. However, the next three years are well simulated by the numerical model. In 1990 model skill is significant at >85%, while in 1991 and 1992 the model skill is significant at >99%.

Several sources of error in the numerical model can be attributed to the poor agreement of the model with observations in 1989 and the smaller scale events in the other years. The horizontal resolution of the model within the bay (0.75 km) results in a mismatch in spatial scales of model resolution and observed settlement location. Observations of blue crab settlement occurred at only one location, the Broadkill River (black circle in Fig. 1), while the model settlement zone extends throughout the mouth of the bay. Comparison of the modeled settlement events as a function of several different settlement locations (not shown) reveals that the modeled settlement events best match the observed events when the entire bay is designated as the settlement site. This result is not surprising; the model's horizontal resolution is unable to resolve the small-scale flow features that are necessary for the accurate simulation of spatial variations in larval settlement within Delaware Bay. Additionally, the model does not incorporate larval responses to variations in salinity, temperature, or turbulent kinetic energy, which have been shown to govern the final settlement of larvae (Forward *et al.*, 2003). Although the model is unable to resolve small-scale flow features within the bay, it is able to accurately simulate those mechanisms responsible for the transport of larvae onto the shelf and back into the bay (i.e. buoyant discharge, tides, and wind-driven transport). The overall agreement between the model settlement and the observed settlement within the Broadkill River indicates that during events when a large number of settlement-age larvae enter the bay, small-scale flow features not present in the model typically result in the settlement of larvae at the mouth of the Broadkill River.

The overall agreement between the modeled and observed settlement events allows us to examine the large-scale dynamics of the model and determine their relative effects on larval recruitment. A striking feature of these simulations is the number of spawned larvae that are lost to their parent estuary by unfavorable advection (Table 1). The percentage of spawned larvae that returns to the bay for settlement ranges from 1.3% to 7.0%. Although the number of larvae spawned each year in the model is constant, the total number of larvae that settle in the bay varies by a factor of five (372 to 1887 total settled larvae), which is significantly larger than the observed variations (ranging from 206 to 355 total settled larvae). The lack of knowledge of actual spawning and mortality rates restricts the model's

Table 1. Categories of successfully settled larvae for years 1989–1992.

Year	Larvae that remain near mouth*	Larvae that enter buoyant flow**	Larvae that are primarily wind-driven***	Total settled larvae
1989	0.3%	0.7%	2.5%	3.5%
1990	0.2%	0.1%	1.0%	1.3%
1991	0.7%	2.0%	4.3%	7.0%
1992	0.5%	1.8%	2.1%	4.4%

\*Defined as those larvae that remain within the black box in Figure 6.

\*\*Defined as those larvae that migrate downshelf of  $X = 10$  km.

\*\*\*Defined as those larvae that exit the black box but remain upshelf of  $X = 10$  km.

ability to predict total larval settlement on an inter-annual basis. Examination of Table 2 reveals that the year of maximum simulated larval settlement (1991) corresponds to the minimum observed larval settlement. However, the timing of the simulated settlement events agree quite well with observations for three of the four years, indicating that the physical mechanisms present in the model are able to account for the observed intra-annual variations in settlement data.

#### *b. Successful larval trajectories*

The large variations in total settlement reveal that the transport pathways followed by larvae during their return to Delaware Bay can be dramatically altered by fluctuations in winds. Investigation of the trajectories of successfully settled larvae (Fig. 5) reveals that most larvae are initially removed from the bay by offshore transport and return with onshore surface transport. While on the shelf, the larvae can travel large distances before returning to the bay. Larvae that enter the buoyancy-driven current can be transported more than 50 km downshelf from the mouth of the bay. Those that are entrained into upshelf currents associated with upwelling winds can be transported more than 100 km upshelf before returning to the bay. Closer analysis of the trajectories reveals that successfully settled larvae can be grouped into three categories: (1) those that remain within the region of the mouth of Delaware Bay, (2) those that enter the buoyancy-driven flow and are transported downshelf before an upwelling event brings them back upshelf, and (3) those

Table 2. Model-data comparison of settled larvae from 1989–1992.

Year	Total number of observed larvae	Total number of modeled larvae
1989	291	959
1990	355	372
1991	206	1887
1992	245	1188

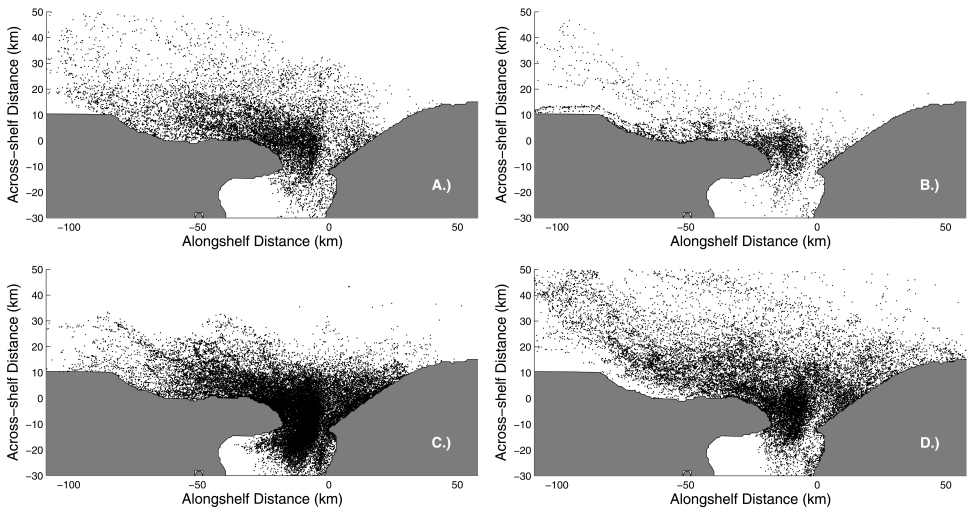


Figure 5. Trajectories of all successfully settled larvae for the years (a) 1989, (b) 1990, (c) 1991, and (d) 1992. The location of each larva at every 10th time step is represented by a black dot.

