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# Circulation and behavior controls on dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay

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## ABSTRACT

The relative contributions of the spring-neap tides, river discharge and vertical behavior to the dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay is investigated with a coupled circulation-individual-based larvae model. The coupled model simulates larval growth and behavior along particle trajectories using temperature and salinity conditions obtained from an implementation of the Regional Ocean Model System (ROMS) for Delaware Bay. Particles, representing oyster larvae, are released at five-day intervals during the spawning seasons (mid-June to mid-September) of 1984, 1985, 1986, 2000 and 2001 from areas that correspond to natural oyster reefs in Delaware Bay. Successful larvae are those that reach a settlement size of 330  $\mu\text{m}$  within the planktonic larval duration of 30 days, as calculated from the growth model. The fortnightly variability of the along-estuary flow associated with the spring-neap tides is the primary factor affecting larval dispersion. Larvae released during neap tides are transported mostly up-estuary into areas with reduced salinity, which decreases growth rates and reduces the chance of reaching settlement size within 30 days. Fewer than 20% of the larvae released from upper bay reefs reach settlement size. However, connectivity to mid-bay oyster reefs by the up-estuary transport provides a potential source of larvae to maintain the upper bay oyster reefs. Larvae released during spring tides are often transported down-estuary into regions of higher salinity, which provide the majority of the potential recruits for down-estuary oyster reefs. Low salinity caused by periods of high river discharge overwhelms the up-down estuary transport associated with the spring-neap tides and reduces the ability of the oyster larvae to reach settlement size. Simulated larval trajectories show that vertical behavior makes a small contribution to larval dispersion and that turbulent mixing can overwhelm this process. Thus, for average river discharge conditions, the intra-seasonal dispersion of eastern oyster larvae in Delaware Bay is mostly controlled by the spring-neap tides and the timing of spawning relative to the occurrence of these tides may determine patterns of transport and movement eastern oyster larvae among oyster reefs in Delaware Bay.

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## 1. Introduction

The horizontal dispersion and subsequent recruitment of eastern oyster (*Crassostrea virginica*) larvae are integral to the location and productivity of natural oyster reefs (Carriker, 1951). The natural oyster reefs in Delaware Bay tend to be aggregated along the New Jersey (northern) side and concentrated in the middle reaches of the Bay (Fig. 1). These reefs are maintained by oyster larvae recruitment that is characterized by large variability within the spawning season (intra-seasonal) and between years (interannual) (e.g., Kennedy, 1996; Powell *et al.*, 2008). Lagrangian particle tracking simulations show that the natural oyster reefs in the upper bay on the New Jersey side (areas 6–7, Fig. 1) receive low larval inputs from local and middle bay reefs (Narváez *et al.*, this issue). Mid-bay reefs (areas 2–5, Fig. 1) receive larval inputs from up-estuary regions as well as from larvae that settle where they were spawned, i.e., self-settlement regions (Narváez *et al.*, this issue). Regions farther down-estuary tend to have higher self-settlement rates and smaller contributions from up-estuary reefs (Narváez *et al.*, this issue). The general down-estuary transport of oyster larvae in Delaware Bay is consistent with observed and simulated patterns of oyster larvae recruitment, which is low for the upper bay oyster reefs and increases for the middle and particularly lower bay reefs (Powell *et al.*, 2008; Narváez *et al.*, this issue). Interannual variations in the simulated larval success are in part attributable to periods of high and low river discharge, which affect larval growth by modifying the salinity field (Narváez *et al.*, this issue).

The patterns of transport and settlement of eastern oyster larvae are also influenced by ontogenetic vertical migration and by diurnal and semi-diurnal tidal flow. During the first 10–20 days, the younger stages of eastern oyster larvae (early-stage, veliger) tend to swim upward and be more concentrated in the upper water column; whereas, the older stages (late-stage, pediveliger), which develop an outer shell, sink and are found near the bottom (Carriker, 1951; Andrews, 1983; Baker, 1991). In addition, larvae move up during flood tides in response to increased salinity and downward during ebb tides in response to decreased salinity (Carriker, 1951; Kennedy, 1996). This behavior is pronounced for intermediate-sized oyster larvae (Dekshenieks *et al.*, 1996). The importance of the ontogenetic vertical migration coupled with the response to diurnal and semi-diurnal tidally-induced salinity changes in determining the distribution and dispersion of eastern oyster larvae has been suggested from observational (Wood and Hargis, 1971; Mann, 1988) and modeling studies (Dekshenieks *et al.*, 1996). However, the relative importance of physical and biological transport in oyster larvae dispersion varies in estuarine environments (Andrews, 1983; North *et al.*, 2008; Kim *et al.*, 2010).

This study extends the results in Narváez *et al.* (this issue) to investigate intra-seasonal (within the spawning season) variability in oyster larvae dispersal and potential settlement. The fortnightly variability in the circulation associated with spring-neap tides is of the same order as the planktonic larval duration. Thus, the salinity and circulation variations resulting from the spring and neap tides coupled with the diurnal and semi-diurnal tidally-induced vertical behavior are potentially important contributors to eastern oyster larvae dispersal and growth in Delaware Bay.



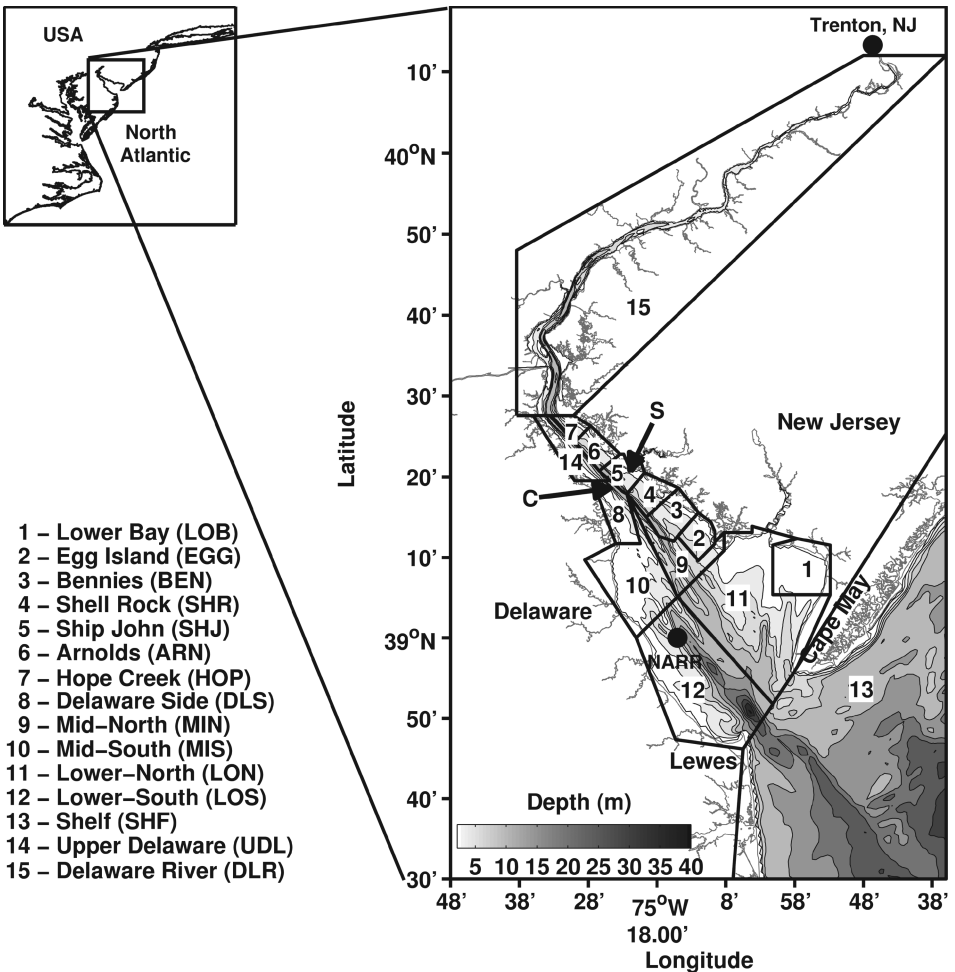


Figure 1. Map and bathymetry of the Delaware Bay system. The release sites for the Lagrangian particle simulations (areas 1–8) generally correspond to the locations of natural oyster reefs in Delaware Bay (see listing). These release sites and an additional seven regions (areas 9–15) were used to analyze the settlement patterns obtained from the Lagrangian particle tracking simulations. River discharge measurements were obtained from U.S. Geological Survey (USGS) gauges at Trenton, NJ. The wind measurements were obtained from the National Centers for Environmental Prediction North American Regional Reanalysis (NARR) product, which has one grid point (●) in the Delaware Bay region. Temporal variability in the vertical distribution of along-estuary flow and salinity were analyzed for a location in the upper-middle bay in the channel (C) and over the shoals (S).

The model configuration and analysis methods used to evaluate the relative effects of circulation variability and larval behavior on transport pathways and potential settlement of eastern oyster larvae in Delaware Bay are given in the following section. The simulation results focus on the effects of the spring-neap tidal forcing, episodic increases and decreases in river discharge, and vertical behavior in determining larval growth and potential settlement sites. These results are discussed in the context of what is known about oyster larvae transport and settlement in Delaware Bay and other systems.

## 2. Methods

### *a. Coupled circulation-larvae model*

The circulation model used in this study is based on the Regional Ocean Model System (ROMS, [www.myroms.org](http://www.myroms.org); Shchepetkin and McWilliams, 2005) that is configured for Delaware Bay and its adjacent continental shelf. Details of the model configuration and validation are given in Wang *et al.* (this issue). This model configuration includes realistic wind forcing, observed river discharges and tidal boundary conditions, but does not include effects due to nontidal currents over the open shelf. The eastern oyster larvae growth model is based on the model described in Deksheniaks *et al.* (1993; 1997), which simulates growth in response to temperature, salinity, food supply and turbidity conditions. The vertical movement of the oyster larva is based on the model given by Deksheniaks *et al.* (1996; 1997). The oyster larvae are represented as particles that move in the simulated circulation field.

The particle tracking module already implemented in ROMS was modified to include the model for eastern oyster larvae growth and behavior so that larval growth, development and movement were calculated simultaneously with the circulation model. The growth rate is determined by the salinity, temperature, and food and turbidity concentrations that the particle encounters. The ontogenetic vertical swimming and sinking behavior is dependent on larval size which is determined by growth. The vertical displacement in response to the diurnal and semi-diurnal tidally-varying salinity is calculated from the salinity experienced along the particle trajectory (see Deksheniaks *et al.*, 1996 for details). Details of the coupled circulation-larval model as well as limitations of this modeling approach are given in Narváez *et al.* (this issue).