that do not enter the buoyancy-driven flow but instead proceed directly offshore and upshelf during an upwelling event. The last two categories require an extended downwelling event to transport the larvae back into the bay for successful recruitment, while the first does not. Example trajectories of larvae from each category are shown in Figure 6. The green trajectory represents a typical pathway followed by a larva that remains near the mouth of the bay for its entire larval stage. The blue trajectory represents the pathway of a larva that first enters the buoyancy-driven current and proceeds downshelf but is then transported offshore during an upwelling event and back upshelf. A subsequent downwelling event transports it back to the mouth of the bay for settlement. The red trajectory represents the pathway of a larva that is primarily affected by wind-driven transport. It is immediately transported offshore and upshelf due to an upwelling event and never enters the buoyancy-driven current. A later downwelling event returns the larva to the mouth of the bay.

The distribution of larvae that follow the transport pathways described above varies greatly over the four years (Table 1). During year 1992, a significant amount of the larvae behave in a manner similar to that described by Epifanio and Garvine (2001). They are removed from the bay and follow the buoyancy-driven flow downshelf. Later an upwelling event transports them offshore and upshelf. Examination of the trajectories of those larvae released during 1992 (Fig. 5d) reveals a large number of larvae spend a significant portion of time downshelf of the bay. Some travel over 60 km downshelf. However, during years 1989–1991, the majority of the larvae do not enter the buoyancy-driven flow but instead are directly transported offshore and upshelf. Trajectories of the larvae during these years (Fig. 5a–c) reveal that most larvae spend little time downshelf and are found primarily upshelf of the bay.

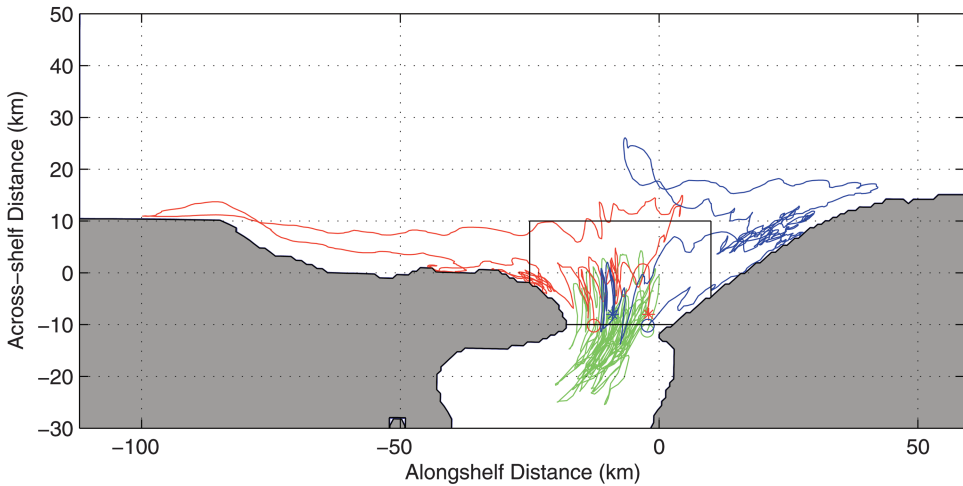


Figure 6. Trajectories of three larvae representing the different categories of successfully settled larvae. The green line represents the trajectory of a larva that remains near the mouth for the duration of its larval stage. The blue line represents the trajectory of a larva that enters the boundary-driven current before returning upshelf due to upwelling winds. The red line represents the trajectory of a larva that is immediately transported offshore and upshelf. The black box is used to define the three categories of larvae: those larvae that remain near the mouth (remain in the box), those that enter the buoyant flow (migrate downshelf of  $X = 10$  km), and those that are primarily wind-driven (exit the box but do not migrate downshelf).

### c. Wind and buoyancy effects on settlement events

Although previous studies of Delaware Bay (Jones and Epifanio, 1995; Garvine *et al.*, 1997; Schwalm, 1999) have suggested that settlement events are governed by downwelling wind events, attempts at statistical analysis of the observed data in conjunction with wind events have not been conclusive, indicating that the relationship between wind forcing and settlement may be more complex than the conceptual model described by Epifanio and Garvine (2001). Output from the present model provides an ideal tool to examine this relationship. Comparison of wind stress and settlement data reveals that larval settlement is most correlated with wind events that are directed nearly downshelf with just a small angle (approximately  $20^\circ$ ) inclined onshore. This result agrees with recent studies that have demonstrated that the surface across-shelf transport is primarily due to alongshelf winds with an additional contribution from across-shelf winds near the coast (Tilburg, 2003) and at the mouth of estuaries (Janzen and Wong, 2002). A comparison of the wind stress component oriented  $20^\circ$  from alongshelf with modeled larval settlement (Fig. 7) reveals that, although some recruitment events do coincide with downwelling events (e.g. days 230 and 262 in 1989, day 246 in 1990, day 264 in 1991, and day 268 in 1992), there are a significant number of events (e.g. days 254 and 284 in 1989 and day 280 in 1991) that do not.



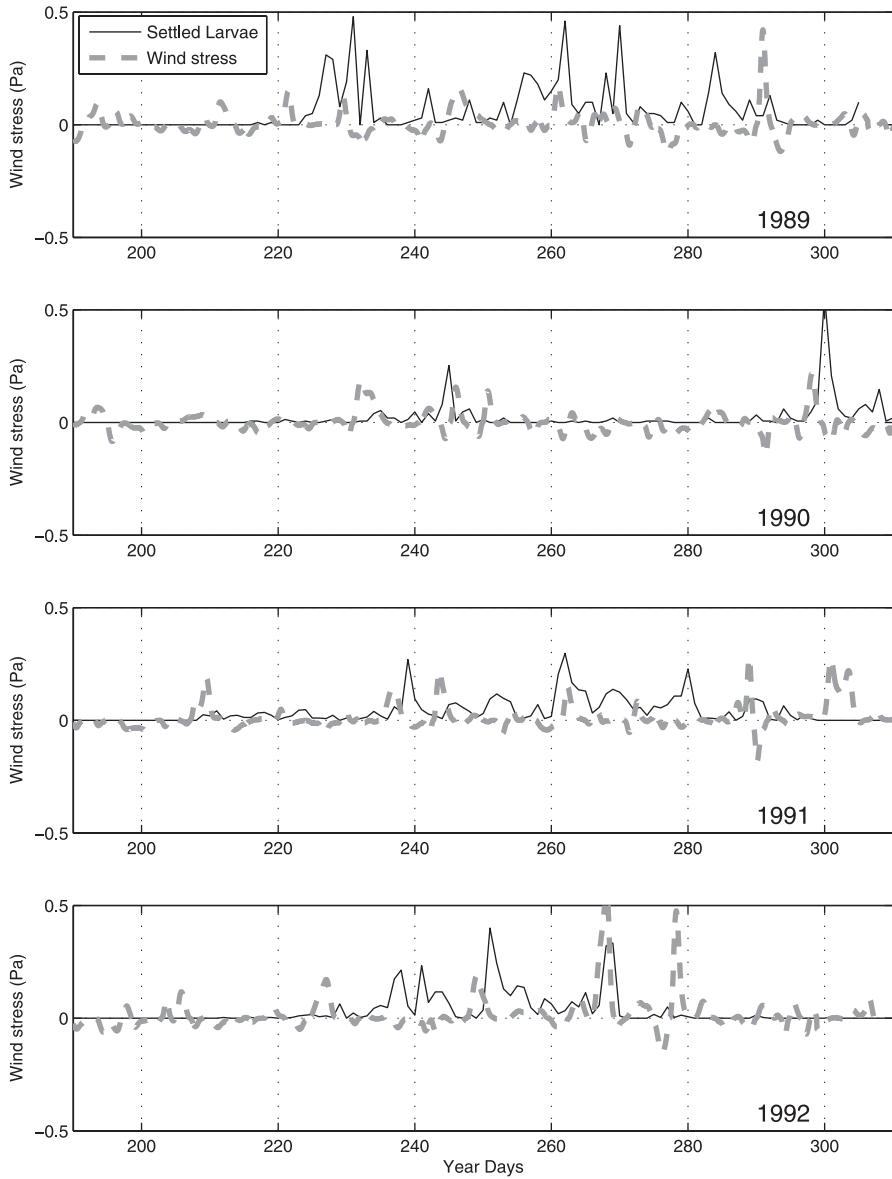


Figure 7. Modeled blue crab settled larvae (solid line) and the wind stress (Pa) component oriented  $20^\circ$  from downshelf (dashed line). The modeled settlement data has been multiplied by an arbitrary constant for easier comparison with the wind stress data.

Closer examination of the model trajectories reveals that the settlement of larvae is governed by more than just wind-driven transport. Larval settlement events occur when megalopa stage larvae are within the mouth of the bay. However, the larvae may be present

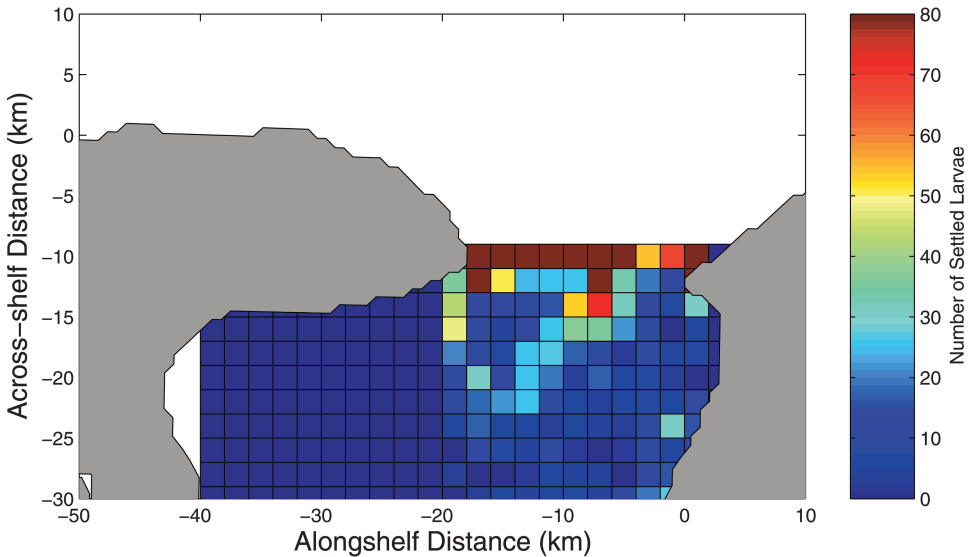


Figure 8. Settlement locations of larvae for all years. The colors indicate the total number of larvae that successfully settle in each location.

in this region due to light winds that never remove the larvae (i.e. the green trajectory in Fig. 6) or an earlier downwelling event that returns immature larvae to the bay, which then remain until they reach the megalopal stage and are able to settle. Examination of the settlement location of the larvae (Fig. 8) reveals that a majority of the larvae settle at the entrance of Delaware Bay (i.e. near black line at  $Y = -10$  km in Fig. 6), indicating that they enter as mature larvae and settle as soon as they enter the bay. However, a number of larvae settle in locations far up the bay, revealing that they enter the bay as immature larvae and settle when they reach the megalopa stage. Most successfully settled larvae remain on the shelf for less than 15 days (Fig. 9a) and inhabit Delaware Bay for 7–10 days before settlement. Hence, the settlement of a majority of larvae should not be expected to coincide with a particular downwelling event. The retention of larvae within the bay before settlement is also supported by the distribution of ages of larvae at settlement (Fig. 9b). The majority of larvae (1946 out of a total of 3500) settle at an age of 22 days or as soon as they reach the megalopal stage, indicating that larval development and not the time of an individual wind event determines time of settlement. This behavior makes it particularly difficult to predict larval settlement using an empirical model derived from winds. Interestingly, observations (Steppe and Epifanio, 2005) revealed very few late stage larvae within Delaware Bay suggesting that the presence of more predators in the bay (Morgan and Christy, 1995) greatly reduces the number of immature larvae that are retained in the bay before settlement.