Food supply and turbidity, which regulate growth, are held at a constant value of  $4 \text{ mg C L}^{-1}$  and  $0 \text{ g L}^{-1}$  along the particle trajectory (Narváez *et al.*, this issue). Larvae growth is minimal at temperatures below  $15^\circ\text{C}$ , salinity below 5, food concentrations less than  $1 \text{ mg C L}^{-1}$ , and turbidity concentrations above  $0.1 \text{ g L}^{-1}$  (Deksheniaks *et al.*, 1993). Growth rate increases with warmer temperatures ( $>25^\circ\text{C}$ ), salinities of 17.5–25, food concentrations  $>3.0 \text{ mg C L}^{-1}$ , and turbidity  $<0.1 \text{ g L}^{-1}$ . The constant food and turbidity concentrations used in the larval model represent optimal conditions for growth (Deksheniaks *et al.*, 1993). The effects of different food and turbidity concentrations on larval growth in Delaware Bay are considered in Narváez *et al.* (this issue).

The particle location is modified by the three-dimensional advective velocity, vertical diffusion, and displacement due to larval swimming (early stage, veliger) and sinking (late stage, pediveliger), and the response to the time-varying salinity that is produced by ebb and flood tides. The vertical advective velocity was obtained from the circulation model. Vertical diffusion, which is calculated by the circulation model, was added to the vertical positions as a random vertical walk to account for sub-grid scale turbulent motions (Hunter *et al.*, 1993; Visser, 1997). The particle trajectories end when a larva reaches a settlement size of 330  $\mu\text{m}$  (Deksheniaks *et al.*, 1993) or fails to reach this size within 30 days after release. The 30-day planktonic larval duration is based on the time estimated for eastern oyster larvae to reach settlement size for environmental conditions characteristic of Delaware Bay (Deksheniaks *et al.*, 1993).

### *b. Simulation design and analysis*

Particles were released within areas in the Delaware estuary that correspond to the existing natural oyster reefs (areas 2 to 7, Fig. 1). Additional release areas where less extensive oyster reefs exist were included in the lower bay (area 1, Fig. 1) and along the Delaware (southern) side of the bay (area 8, Fig. 1). Two hundred particles are released from each area (areas 1 to 8, Fig. 1); particles are released from 40 locations evenly distributed within each release area and 5 particles are released at each location. All particles are simultaneously released at midnight from each area, which makes the release time independent of the tidal phase. The releases are repeated at five-day intervals from mid-June to mid-September which encompasses the spawning period of eastern oysters in mid-latitude estuaries, such as Delaware Bay (Thompson *et al.*, 1996). Thus, 18 spawning events were simulated in each area, resulting in a total of 28,800 particles (1600 per spawning event) released over the entire season.

The particle tracking simulations used environmental conditions from 1984, 1985, 1986, 2000, and 2001 (see Narváez *et al.*, this issue). The velocity, temperature, and salinity conditions encountered by a particle along its trajectory are obtained, as are larval size, swimming/sinking speed, and swimming time. Analysis of the simulated particle trajectories provide transport and transfer rates between release and potential settlement locations.

Larval success is estimated for each release area and spawning event (release time) by the number of particles that reach settlement size within 30 days. Larval transport is estimated at one-hour intervals (Lagrangian model integration time) as the linear distance and angle of each particle (i.e., larva) from its release position to its current location. This information is used to construct frequency histograms that show the transport length scales and orientation relative to each particle release location. Larval dispersion is obtained from connectivity matrices that relate the percent of the total larvae released in an area that could successfully settle in the same or another area. The resulting percentages provide estimates of transfer rates among regions and potential settlement of larvae in the different areas of Delaware Bay.

The relative contribution of local estuarine circulation and behavior to larval dispersion is determined by comparing results of simulations with passive particles (no larval growth and behavior) to those with particles that had growth and behavior. The former includes only the effects of physical processes that affect the estuarine circulation and salinity fields and provides estimates of physical transport. The latter provides the additional contribution to transport from behavior. The influence of vertical mixing relative to larval behavior is assessed by comparing simulations with and without sub-grid scale turbulent motions (i.e., random vertical walk).

Flow conditions in different years are compared using the simulated along-estuary flow and salinity from locations in the main stem channel in Delaware Bay and over the shoals in the mid-reaches of Delaware Bay near the natural oyster reefs (Fig. 1). The hourly time series of along-estuary flow and salinity were filtered to remove higher frequency variability caused by the semi-diurnal and diurnal tides. The residual (i.e., sub-tidal) circulation and salinity were analyzed using spectral and cross-correlation analysis to provide the dominant variability periods for different environmental conditions, which were then related to simulated larval success, transport, potential settlement, and retention patterns.

The simulated transport patterns are used to estimate spatial and temporal variability in larval retention in four representative regions in the estuary. These regions included the low salinity regions in the upper bay (areas 6, 7, 14, 15; Fig. 1), the high salinity oyster reefs in the lower bay (area 1; Fig. 1), the oyster reefs on the Delaware side of the bay (area 8; Fig. 1) and the natural oysters reefs in the middle reaches of the bay (areas 2 to 5; Fig. 1). For each region and release time, larval retention was estimated from the number of particles that remained in an area each day between release and settlement. The daily number of particles in a region was then divided by the total number of particles released at each location to obtain an estimate of the fraction of particles remaining in a region. Larval retention was estimated in this way for each of the release times for each of the five years used for the simulations.

### 3. Results

#### *a. Intra-seasonal variability in residual circulation and salinity*

The residual circulation in the channel in the mid-portion of Delaware Bay is predominantly outward (negative, down-estuary) near the surface (0–4 m) (Fig. 2a, f). Subsurface (4–13 m) flow is alternately up- or down-estuary (Fig. 2a, f) with strong or weak stratification (Fig. 2c, h) associated with neap or spring tides, respectively. Over the shoals, the flow is either in or out with little vertical shear (Fig. 2c, h) with neap or spring tides, respectively. Surface flow at the channel and shoal sites was significantly correlated with the surface elevation with a time lag of 3–5 days ( $r = 0.5$ ,  $p < 0.05$ ), but was not significantly correlated with wind direction and speed. However, surface elevation, salinity, and sub-surface along-estuary flow had a significant energy peak at 10–15 days (determined with spectral analysis), suggesting that all properties are responding to the same forcing.

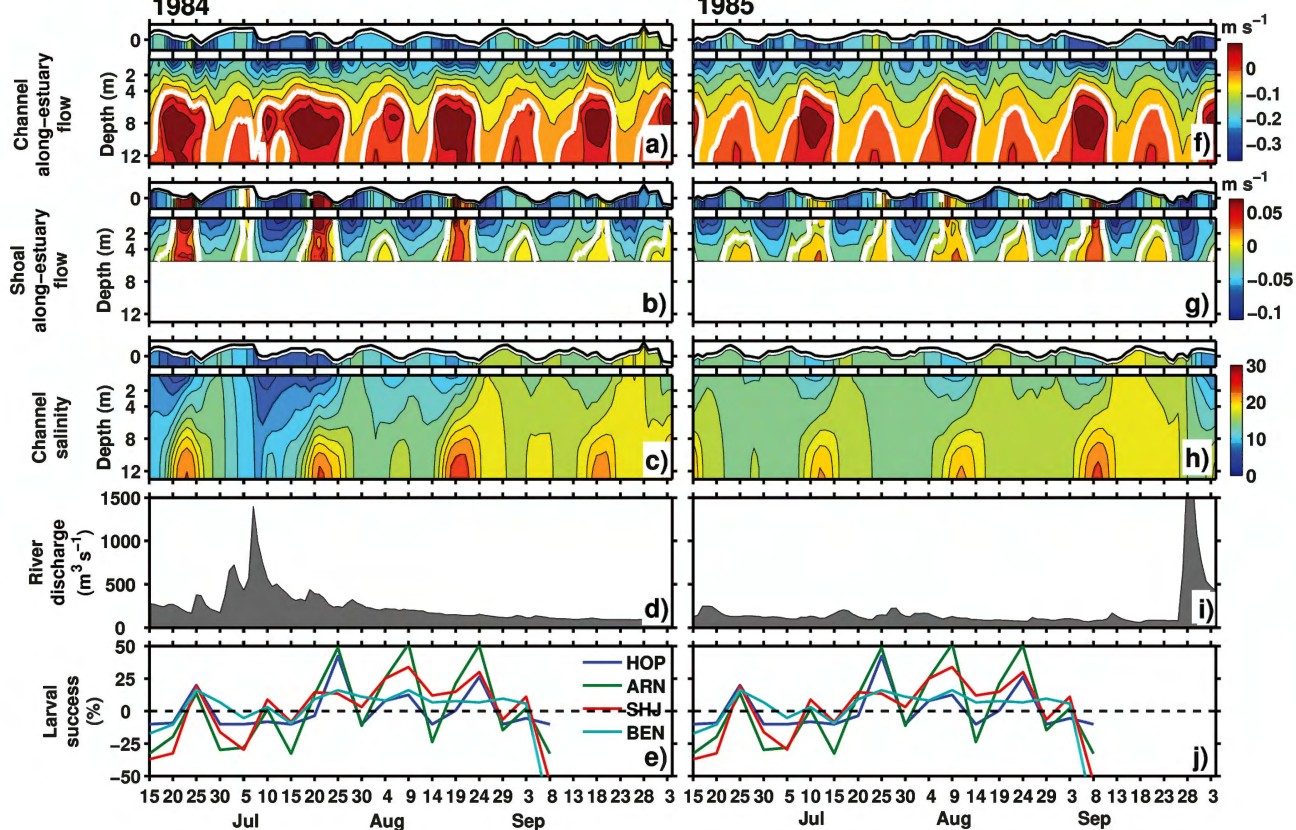


Figure 2. Time series for the spawning season of 1984 and 1985 showing the simulated depth-time distributions of (a, f) along-estuary flow in the channel and (b, g) over the shoals, and (c, h) the salinity in the channel for the 1984 (left panel) and 1985 (right panel) spawning seasons. Negative velocities indicate down-estuary flow; positive velocities are up-estuary flow. The transition between inflows and outflows (zero velocity-contour, white line) is indicated. The surface elevation is indicated in the panel above the flow and salinity depth-time distributions. The time series of river discharge (d, i) was obtained from the USGS gauge at Trenton, NJ. Larval success time series were estimated for four oyster reefs (e, j) identified as: HOP-Hope Creek, ARN-Arnolds, SHJ-Ship John, and BEN-Bennies. Reefs locations are shown on Figure 1. The larval success time series were constructed from the simulated Lagrangian trajectories as described in the text.

The strongest up-estuary flows bring high salinity (>25) water into the upper estuary (e.g., 1984: 6/20, 7/20, 8/19, in Fig. 2c and 1985: 7/10, 8/9, 9/8 in Fig. 2h) with significant correlations between near bottom velocity and salinity ( $r = 0.6$ ,  $p < 0.05$  lag = 0–2 days). These flows are associated with the strongest neap tide of the lunar cycle. During spring tides, salinity is around 15 and is vertically homogenous (e.g., 8/4/84, 7/30/85). Disruptions to this pattern occur during high river flow events (such as in early July of 1984) (Fig. 2d). Low river discharge in 1985 (Fig. 2i) results in overall higher salinity (Fig. 2h). For all the simulated years, the fortnightly variability driven by the neap-spring cycle dominates the current and salinity (Figs. 2, 3). However, high river discharge events (such as in early July 1984 (Fig. 2d), 1986 (Fig. 3a, b, c) and August 2000 (Fig. 3e, f, g)) produce large salinity changes that overwhelm the fortnightly salinity variability.