Buoyancy-driven transport provides the mechanism for low-frequency transport of spawned larvae out of Delaware Bay. A comparison of the river discharge used to drive the

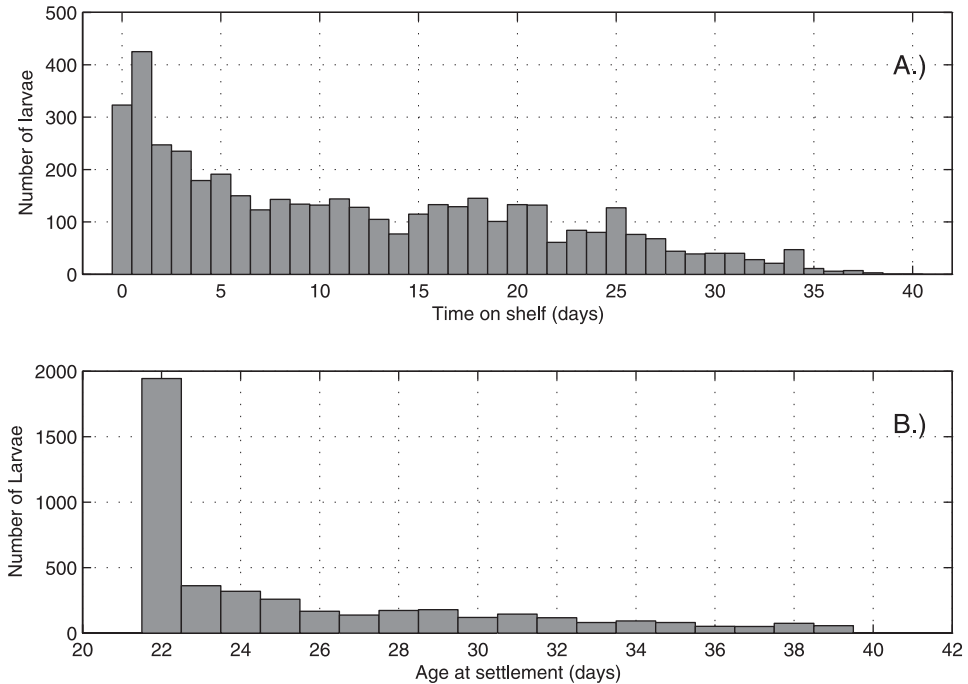


Figure 9. Histograms indicating (a) the distribution of time each successfully settled larva remains offshore of  $Y = 0$  km and (b) the distribution of ages of larvae at time of settlement.

numerical model (Fig. 10) reveals that the average discharge during the simulated time periods varies between 150 and 200  $\text{m}^3/\text{s}$  for each year, but there are large but short-lived discharge events in 1989 and 1991. While lower frequency fluctuations in river discharge might have significant effects on larval transport by overcoming wind-driven flow and transporting more larvae downshelf away from the estuary, the short-lived increases in river discharge appear to have little effect on successful larval recruitment. In 1989 and 1992, wind-driven processes determine the trajectories of most successfully settled larvae and do not result in a greater than expected loss of settlement to the bay (Table 1). However, the increase in river discharge in 1992 may have resulted in a greater number of larvae exiting the bay and traveling downshelf before returning to the bay.

#### d. Mortality and diffusion

The comparison of the timing of the modeled and observed settlement events is relatively straightforward, but the lack of available information on the number of larvae spawned each year or the rate of larval mortality prevents any attempt at comparing the absolute magnitude of the modeled and observed settlement events. However, we can examine the relative effects of different mechanisms on the total larval settlement by performing a series of simulations for year 1991 in which the larval mortality (Tables 3 and