The high river discharge in early July 1984 produced a low-salinity surface plume that extended along the main axis of the estuary (Fig. 4a) with corresponding down-estuary surface currents. The strongest flows occur along the main channel (Fig. 4b). Weak near-bottom currents are directed into the bay (Fig. 4c). The surface-to-bottom salinity difference is in excess of 10 along the main channel (Fig. 4d), suggesting that this part of the bay is strongly stratified. The shoal regions remain relatively well-mixed (Fig. 4d).

Spring tides produce a surface salinity distribution with less saline water on the north side of the bay (in the shallower area behind Cape May) and more saline water on the south side (Fig. 5a). This pattern is due to stronger vertical mixing during spring tide combined with the higher salinity water in the deep channel along the axis of the bay. Along-estuary flows are outward at the surface (Fig. 5b) and inward at the bottom (Fig. 5c). The surface to bottom salinity difference is small (Fig. 5d). The down-estuary movement of the surface isohalines during neap tides (Fig. 5e) is comparable to that associated with high river discharge events (Fig. 4a). The surface and bottom flows are also similar, although reduced in magnitude (Fig. 5f, g). The surface-bottom salinity difference during neap tides is large along the main channel portion of the bay due to reduced vertical mixing and is reduced over the shoals (Fig. 5h) due to the shallower depths.

### *b. Intra-seasonal variability in larval success*

Narváez *et al.* (this issue) linked the spatial variability in larval success to the along-estuary salinity, with success rates of larvae released in the lower bay almost double those of larvae released in the low salinity upper bay. To obtain a time series of success that is comparable between areas, this along-estuary gradient in success was removed by subtracting the average larval success calculated from all releases at each release location. This time series gives the temporal variation in larval success at a location relative to the average spawning season success. The time series obtained for 1984 and 1985 (Fig. 2e, j) and for 1986, 2000 and 2001 (Fig. 3d, h, l) for locations in the upper and middle Delaware Bay shows two types of variations. The first consists of two or more consecutive spawning events with lower than average larval success, as occurred from mid-June to late July in 1984 (Fig. 2e). The second type is synchronized increases (e.g., 1984: 7/25, 8/24; 1985: 6/30, 8/24)

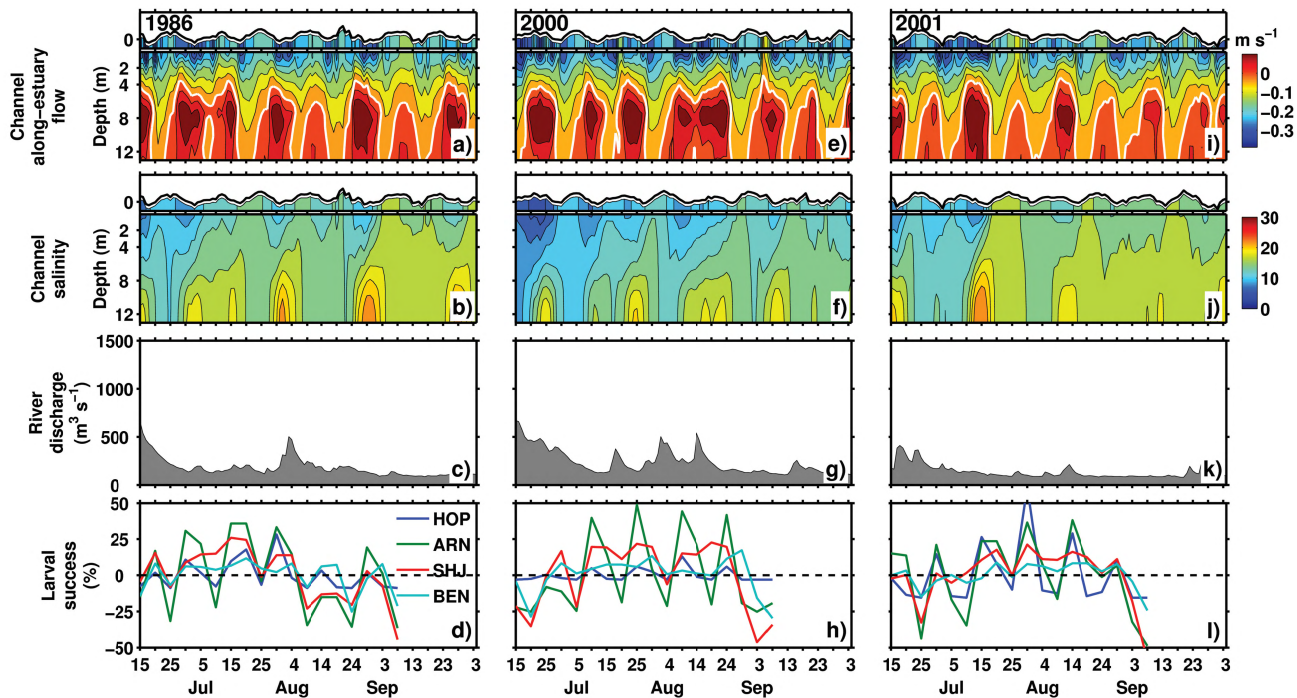


Figure 3. Depth-time distributions of simulated (a, e, i) along-estuary flow in the channel and the (b, f, j) salinity in the channel obtained for the 1986, 2000 and 2001 spawning seasons. Negative velocities indicate down-estuary flow; positive velocities are up-estuary flow. The transition between inflows and outflows (zero velocity-contour, white line) is indicated. The surface elevation is indicated in the panel above the flow and salinity depth-time distributions. The time series of river discharge (c, g, k) were obtained from USGS gauges at Trenton, NJ. Larval success time series were estimated for four oyster reefs (d, h, l) identified as: HOP-Hope Creek, ARN-Arnolds, SHJ-Ship John, and BEN-Bennies. Reefs locations are shown on Figure 1.

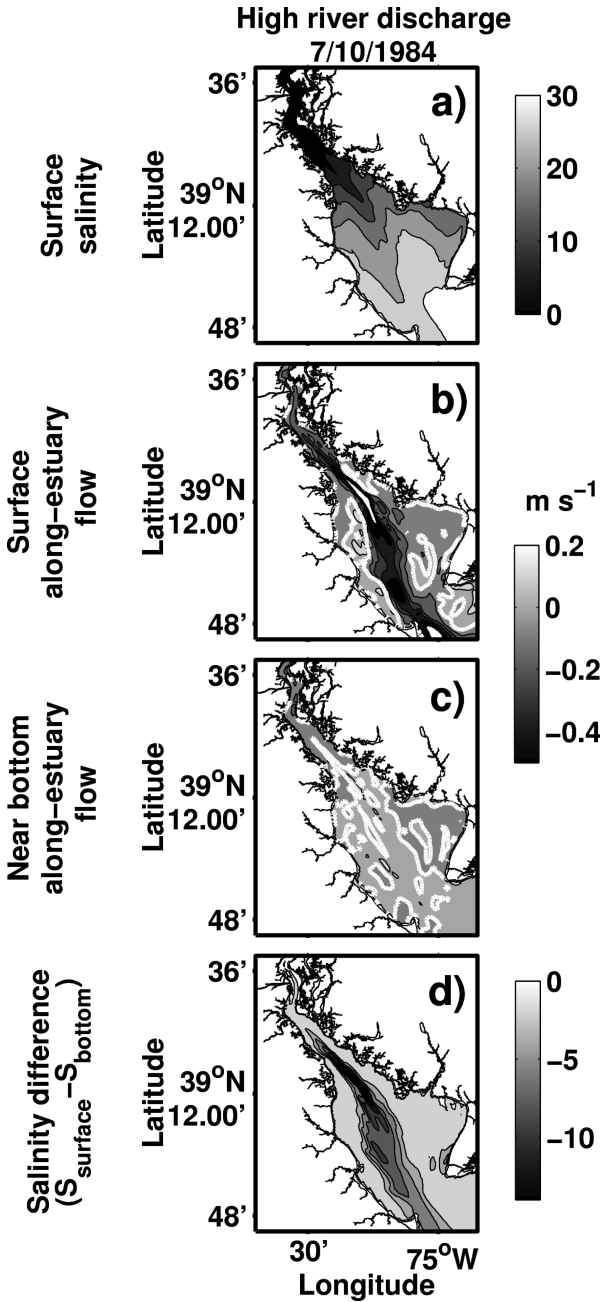


Figure 4. Distribution of simulated (a) surface salinity, (b) surface along-estuary flow, (c) bottom along-channel flow, and (d) the difference in surface and bottom salinity (a measure of stratification) obtained for high river discharge conditions. The transition between inflows and outflows (zero velocity-contour, white line) is indicated.



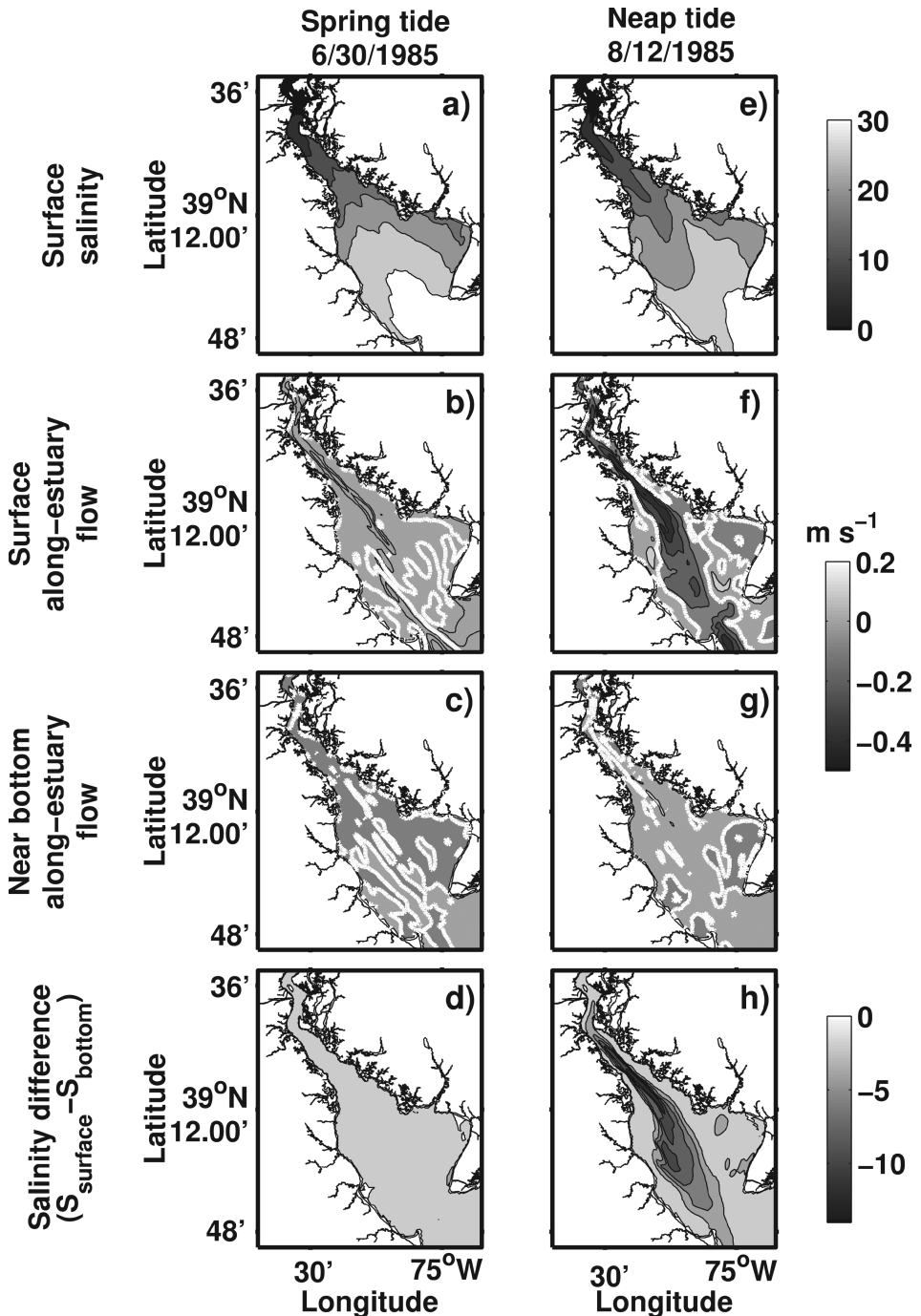


Figure 5. Distribution of simulated (a, e) surface salinity, (b, f) surface along-estuary flow, (c, g) bottom along-channel flow and (d, h) the difference in surface and bottom salinity (a measure of stratification) obtained for spring tide (left panel) and neap tide (right panel) conditions. The transition between inflows and outflows (zero velocity-contour, white line) is indicated.

and decreases (e.g., 1984: 7/30, 8/14; 1985: 7/5, 8/4) in larval success. High success, such as the ~50% observed on 25 July 1984 is followed by a period of low success centered on 30 July 1984 (Fig. 2e). Similar synchronized high/low larval success events occur in the remainder of 1984, throughout the spawning period in 1985 (Fig. 2j), and in the other years included in this study (1986, 2000 and 2001, Fig. 3d, h, l).

The prolonged period of below-average larval success in the early spawning season of 1984 (Fig. 2e) is associated with high river discharge (Fig. 2d), which produces low salinity conditions through Delaware Bay (Fig. 4) for extended periods (Figs. 2, 3). Following the return to more typical salinity conditions in late July 1984, larval success improved. The synchronized increases in larval success observed for the 1984 and 1985 spawning seasons tends to be associated with the general outflow associated with spring tides (Fig. 2a, b, f, g). Similar results occurred in the others years (Fig. 3).

The times when the percent of larvae that reach settlement size exceeds the average in the upper and middle estuary regions coincide with persistent outflow in the channel and over the shoals in the 3–5 days following larval release (Figs. 2 and 3). These periods of unidirectional outflow throughout the water column occur during spring tides. When larvae experience up-estuary flows following release (typically during neap tides), such as 30 July 1984 and 5 July 1985 (Fig. 2), decreased survival occurs. This general pattern is seen for the five years included in the analysis (Table 1). With few exceptions, increased larval success occurred during spring tides and during transitions from neap to spring tides. Decreased larval success was associated with neap tides and transitions from spring to neap tides (Table 1). The exceptions to these general patterns are associated with periods of high river discharge (e.g., early July 1984 and 1986) and reduced temperature (e.g., August 1986, discussed in Narváez *et al.*, this issue).

The fortnightly variability in the residual flow produced by spring and neap tides directly affects larval success by transporting larvae up- or down-estuary following their release. Low success (e.g., 30 July and 29 August 1984 in Fig. 2e and 20 June and 5 July 1985 in Fig. 2j) occurred during periods of up-estuary transport (Fig. 6); high larval success in 1984 and 1985 are associated with down-estuary transport (Fig. 7). Similar results were obtained for the synchronized high/low larval success events in 1986, 2000 and 2001 (not shown).

The correspondence between larval success and timing of the spring-neap tides is shown by comparing larval success for releases from natural reef sites in the upper and middle reaches of Delaware Bay with the along-estuary bottom flow in the channel (Fig. 8). Bottom flow provides a reliable indicator of in- or outflows (Figs. 2, 3). The flow used in the comparison is the mean over the first 5 days following a release, which provides independent estimates for larvae released at 5-day intervals. High success releases are those that exceed the mean success for an individual year.

Larval success at Hope Creek (in the upper estuary) is generally less than the mean success in each year (Fig. 8a). The average salinity encountered by a larva in this part of the bay was 14 or below (Fig. 9a). Larval growth is reduced for salinity below 15 and ceases below 12 (Deksheniaks *et al.*, 1993). Thus, larvae transported to Hope Creek are in a salinity

Table 1. Summary of flow conditions and larval success obtained from simulations in which particles were released at five-day intervals during the Delaware Bay spawning season from Arnolds and Ship John oyster reefs (locations on Fig. 1) for the five simulation years. The flow conditions during each five-day period in each year are indicated as high river discharge (D), spring (S) tide, neap (N) tide, and transition periods from spring to neap tides (S-N) and from neap to spring tides (N-S). Larval success was determined by comparison to the average of success from all five years and is given as low (L), high (H), reduced high (RH) and no change (NC). Periods when larval success exceeded the average success (H, RH) are indicated by bold text. Low success in August 1986 (indicated by \*) resulted from cooler water temperatures (see Narváez *et al.*, this issue), which is not included in this analysis. High or low success that occurred only at Arnolds is indicated as (ARN).

Release Time	Years				
	1984	1985	1986	2000	2001
15-Jun	S-N (L)	<b>N-S (RH)</b>	D-N (L)	S-N (L)	<b>N (H-ARN)</b>
20-Jun	N (L)	N (L)	<b>S (H)</b>	N (L)	<b>S (RH-ARN)</b>
25-Jun	<b>N-S (H)</b>	N-S (L)	S-N (L)	N-S (L)	N (L)
30-Jun	S-N (L)	<b>S (H)</b>	<b>N (H)</b>	S (L-ARN)	<b>N-S (H)</b>
5-Jul	D-N (L)	N (L)	<b>D-N-S (RH)</b>	N (L)	S-N (L)
10-Jul	D-(RH)	<b>N-S (RH)</b>	D-N (L-ARN)	<b>N-S (H)</b>	N (L)
15-Jul	D-N (L)	<b>S (H)</b>	<b>N-S (H)</b>	<b>S-N (RH)</b>	<b>N-S (H)</b>
20-Jul	<b>N (RH)</b>	N (L)	<b>S (H)</b>	N (L)	<b>S-N (H)</b>
25-Jul	<b>N-S (H)</b>	<b>N-S (RH)</b>	N (NC)	<b>N-S (H)</b>	N (NC)
30-Jul	S-N (L)	<b>S-N (H)</b>	<b>N (H)</b>	<b>S-N (RH)</b>	<b>N-S (H)</b>
4-Aug	<b>N (RH)</b>	N (L)	<b>N-S (RH)</b>	D-N (L)	<b>S-N (H)</b>
9-Aug	<b>S (H)</b>	<b>N (H)</b>	N (L)*	D-N (H)	N (L)
14-Aug	N (L)	<b>S (H)</b>	N-S (L)*	D-S-N (RH)	<b>N-S (H)</b>
19-Aug	<b>N-S (H)</b>	N (L)	S-N (L)*	D-N (L)	<b>S-N (RH)</b>
24-Aug	<b>S (H)</b>	<b>N-S (H)</b>	N (L)*	<b>N-S (H)</b>	N (NC)
29-Aug	N (L)	<b>S-N (H)</b>	<b>N-S (H)</b>	S-N (L)	<b>N-S (H)</b>
3-Sep	N-S (NC)	N (L)	S-N (L)	N (L)	N (L)
8-Sep	S-N (L)	<b>N (H)</b>	N (L)	N (L)	N (L)

environment that is not conducive to growth and development. At Arnolds, Ship John, and Bennies, larval success is higher than the mean during periods of outflow (down-estuary transport) associated with spring tides, especially for 1985 and 2001 (Fig. 8b, c, d). At these sites, the enhanced success rates are associated with an average salinity above 13 (Fig. 9b, c, d). The Ship John and Bennies sites tend to have higher larval success (Narváez *et al.*, this issue) but down-estuary flows further enhance success (Table 2). Reduced larval success at these three sites is associated with up-estuary transport during neap tides, although this correspondence was not as strong as that for outflows (Table 2).

During times of high river discharge in 1984 (Fig. 10), potential larval settlement in the upper and middle bay is significantly reduced. This reduction in potential settlement is largest for the reef sites in the upper bay which have longer exposure to low salinity water.

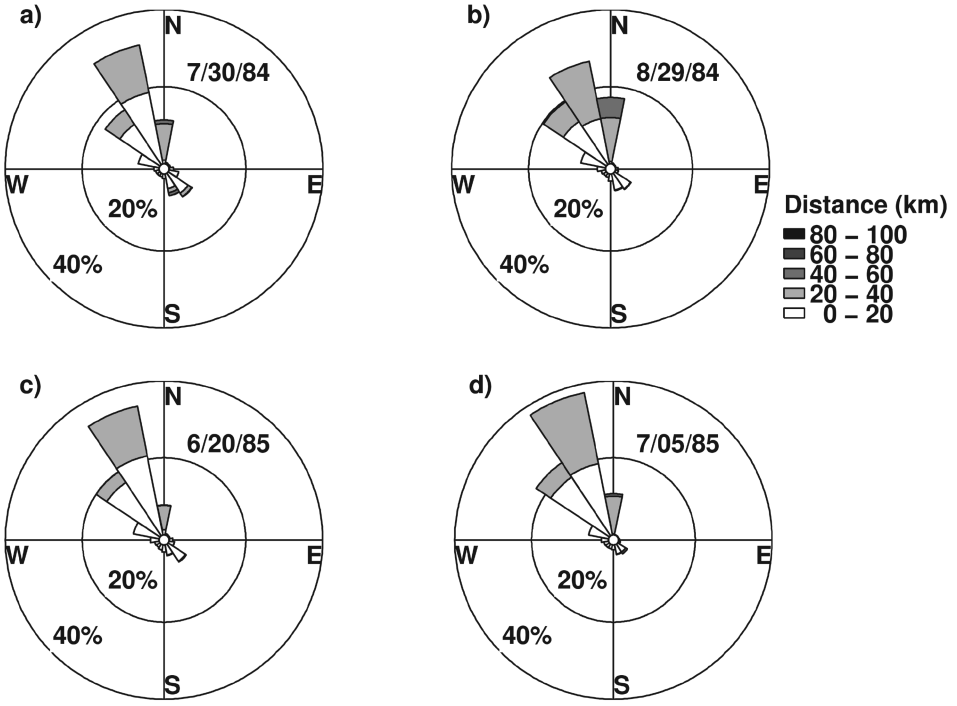


Figure 6. Larval transport histograms for larvae released from Arnolds on (a) 30 July 1984, (b) 29 August 1984, (c) 20 June 1985, and (d) 7 July 1985. The histograms are based on the linear distance (magnitude) and angle (direction) estimated for each larva from its release position to its current location at one-hour intervals (Lagrangian model integration time step).