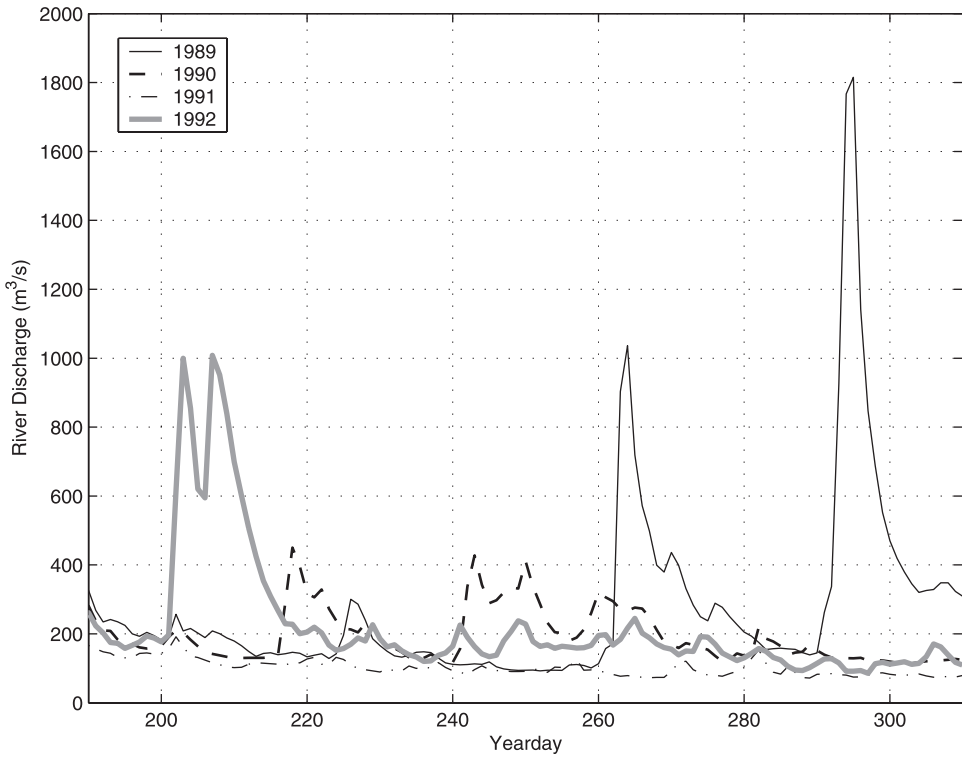


Figure 10. Discharge of the Delaware River ( $\text{m}^3/\text{s}$ ) obtained from the United States Geological Survey daily discharge records at Trenton, NJ.

4) and diffusion (Table 5) are systematically varied. The effect of mortality on larval settlement is expected; the number of settled larvae systematically decreases as the mortality rate within the model is increased. As the mortality rate is increased from 0 to  $0.5 \text{ day}^{-1}$ , the total larval settlement decreases from 7.0% to 0.0026% (Table 3). A mortality rate of  $0.1 \text{ day}^{-1}$  applied to the simulation of year 1991, which results in an order of magnitude decrease in total larval settlement (7.0% to 1.3%), is comparable to settlement fluctuations resulting from interannual variations in transport (Table 1).

Table 3. Total settled larvae as a function of mortality for year 1991.

Mortality rate ( $\text{day}^{-1}$ )	Total settled larvae
0	7.0%
0.025	4.6%
0.05	3.1%
0.1	1.3%
0.2	0.25%
0.5	0.0026%

Table 4. Categories of successfully settled larvae as a function of mortality within the bay for year 1991.

Mortality rate in bay ( $\text{day}^{-1}$ )	Larvae that remain near mouth*	Larvae that enter buoyant flow**	Larvae that are primarily wind-driven***	Total settled larvae
0	0.7%	2.0%	4.3%	7.0%
0.05	0.7%	1.9%	3.6%	6.2%
0.1	0.4%	1.7%	2.8%	4.9%
0.2	0.2%	1.5%	2.0%	3.7%
0.5	<0.1%	1.2%	1.2%	2.4%

\*Defined as those larvae that remain within the black box in Figure 6.

\*\*Defined as those larvae that migrate downshelf of  $X = 10$  km.

\*\*\*Defined as those larvae that exit the black box but remain upshelf of  $X = 10$  km.

A common explanation for the transport of blue crabs from their spawning sites in estuaries to the continental shelf during their larval stage is the avoidance of predators, whose population is much larger within the estuaries (e.g., Morgan and Christy, 1995). The effectiveness of this migration can be illustrated using a series of simulations for the year 1991 in which the mortality rate in Delaware Bay is varied (Table 4). As the mortality rate is increased within the bay, the total number of settled larvae decreases. A mortality rate of  $0.5 \text{ day}^{-1}$  within the bay results in a decrease of settlement from 7.0% to 2.4% for the year 1991. Settlement of wind-driven larvae decreases from 4.3% for no mortality to 1.2% for a mortality rate of  $0.5 \text{ day}^{-1}$  (Table 4). The majority of the wind-driven larvae enter the bay as immature larvae and are subjected to high mortality within the bay as they mature into megalopae. Those larvae that enter the buoyant flow are transported downshelf and return to the bay as megalopae suffer less from high mortality rates in the bay (2.0% for no mortality vs. 1.2% for a mortality rate of  $0.5 \text{ day}^{-1}$ ). However, those larvae that remain near the mouth are drastically affected by high mortality rates within the bay. The number of successfully settled larvae decreases by an order of magnitude from 0.7% to <0.1% as the mortality increases, indicating that the removal of larvae from the bay by either wind-driven or buoyancy-driven transport dramatically weakens the effect of any localized mortality and greatly increases the probability of successful recruitment.

Variations in diffusion do not result in a monotonic increase or decrease in total larval settlement (Table 5). Increased diffusion results in greater mixing of the particles which

Table 5. Total settled larvae as a function of diffusion for year 1991.

$B$	Total settled larvae
$\infty$	6.8%
2	7.2%
1	7.0%
0.75	4.7%

can result in more or less larvae present near the mouth during a downwelling event or within the bay when the larvae mature into megalopae. Increased diffusion does, however, result in a decrease in the magnitude of settlement events, since it results in less deterministic behavior of the larvae in response to wind events and a gradual departure from the episodic nature of the larval settlement.

#### *e. Spawning locations*

Because the larval stage of blue crabs is transported to the coastal shelf before entering an estuary to settle, mixing with other stocks may occur (Epifanio, 1995). Kahn *et al.* (1998) in their examination of Delaware Bay blue crab stock discussed this possibility but ultimately determined that the stock within the bay was probably the source of its own recruits. They based this decision on the relative size of the Delaware Bay stock to that of nearby regions, the distance to the next comparable size stock (Chesapeake Bay), and assumptions of local coastal circulation. Here, the numerical model provides an ideal tool to test these assertions and determine the probable spawning sites for blue crab larvae that eventually settle in Delaware Bay. Simulations are conducted for each year in which larvae are instantaneously placed into the flow field during high slack tide along lines that approximated the 10 m isobath (see black lines in Fig. 2b). Separate simulations are performed for those larvae originating upshelf and downshelf.