By late July, the low salinity water is replaced by that with more typical salinity (Fig. 2) and larval success increases at the upper bay sites (Fig. 10a, b). Periods with low river discharge (e.g., 8/4/84) have increased transfer rates for the mid-bay reef sites (Fig. 10).

The fortnightly tidal variability also modifies larval transfer rates (Fig. 11). In general, larval releases during spring tides result in a higher percent exchange with downstream sites (Fig. 11). For example, larvae released at Shell Rock during outflows (e.g., 6/30/84, 7/15/84, 8/14/84) increase their exchanges with Bennies, Egg Island and the lower part of Delaware Bay (Fig. 11). Larvae released during neap tides provide increased inputs to sites upstream of the release area. Higher exchange rates at mid-bay sites, such as Ship John and Shell Rock, occur when larvae are released during neap tides (Fig. 11).

The transfer rates suggest that portions of Delaware Bay retain or export more larvae than others (Figs. 10, 11). The general pattern of larval export and retention is obtained by averaging over larger representative regions of Delaware Bay for each release time and for the entire spawning season. In the upper bay the general pattern is one of high particle retention (Fig. 12a). The decrease in retention in 1984 and 2000 is associated with the high

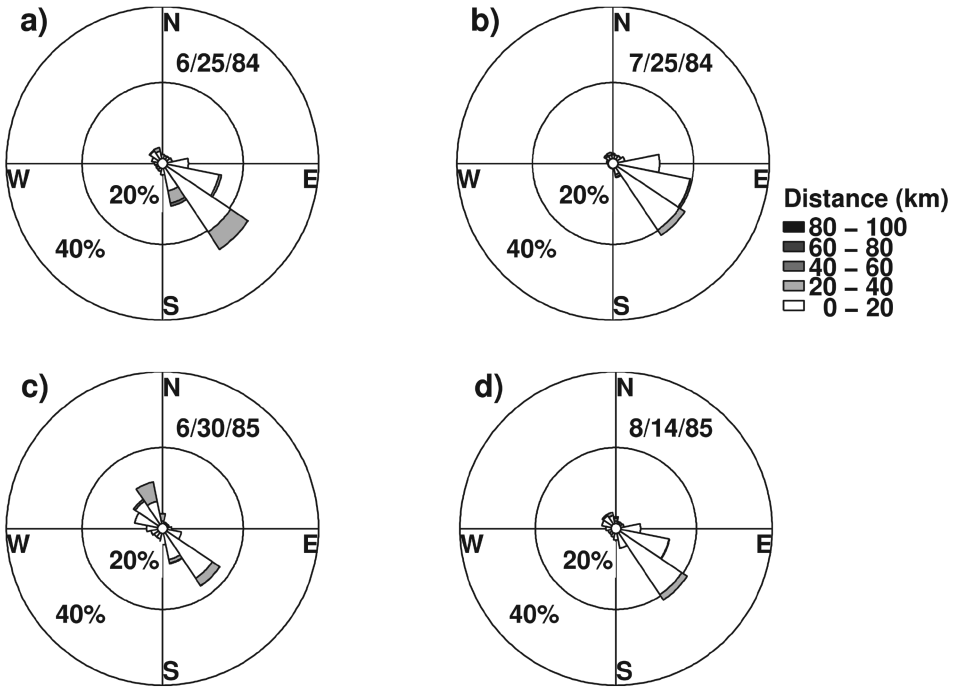


Figure 7. Larval transport histograms for larvae released from Arnolds on (a) 25 June 1984, (b) 25 July 1984, (c) 30 June 1985, and (d) 14 August 1985. The histograms are based on the linear distance (magnitude) and angle (direction) estimated for each larva from its release position to its current location at one-hour intervals (Lagrangian model integration time step).

river discharge that occurred during these years. Particle transport into the upper bay is enhanced during neap tides and particle export increases during spring tides (Fig. 13a). Along the Delaware side of the bay, the average particle retention is about 50% (Fig. 12b) but considerable variability is introduced by the spring-neap cycle (Fig. 13b). Neap tides tend to be associated with reduced larval retention and spring tides result in higher retention (Fig. 13b). These counter-intuitive results arise because outflow conditions driven by spring tides provide larvae from the upper bay to the mid- and lower bay while inflow during neap tides moves larvae to the upper bay. Particle retention in the middle reaches of the bay is relatively constant at about 30% (Fig. 12c) and variability produced by the neap tides is small (Fig. 13c). However, particle retention increases during spring tides because of the contribution from upstream regions. Particle retention is uniformly high in the lower bay (Fig. 12d), but overall the fortnightly variability has little effect on particle retention (Fig. 13d).

### c. Effects of behavior on larval dispersion

The effect of vertical behavior and vertical mixing on larval dispersion was assessed by comparing the previous results with simulations that use passive particles (i.e., without larval

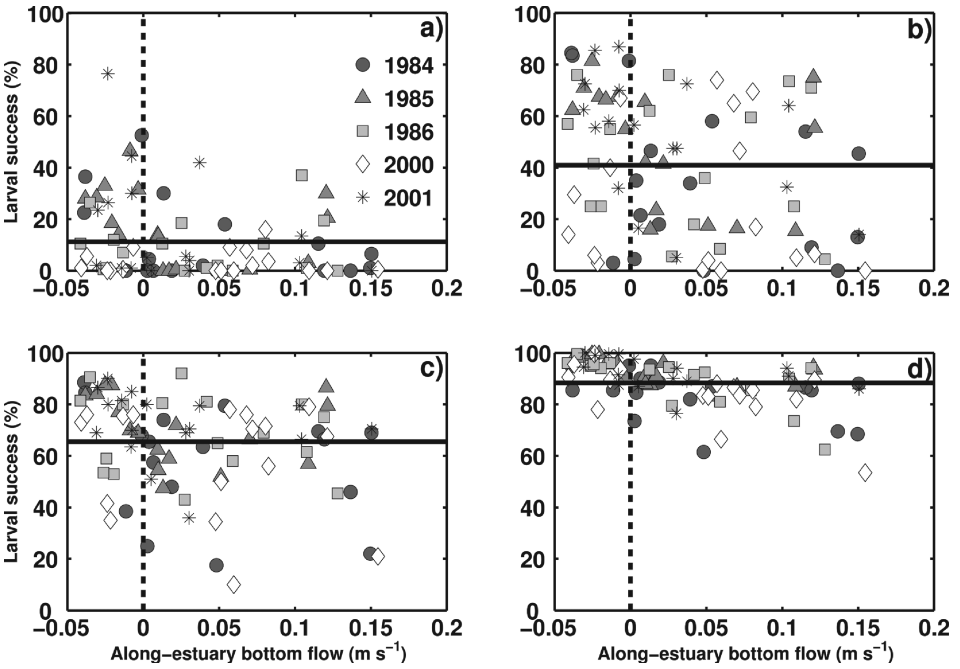


Figure 8. Relationship between along-estuary bottom flow and larval success for the 5 years included in this study for larvae released from (a) Hope Creek, (b) Arnolds, (c) Ship John, and (d) Bennies reefs (locations in Fig. 1). The five-year average success for each release area is indicated (horizontal lines) as is the zero velocity (vertical lines) which marks the shift from down-estuary flow (negative velocities) to up-estuary flow (positive velocities).

growth and behavior) and with simulations that include growth and behavior but no sub-grid vertical mixing (i.e., without the random vertical walk), respectively. For these simulations, particles are released at the same locations and times used for the year 2000 simulations. The final settlement location for the passive particles was taken from corresponding trajectories in the simulations with larval growth and behavior at the time and location the larvae reached settlement size. Comparison of the dispersion obtained for particles with and without larval growth and behavior that were released at Ship John on 20 June 2000 shows that those with behavior were mostly retained in the upper-middle estuary (Fig. 14a). Passive particles tend to move down-estuary toward the southwestern side of the lower estuary (Fig. 14b). The transport histograms show that differences in distance traveled for the two types of particles are about 5–10% (Fig. 14c, d).

The connectivity matrix for the spawning season shows that the majority of the particles with larval growth and behavior reach settlement size mostly between Arnolds and Egg Island, and that most of the particles potentially settle within the estuary (Fig. 15a, b). Overall larval success is highest in the mid-reaches of the estuary (Fig. 15c). The connectivity matrix for the passive particles is similar but with slightly larger dispersal scales (Fig. 15d, e). For

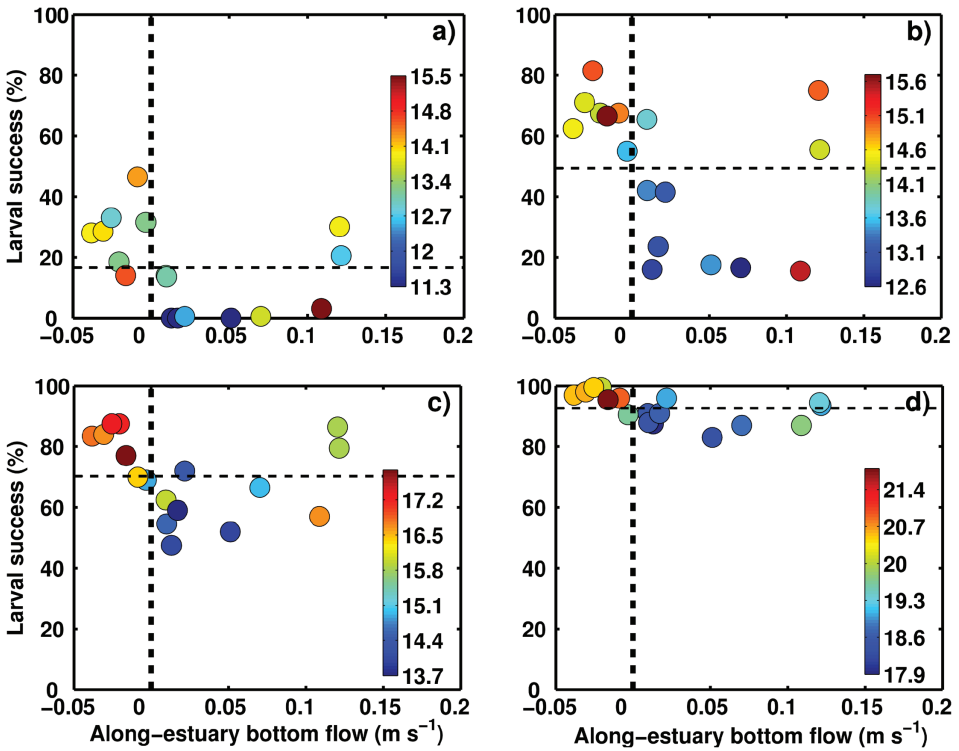


Figure 9. Relationship between along-estuary bottom flow, larval success, and salinity for 1985 for larvae released from (a) Hope Creek, (b) Arnolds, (c) Ship John, and (d) Bennies reefs. The average success at each release location is indicated (horizontal lines) as is the zero velocity (vertical lines) which marks the shift from down-estuary flow (negative velocities) to up-estuary flow (positive velocities).

Table 2. Percentage of success events and corresponding spring-neap tide for larvae released from four natural oyster reefs (locations shown in Figure 1) that exceeded the five-year average success rate.

Release area	Spring tide	Neap tide
Hope Creek	55	65
Arnolds	72	62
Ship John	66	55
Bennies	90	55

example, more particles are transported to the upper estuary regions and to the continental shelf (Fig. 15a, b versus 15d, e). The larger dispersal scales also result in a lower percent of potential settlement on the natural oyster reefs (Fig. 15e), which results in decreased larval success for these regions (Fig. 15f).

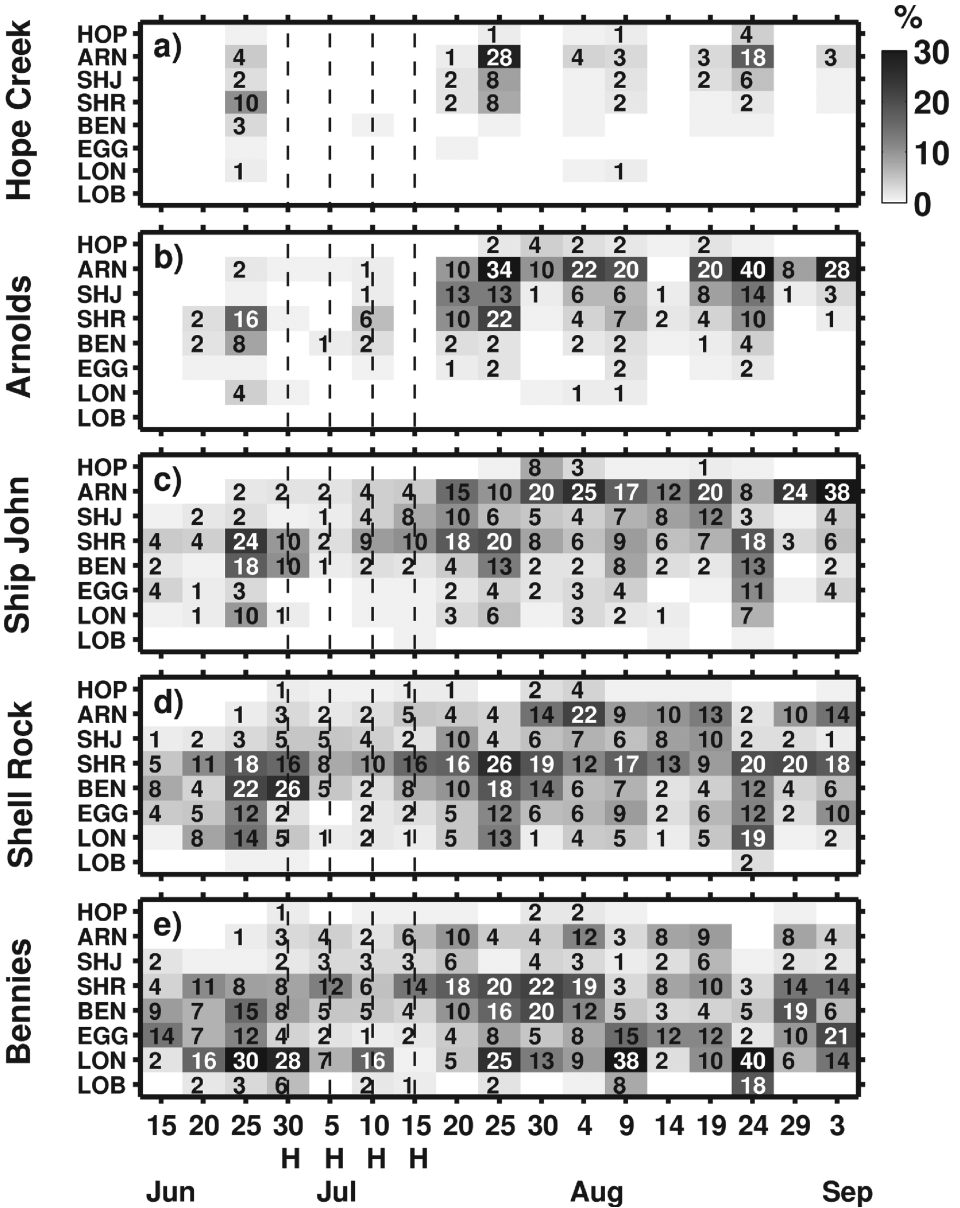


Figure 10. Time variability in the percent of successful larvae released from (a) Hope Creek, (b) Arnolds, (c) Ship John, (d) Shell Rock and (e) Bennies that potentially settled in the same or another location (y axis) for the spawning season of 1984. Periods of high river discharge (H) are indicated by the vertical dashed lines. Values greater than 1% are shown and the degree of connectivity is indicated by the shading. With darker shades associated with higher connectivity. The settlement areas are abbreviated as: HOP-Hope Creek, ARN-Arnolds, SHJ-Ship John, SHR-Shell Rock, BEN-Bennies, EGG-Egg Island, LON-Lower Bay North and LOB-Lower Bay.



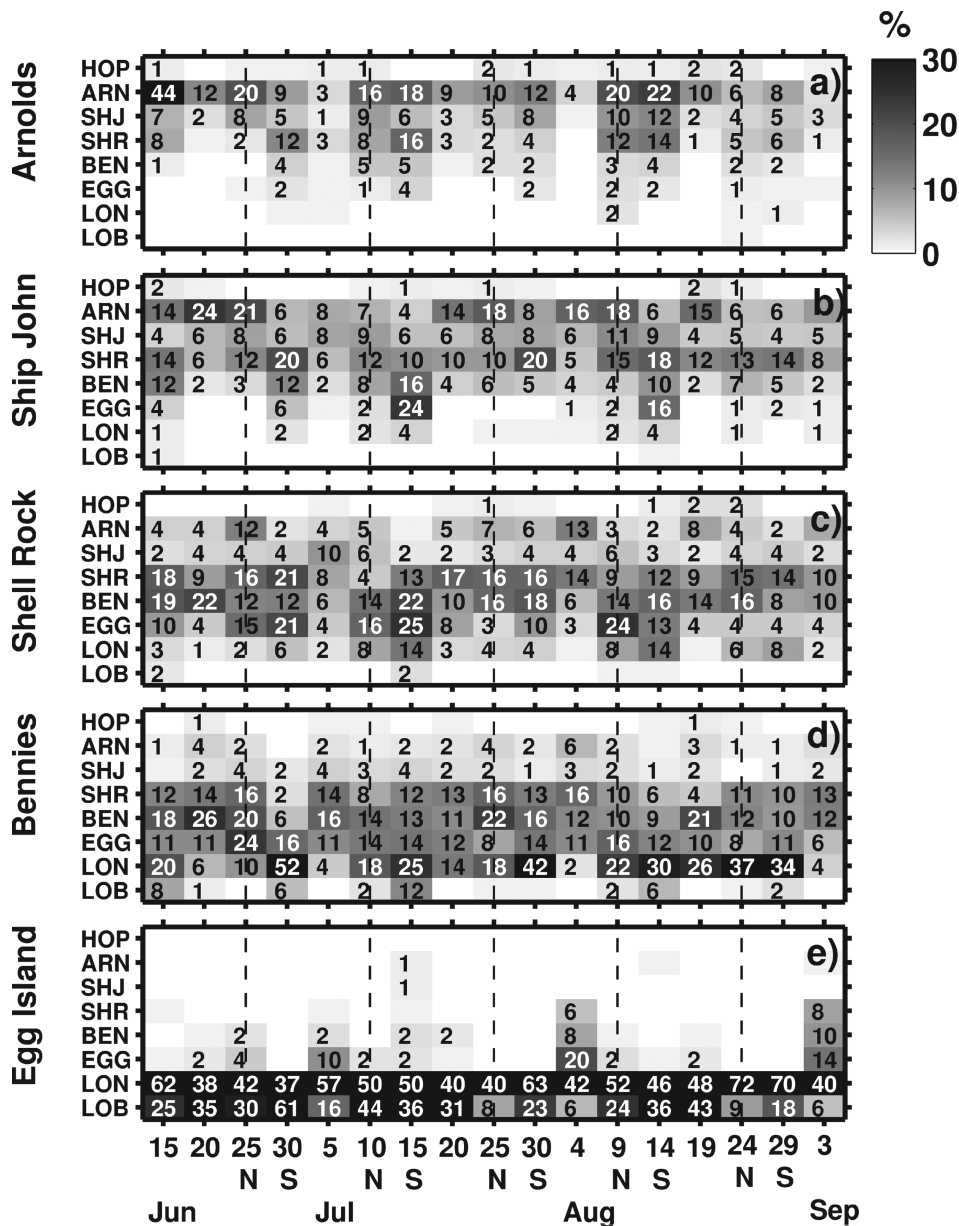


Figure 11. Time variability in the percent of successful larvae released at (a) Arnolds, (b) Ship John, (c) Shell Rock, (d) Bennies, and (e) Egg Island that potentially settled in the same or another location (y axis) for the spawning season of 1985. Periods of neap tides (N) are indicated by the vertical dashed lines; spring tides (S) occurred following the neap tides. Values greater than 1% are shown and the degree of connectivity is indicated by the shading, with darker shades associated with higher connectivity. The settlement areas are abbreviated as: HOP-Hope Creek, ARN-Arnolds, SHJ-Ship John, SHR-Shell Rock, BEN-Bennies, EGG-Egg Island, LON-Lower Bay North and LOB-Lower Bay.

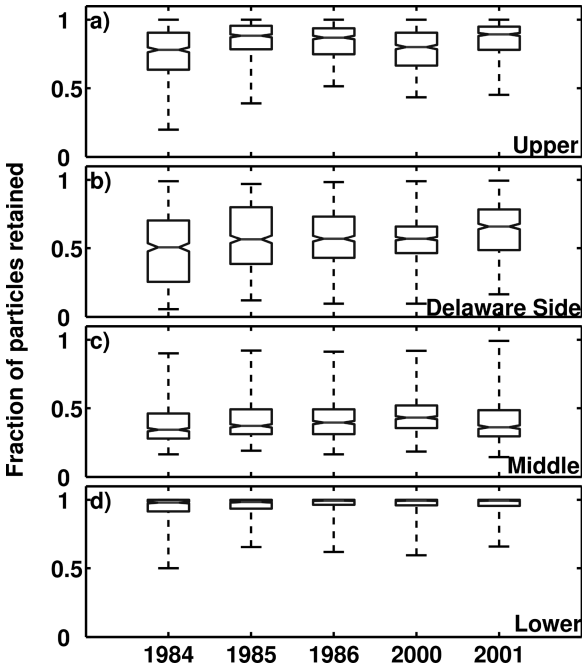


Figure 12. Interannual variability in larval retention calculated for the (a) Upper (areas 6, 7, 14, 15, Fig. 1), (b) Delaware Side (area 8, Fig.1), (c) Middle (areas 2 to 5, Fig. 1) and (d) Lower (area 1, Fig. 1) estuary regions of Delaware Bay from the simulated Lagrangian trajectories. The size of each box represents the 25<sup>th</sup> and 75<sup>th</sup> percentiles; the maximum and minimum values for each are represented by the vertical bars. The median of the estimates is given by the horizontal line and the degree of indentation for each box indicates the significance level of the median. If two intervals overlap, the medians are not significantly different at the 5% significance level.