Comparison of settlement number for those larvae spawned downshelf with those spawned at the mouth of the bay shows that downshelf larvae rarely settle within the bay. Over the years 1989–1992, an average of 4.1% of larvae spawned within Delaware Bay returned to the bay, while only 0.6% of larvae that spawned downshelf eventually settled in the bay. However, those larvae that are spawned upshelf of the bay are efficiently transported to the bay to settle. An average of 5.0% of larvae spawned upshelf of Delaware Bay eventually settled in the bay. Comparison of the settlement events of these larvae to the observations (Fig. 11) reveals little agreement. This disagreement is due to the relatively small number of crabs that inhabit the regions upshelf of Delaware Bay. A five-year study of blue crab landings in New Jersey (Stehlik *et al.*, 1998) reveals that, for the time period 1991–1995, a yearly average of 1.15 million pounds of blue crabs were caught within Raritan Bay and the Atlantic coastal estuaries and sounds within New Jersey. At the same time a yearly average of 8.38 million pounds of blue crabs were caught within Delaware Bay (Stehlik *et al.*, 1998; Helser and Kahn, 2001). Although larvae spawned upshelf of Delaware Bay are more efficiently settled in Delaware Bay (5.0% vs. 4.1%) than those that are spawned within the bay, the number of crabs available to spawn larvae is less than 14% of those in Delaware Bay, resulting in little influence on Delaware Bay settlement rates and fluctuations in the overall population.

## **4. Conclusions**

Using a coupled numerical model, we examine the physical mechanisms responsible for larval settlement in Delaware Bay and determine those pathways in the coastal ocean

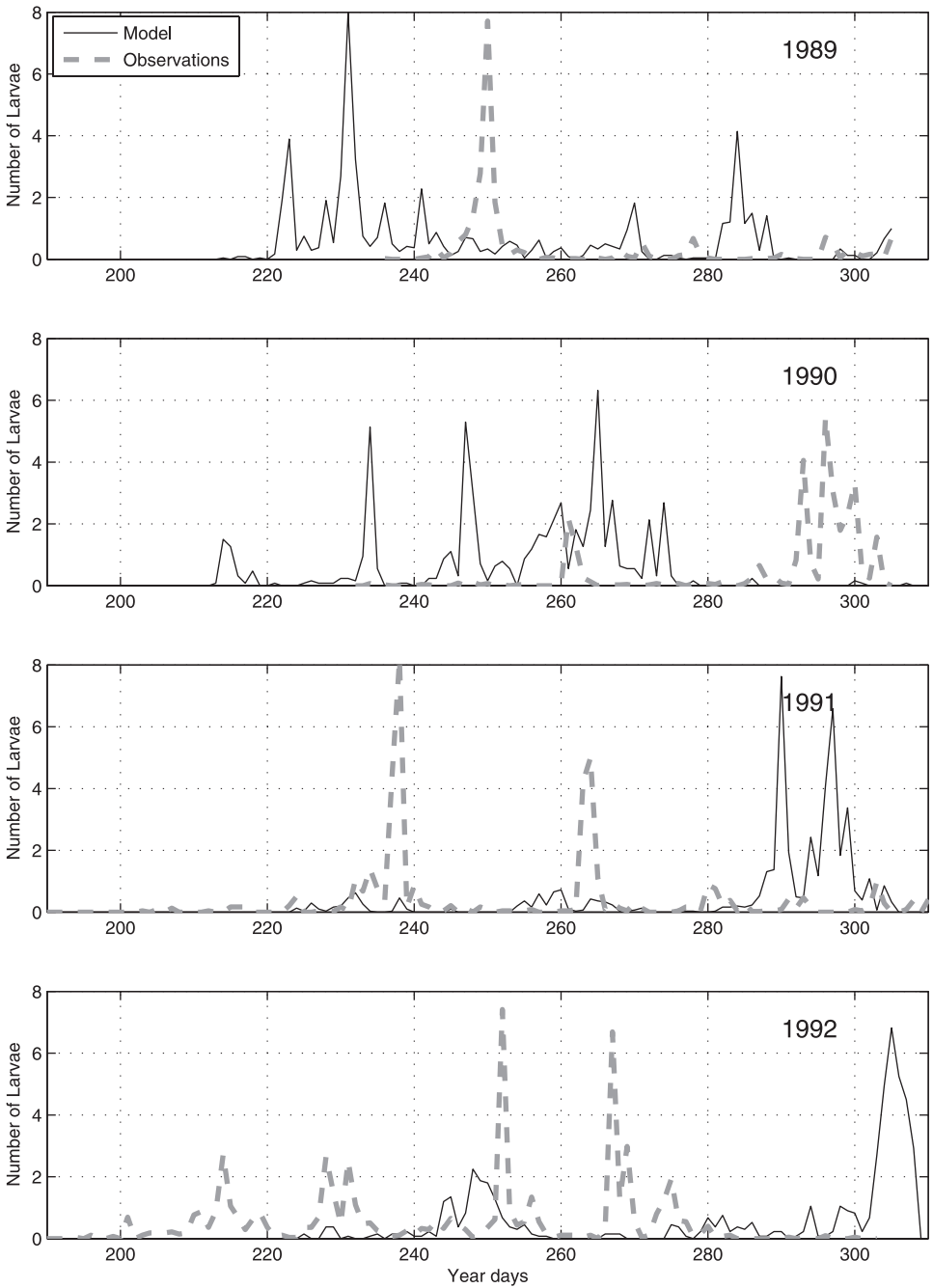


Figure 11. Settled larvae from simulation in which larvae were spawned upshelf of the bay (solid line) and observed blue crab settled larvae (dashed line) for the years 1989–1992. Observed settlement data were obtained from daily measurements in the Broadkill River. Both modeled and observed settlement data have been nondimensionalized by dividing all values by their standard deviation.



followed by successfully recruited larvae. The numerical model whose domain encompasses Delaware Bay and the adjoining coastal ocean includes daily wind-forcing, daily river discharge, and tides. Simulated settlement events from a particle advection scheme coupled to a physical circulation model agree quite well with blue crab larval settlement observed in the Broadkill River for three of the four years. The coupled model reproduces most major observed settlement events using a simple, deterministic scheme for the spawning and settlement of larvae, indicating that the transport and settlement larvae is primarily driven by the surface currents governed by winds, river discharge, mixing, and tides. Comparison of simulations in which larvae are spawned upshelf, downshelf, and within the bay reveals that Delaware Bay is most likely the source for its own recruits.