The vertical distribution of particles with (Fig. 16a) and without (Fig. 16b) larval growth and behavior for releases from Shell Rock on 24 August 2000 shows that most were concentrated between the surface and 4 m. The Delaware estuary has large areas with depths <5 m (Fig. 1), so larvae have a higher probability of encountering shallow areas than the deeper areas and channels. The particles with and without larval growth and behavior have similar vertical distributions (Fig. 16a, b).

Removing the subgrid scale vertical mixing gives more distinct vertical locations at different times (Fig. 16c), characterized by upward swimming following release, maintenance in surface waters during the intermediate portion of planktonic life, and descent in the older larval stage. These results suggest that vertical mixing can overwhelm larval behavior, especially in a shallow system that is tidally mixed. This may account for the small differences in dispersal patterns for the particles with and without larval growth and behavior.

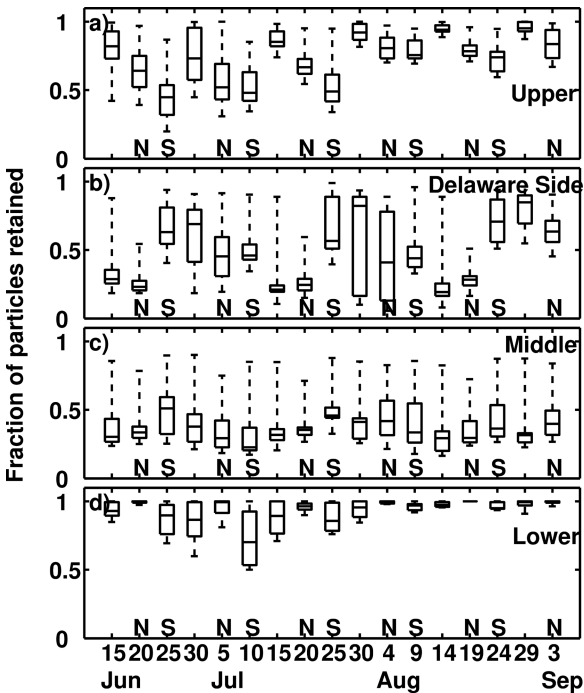


Figure 13. Intra-seasonal variability in larval retention calculated for 1984 for the (a) Upper (areas 6, 7, 14, 15, Fig. 1), (b) Delaware Side (area 8, Fig. 1), (c) Middle (areas 2 to 5, Fig. 1) and (d) Lower (area 1, Fig. 1) estuary regions of Delaware Bay from the simulated Lagrangian trajectories. The size of each box represents the 25<sup>th</sup> and 75<sup>th</sup> percentiles, the maximum and minimum values for each are represented by the vertical bars. The median of the estimates is given by the horizontal line and the degree of indentation for each box indicates the significance level of the median. If two intervals overlap, the medians are not significantly different at the 5% significance level. Times when spring tides (S) and neap tides (N) occurred are indicated.

#### 4. Discussion

In this study, larval success (as measured by survival to settlement size) and larval transport (including physical transport and behavior) are used to determine relationships among residual estuarine circulation, salinity, and larval growth and behavior that control intra-seasonal dispersion and potential settlement of oyster larvae in Delaware Bay. The simulated settlement regions show general agreement with observed regions of high and low recruitment (Narváez *et al.*, this issue). However, the magnitude of the observed interannual variability in recruitment is not reproduced by the simulations (Narváez *et al.*, this issue). The oyster larvae model does not include effects of predation and general mortality (e.g., Deksheniaks *et al.*, 1997), spawning and settlement cues (e.g., Hidu and Haskin, 1971), variability in food quantity and quality (e.g., Powell *et al.*, 2002; Powell *et al.*, this issue), or post-settlement processes, all of which influence larval survival and recruitment. Also,

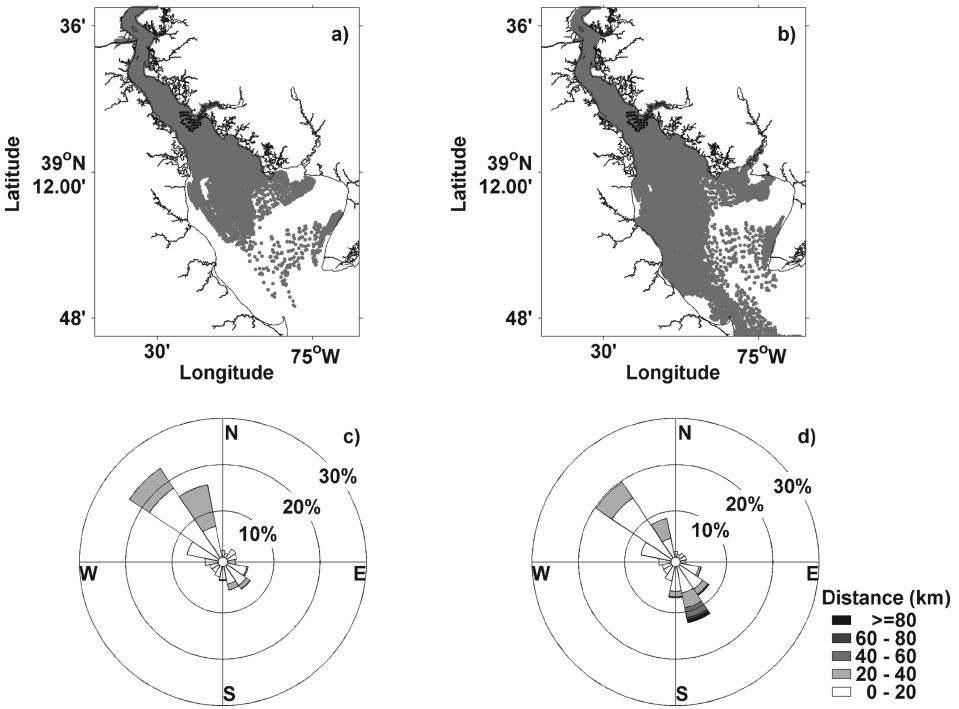


Figure 14. Distribution of particles released on 20 June 2000 from Ship John (black dots) (a) with larval growth and behavior and (b) without larval growth and behavior (passive particles). The larval transport histograms were estimated for particles (c) with and (d) without larval growth and behavior.

the constant and optimal food and turbidity concentrations that are specified for Delaware Bay over the spawning season likely result in an overestimate of survival and potential settlement for some reef areas.

Even with these limitations, the simulations provide insights into interactions between physical and biological processes that potentially affect the dispersion and success of oyster larvae in Delaware Bay. The spring and neap tides provide consistent flow directions that transport larvae to areas with salinity conditions that can favor or decrease larval survival. The fortnightly periodicity of these changes is within the 30-day life span of an eastern oyster larva in Delaware Bay. In addition, episodic increases in river discharge and concurrent decrease in bay salinity have a negative effect on larval growth. These less regular events can persist for extended times and therefore can have an important effect on oyster larvae success in Delaware Bay. *In situ* observations to evaluate these model-based results do not exist. However, the simulation results provide guidance on the types of data that are needed, such as measurements of oyster larvae settlement at time scales that correspond to

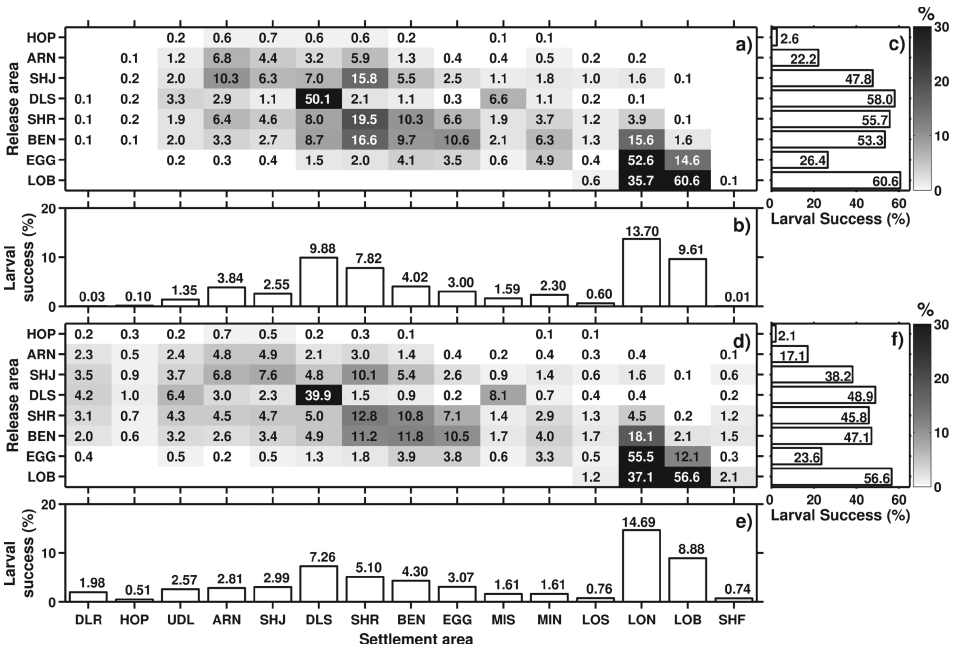


Figure 15. (a) The percent of total larvae released at a particular area (y axis) that potentially settled in the same or another location (x axis), (b) the average percent of particles arriving at each settlement area, and (c) the average percent of particles from the release area that arrived only at the natural oyster reefs (areas 1 to 8, Fig. 1) obtained from simulations done for 2000 that included larval growth and behavior. (d) The percent of total larvae released at a particular area (y axis) that potentially settled in the same or another location (x axis), (e) the average percent of particles arriving at each settlement area, and (f) the average percent of particles from the release area that arrived only at the natural oyster reefs (area 1 to 8, Fig. 1) obtained from simulations done for 2000 that did not include larval growth and behavior. Values greater than 0.05% are shown and the degree of connectivity is indicated by the shading, with darker shades associated with higher connectivity. The abbreviations used for the oyster reefs are given in Figure 1.

the spring-neap cycle, coincident measurements of environmental conditions, particularly food quantity and quality, and larval distributions.

a. Effect of spring-neap tides on larval dispersion

The residual circulation in Delaware Bay is dominated by fortnightly variability associated with spring-neap tides. During neap tides, outflow occurs in the surface layer and inflow in the deep channel and over the shoals. During spring tides, unidirectional outflow occurs throughout the water column in the upper-middle estuary region. The strong currents associated with spring tides increase tidal mixing, which in turn reduce vertical stratification and residual flow. The slower currents associated with neap tides reduce tidal mixing, enhancing stratification and the residual circulation (Geyer *et al.*, 2000; Stacey *et al.*, 2001).

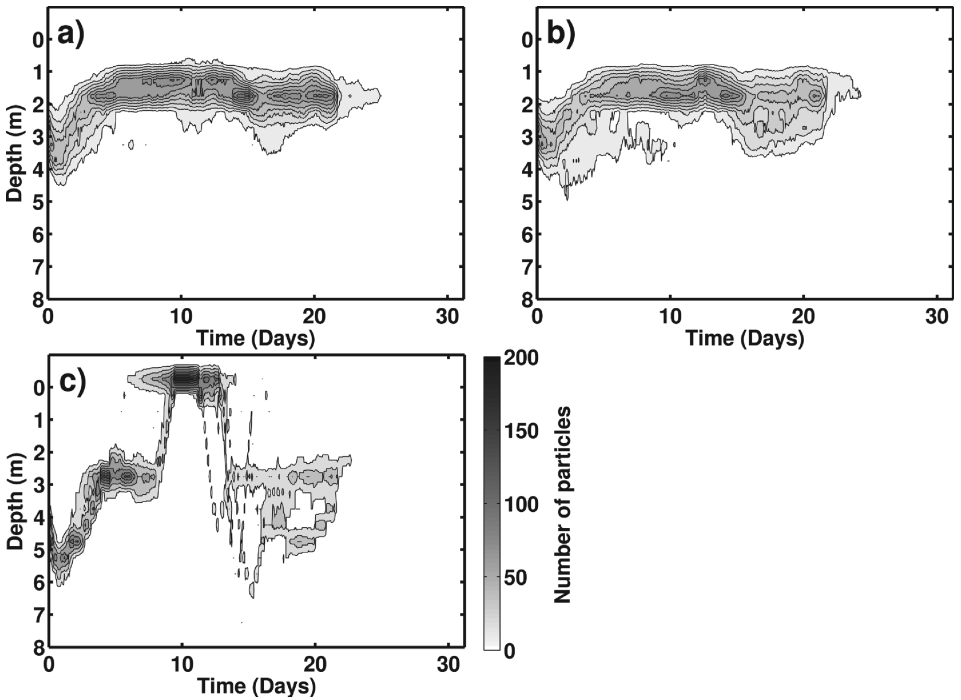


Figure 16. Vertical distribution of particles released from Shell Rock on 24 August 2000 obtained from simulations (a) with growth and behavior, (b) without growth and behavior and (c) with growth and behavior but without sub-grid scale vertical mixing.

Larvae released during unidirectional outflow (i.e., spring tides) are transported down-estuary, where high salinity favors larval success by decreasing the time needed to develop to settlement size. During neap tides, larvae are transported up-estuary during their early stages where low salinity waters increase development times, extending the planktonic larval duration and hence decreasing the probability of success. Larvae entering the upper part of Delaware Bay are more likely to be retained (Fig. 12) where success is decreased. Hence, this transport pathway results in larvae that are potentially lost from the oyster population.

The export of larvae from the middle to upper estuary reef sites is larger when releases occur during neap tides (Fig. 8). For upper estuary regions, where larval success is low, this could be an important mechanism that provides larvae and also maintains connectivity with reefs in other regions of the bay. The supply of new individuals to the upper-most reef site, Hope Creek, is low, suggesting limited connection to the other Delaware estuary reefs. He *et al.* (this issue) show that the oyster populations from Arnolds to Egg Island are genetically homogeneous and that Hope Creek is genetically different from the other populations in the estuary. The limited up-estuary transport and low survival at Hope Creek

may help maintain these genetic differences. Although larval dispersal provides the mechanism for gene transfer, Munroe *et al.* (this issue) suggest that the characteristics of the adult oyster population (such as abundance and mortality) are also important in maintaining and establishing genetic traits.

In mid-latitude estuaries such as Delaware Bay, eastern oysters typically spawn 2–3 times during the spring-summer season (Deksheniaks *et al.*, 1993; Kennedy, 1996). However, these spawns occur at different times and locations in the bay, i.e., they are not synchronized over the bay. An analysis of gonadal tissue obtained from oysters sampled during the spawning seasons of 1964 and 1965 from natural and leased reefs that span upper to lower bay show that peak spawning occurs at different times throughout Delaware Bay (Mesquita and Ford, unpublished data). In 1964, spawning began in the lower bay in June, proceeded up-estuary during the summer, and occurred at upper bay sites in late July and early August. Peak spawning in 1965 began in the lower bay but the upper bay reefs spawned just prior to the mid-bay sites. This along-estuary gradient in peak spawning would favor contributions from different reef areas as the spawning season progresses. Depending on when and where peak spawning occurs, the fortnightly tide could potentially determine which reefs are sources or sinks of larvae and where successful larvae potentially settle.

The simulated particle trajectories show the importance of high salinity in moderating larval growth and total planktonic larval duration. Release from a particular location during neap tide, which favors up-estuary transport, may significantly reduce the potential set; whereas, release during down-estuary flow (spring tide) may enhance survival and hence potential settlement. The effects of spring-neap tides on the horizontal larval distribution might be even more important for oyster larvae with shorter planktonic life, as occurs in lower latitude estuaries (Deksheniaks *et al.*, 1993; Kennedy, 1996). Relationships between larval transport and tides, internal waves, and bores have been demonstrated (e.g., Shanks, 1986; Shanks and Wright, 1987; Pineda, 1994, 1999), and behavioral responses by some larvae to tides have been shown (e.g., Hill, 1991; Thiebaut *et al.*, 1992; Forward and Tankersley, 2001; López-Duarte and Tankersley, 2009). This study shows that larval growth and potential success is also affected by tidal variability, and this relationship can be more important than behavior or physical transport in determining the dispersion and connectivity of estuarine oyster populations (e.g., Shen *et al.*, 1999).

#### *b. Effects of river discharge on larval dispersion*

High river discharge events (Fig. 2) can decrease the overall spawning season larval success (Narváez *et al.*, this issue). River discharge also affects larval dispersion causing a shift in the fraction of larvae that reach settlement size between upper and middle estuary regions (Fig. 10). More larvae are transported to the upper estuary during low river discharge. The middle and lower estuary regions receive more larvae when river discharge is high. These changes in transport combine with salinity to produce an along-estuary gradient in success and potential settlement. However, increased down-estuary flow during high river

discharge results in increased up-estuary subsurface flow (Figs. 2 and 3). Larvae tended to be well-mixed throughout the water column, so the chances of up- or down-estuary transport are potentially similar, which highlights the importance of salinity in larval growth and success.

Larvae transported to the higher salinity water of the western part of the Cape May Peninsula in the lower Delaware Bay have higher rates of success. The circulation of this region is characterized by slow currents and a gyre that supports retention and local recruitment and allows this region to retain larvae exported from the middle estuary reefs. Also, an area of weak sub-tidal circulation just outside of Delaware Bay has been associated with the retention of crab larvae (Steppe and Epifanio, 2006) that have been exported from the bay. This offshore region could potentially retain oyster larvae that are exported from the bay, providing a mechanism for return to the lower bay. Retention areas have been proposed as important mechanisms that control larval dispersal in other estuarine systems (Sulkin, 1981; Shen *et al.*, 1999). Hence, the success of the oyster reefs in the lower Delaware Bay may be attributable to the existence of a permanent recirculation that retains larvae in high salinity waters which favor larval growth.

### *c. Importance of vertical behavior in larval dispersal*

The simulated particles that include behavior tend to have higher rates of successful settlement on the natural reefs in Delaware Bay, but the transport patterns of these particles relative to those without behavior are not substantially different. Vertical swimming behavior has been identified as an important factor in the dispersion of oyster larvae (e.g., Carriker, 1951; North *et al.*, 2008) and larvae of other marine organisms (e.g., Pineda, 2000; 2007; Largier, 2003; Pineda, 2007; Tilburg *et al.*, 2010). However, Kim *et al.* (2010) reported that although vertical behavior increased the retention of eastern oyster larvae near spawning areas, physical transport dominated the simulated and observed settlement patterns in Mobile Bay, Alabama. This finding was attributed to the regular well-mixed conditions of Mobile Bay. The simulated circulation in Delaware Bay is characterized by a well-mixed water column over the shallow areas of the estuary where the oyster reefs are located. The vertical larval distributions show that turbulent vertical mixing is stronger than the ability of the larvae to change their vertical location. Thus, the retention, dispersal, and ultimate settlement location for eastern oyster larvae are a result of the combined effects of water motion, turbulent mixing and larval success and, to a lesser extent, larval behavior. The combination of variations in flow direction produced by the spring-neap tides, the general estuarine circulation, and a well-mixed vertical distribution of larvae may be required to maintain larvae around the natural oyster reefs and within the estuary. Thus, all three must be represented in models that consider larval dispersal processes. The relatively small contribution of behavior to transport and dispersion of eastern oyster larvae suggests that for some shallow estuarine systems, passive transport simulations might be sufficient to determine population connectivity within the estuary (Haase *et al.*, 2012) and larval transport between estuaries and adjacent coastal zones (Roegner, 2000).



## 5. Summary and conclusions

Observational (e.g., Shanks *et al.*, 2002; Roegner *et al.*, 2007) and modeling studies (e.g., Shen *et al.*, 1999; Pringle and Franks, 2001) have focused on quantifying transport of larvae into or out of a system by tidal motions. These studies showed the importance of tides in larval transport, with the spring-neap tides accounting for as much as 40% of the variation in larval imports to an estuary (Luettich *et al.*, 1999). This study extends these studies by considering the within-estuary variability in larval dispersion pathways and success (as a measure of survival) that is produced by spring-neap tides that are superimposed on the general estuarine gravitational circulation. The transport pathway and the salinity conditions experienced by a larva during dispersal imparts intra-seasonal temporal and spatial variability to larval success, which contribute to the observed variability in oyster larvae settlement patterns in Delaware Bay.

Spring-neap tides are a predictable feature of estuarine circulation and represent an important mechanism for moving larvae from down-estuary locations to upper estuary oyster reefs. However, the low transfer associated with the up-estuary transport are such that this mechanism cannot completely explain the persistence of upper estuary oyster reefs, such as Hope Creek in the upper Delaware Bay. Local recruitment is likely to be important also in these regions.

River discharge also influences larval transfer and can at times be a primary determinant of larval dispersion, success and potential settlement, such as occurred in 1984 in Delaware Bay (Narváez *et al.*, this issue). During these times, river discharge can overwhelm the regular up-down estuary transport associated with the spring-neap tides. However, variations in river discharge are episodic, whereas the spring-neap tides are regular and predictable. In the longer term, the variability imposed by the spring-neap cycle is likely an important determinant of larval transport patterns and hence the patterns of recruitment and genetic dispersal in Delaware Bay and other similar estuarine systems.

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