Quantitative measurement of model skill using a simple randomization test reveals that the model reproduces the observed settlement events at >85% significance for 1990 and >99% for 1991 and 1992. There are several sources of error within the model that can be addressed with greater knowledge of larval behavior and increased resolution of the model. The model reproduces most observed significant settlement events but does also produce several simulated settlement events that are not observed. Previous studies (Garvine *et al.*, 1997) have encountered similar problems, which are most likely due to a mismatch in the modeled and actual spawning events. While spawning is simulated within the model as a regular introduction of larvae into the flow field at high tide, actual spawning is most likely episodic. Spatial resolution of the numerical model in the vicinity of the buoyant outflow and within the bay restricts the ability of the numerical model to include small-scale dynamics at the edge of the buoyant plume and within individual larval patches. A greater understanding of those factors that influence spawning and settlement events as well as increased spatial resolution within Delaware Bay and the adjoining coastal region would greatly increase the accuracy of the model. However, the nature of the trajectories followed by an individual larva allows for large-scale dynamics to govern a majority of the advection and settlement process resulting in good agreement between the model and observations for three of the four years.

Results from this study allow us to expand on the conceptual model developed by Epifanio and Garvine (2001), in which larvae are transported out of the bay and downshelf by a buoyancy-driven flow, return upshelf due to an upwelling event, and are transported back into the bay by a downwelling event. Examination of output from the model supports results from previous studies of larval transport (Jones and Epifanio, 1995; Garvine *et al.*, 1997) that indicate the transport and settlement of larvae is primarily governed by winds. However, the relationship between wind-forcing and settlement events is not as straightforward as previously thought. Although some settlement events coincide with downwelling winds, a majority cannot be identified with particular downwelling wind events. Analysis of the trajectories of the successfully settled larvae indicates that a majority of the larvae return to the bay prior to settlement due to an earlier downwelling event, while others remain in the vicinity of the bay during their entire larval stage due to weak wind-forcing. These larvae are in relatively close proximity to juvenile habitat within the bay, while they

are still in late zoea stages. Thus, settlement occurs shortly after molt to the megalopa stage. The time of their settlement is not dictated by wind events but instead by the time of maturation into megalopae. Additionally, a majority of the larvae that eventually return to the bay do not enter the buoyancy-driven current confined to the Delaware coast but are either directly transported offshore and upshelf due to upwelling winds or remain near the mouth. Sensitivity analyses of mortality rates and diffusion demonstrate that variations in larval mortality and mixing affect the magnitude, but not the timing, of settlement events.

These results provide a new conceptual model that includes the basic components of Epifanio and Garvine (2001) with some slight modifications to the timing of settlement and the transport pathways. The modified conceptual model is described here:

During mid-summer, gravid female crabs migrate to the mouth of Delaware Bay and spawn, releasing larvae that rise to the surface. These larvae remain near the surface and exit the bay during the subsequent ebb tide. Depending on the direction and magnitude of the winds, the larvae can (1) enter the buoyancy driven flow, travel downshelf and return upshelf during an upwelling wind event (blue trajectory in Fig. 6), (2) be transported directly offshore and upshelf by an upwelling event (red trajectory in Fig. 6), or (3) remain near the mouth of the bay (green trajectory in Fig. 6). Downwelling events then return the larvae to the bay. Those larvae that have matured into megalopae settle immediately, while immature larvae remain in the bay until maturation. The success of each pathway in transporting larvae back to Delaware Bay for settlement is determined by larval mortality rates on the shelf and in the bay. Increased predation within the bay can significantly decrease the number of larvae that remain near the mouth of the bay for the duration of their larval stages.

*Acknowledgments.* We would like to thank Alan Blumberg for providing the numerical ocean model ECOM3d. We would like to thank Brandon Jones, Cecily Natunewicz and Chuck Epifanio for providing the observed settlement data. We greatly appreciate the comments on earlier drafts by Rich Garvine, Brandon Jones, Chuck Epifanio, Steve Holland, D. R. Johnson and two anonymous reviewers. This study was supported by funds from the State of Delaware and State of Georgia Sea Grant Programs.

#### REFERENCES

- Austin, J. A. and S. J. Lentz. 2002. The inner shelf response to wind-driven upwelling and downwelling. *J. Phys. Oceanogr.*, 32, 2171–2193.
- Blumberg, A. F. and G. L. Mellor. 1987. A description of a three-dimensional coastal ocean circulation model, in *Three-dimensional Coastal Ocean Models*, N. Heaps, ed., Amer. Geophys. Union, 1–16 pp.
- DeVries, M. C., C. E. Epifanio and A. I. Dittel. 1983. Lunar rhythms in the egg hatching of the subtidal crustacean: *Callinectes arcuatus* Ordway (Decapoda:Brachyura). *Estuar. Coast. Shelf Sci.*, 17, 717–724.
- Egbert, G. D., A. F. Bennett and M. G. G. Forman. 1994. TOPEX/POSEIDON tides estimated using global inverse model. *J. Geophys. Res.*, 99, 24821–24852.
- Epifanio, C. E. 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off Mid-Atlantic states. *Bull. Mar. Sci.*, 57, 713–725.

- Epifanio, C. E. and R. W. Garvine. 2001. Larval transport on the Atlantic continental shelf of North America: A review. *Estuar. Coast. Shelf Sci.*, 52, 51–77.
- Epifanio, C. E., C. C. Valenti and A. E. Pembroke. 1984. Dispersal and recruitment of blue crab in Delaware Bay, U.S.A. *Estuar. Coast. Shelf Sci.*, 18, 1–12.
- Forward, R. B., R. A. Tankersley and J. M. Welch. 2003. Selective tidal-stream transport of the blue crab, *Callinectes sapidus*: An overview. *Bull. Mar. Sci.*, 72, 347–365.
- Garvine, R. W., C. E. Epifanio, C. C. Epifanio and K. C. Wong. 1997. Transport and recruitment of blue crab larvae: a model with advection and mortality. *Estuar. Coast. Shelf Sci.*, 45, 99–111.
- Hannah, C. G., C. E. Naimie, J. W. Loder and F. E. Werner. 1998. Upper-ocean transport mechanisms from the Gulf of Maine to Georges Bank, with implications for *Calanus* supply. *Cont. Shelf Res.*, 17, 1887–1911.
- Helser, T. E. and D. M. Kahn. 2001. Stock assessment of Delaware Bay blue crab (*Callinectes sapidus*) for 2001. Department of Natural Resources and Environmental Control, Delaware Division of Fish and Wildlife, 89 Kings Highway, Dover, DE 19901.
- Hood, R. R., H. V. Wang, J. E. Purcell, E. D. Houde and L. W. Harding. 1999. Modeling particles and pelagic organisms in Chesapeake Bay: Convergent features control plankton distributions. *J. Geophys. Res.*, 104, 1223–1243.
- Houde, E. D. 1989. Subtleties and episodes in the early life history of fishes. *J. Fish Bio.*, 3 (Suppl. A.), 29–38.
- Janzen, C. D. and K.-C. Wong. 2002. Wind-forced dynamics at the estuary-shelf interface of a large coastal plane estuary. *J. Geophys. Res.*, 107, 3138, doi:10.1029/2001JC000959.
- Johnson, D. F. and K. W. Hess. 1990. Numerical simulations of blue crab larvae dispersal and recruitment. *Bull. Mar. Sci.*, 46, 195–213.
- Johnson, D. R. 1985. Wind-forced dispersion of blue crab larvae in the Middle Atlantic Bight. *Cont. Shelf Res.*, 4, 733–745.
- Johnson, D. R. and B. S. Hester. 1989. Larval transport and its association with recruitment of blue crabs in Chesapeake Bay. *Estuar. Coast. Shelf Sci.*, 28, 459–472.
- Johnson, D. R., B. S. Hester and J. R. McConnaugha. 1984. Studies of a wind mechanism influencing the recruitment of blue crabs in the middle Atlantic bight. *Cont. Shelf Res.*, 3, 425–437.
- Jones, M. B. and C. E. Epifanio. 1995. Settlement of brachyuran megalopae in Delaware Bay: a time series analysis. *Mar. Ecol. Prog. Ser.*, 125, 67–76.
- Kahn, D. M., R. W. Cole, S. F. Michels and W. H. Whitmore. 1998. Development of life-stage-specific indices of relative abundance and stock-recruitment relationships for the Delaware Bay blue crab stock. *J. Shellfish Res.*, 17, 529–541.
- Kourafalou, V. H., L.-Y. Oey, J. D. Wang and T. N. Lee. 1996a. The fate of river discharge on the continental shelf. 1. Modeling the river plume and the inner shelf coastal current. *J. Geophys. Res.*, 101, 3415–3434.
- Kourafalou, V. H., T. N. Lee, L.-Y. Oey and J. D. Wang. 1996b. The fate of river discharge on the continental shelf. 2. Transport of coastal low-salinity waters under realistic wind and tidal forcing. *J. Geophys. Res.*, 101, 3435–3455.
- Mele, M. 2002. Modeling patch formation and dynamics of blue crab larvae (*Callinectes sapidus*) in an estuarine dispersal and transport regime. M.S. Thesis, University of Delaware, 59 pp.
- Morgan, S. G. 1987. Adaptive significance of hatching rhythms and dispersal patterns of estuarine crab larvae: avoidance of physiological stress by larval export? *J. Exp. Mar. Biol. Ecol.*, 113, 71–78.
- Morgan, S. G. and J. H. Christy. 1995. Adaptive significance of the timing of larval release by crabs. *Am. Nat.*, 145, 457–479.
- Natunewicz, C. C., C. E. Epifanio and R. W. Garvine. 2001. Transport of crab larval patches in the coastal ocean. *Mar. Ecol. Prog. Ser.*, 222, 143–154.

- Roughgarden, J., S. Gaines and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science*, *241*, 1460–1466.
- Schwalm, S. M. 1999. The effect of wind conditions on *Callinectes sapidus* population fluctuations in Delaware Bay. M.S. Thesis, University of Delaware, 102 pp.
- Smagorinsky, J. 1963. General circulation experiments with the primitive equations, 1. The basic experiment. *Mon. Weath. Rev.*, *91*, 99–164.
- Stehlik, L. L., P. G. Scarlett and J. Dobarro. 1998. Status of the blue crab fisheries of New Jersey. *J. Shellfish Res.*, *17*, 475–485.
- Steppe, C. N. and C. E. Epifanio. 2005. Distribution of brachyuran larvae in Delaware Bay and on the adjacent continental shelf: Influence of near shore hydrographic regimes. *Est. Coast Shelf Sci.*, (submitted).
- Sutherland, J. P. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology*, *71*, 955–972.
- Tilburg, C. E. 2003. Across-shelf transport on a continental shelf: Do across-shelf winds matter? *J. Phys. Oceanogr.*, *33*, 2675–2688.
- Whitney, M. M. 2003. Simulating the Delaware Coastal Current. Ph.D. dissertation, University of Delaware, 284 pp.
- Whitney, M. M. and R. W. Garvine. 2005. Simulating a coastal buoyant outflow: Comparison to observation. *J. Phys. Oceanogr.*, (in press).

Received: 18 June, 2004; revised: 9 November, 2004.