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MODELING THE DISPERSION OF EASTERN OYSTER LARVAE (*CRASSOSTREA VIRGINICA*) AND ITS EFFECTS ON THE MOVEMENT OF DISEASE RESISTANT GENES IN THE DELAWARE BAY ESTUARY

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A Dissertation Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
Requirements for the Degree of

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ABSTRACT

MODELING THE DISPERSION OF EASTERN OYSTER LARVAE (*CRASSOSTREA VIRGINICA*) AND ITS EFFECTS ON THE MOVEMENT OF DISEASE RESISTANT GENES IN THE DELAWARE BAY ESTUARY

Diego A. Narváez
Old Dominion University, 2012
Director: Dr. John M. Klinck

This study combines several models to address two primary research questions. How does the interaction of larval biology and environmental variability determine the spatial distribution of oyster larvae in Delaware Bay? What is the role of larval dispersion in the transference of disease-resistant genes? The particle-tracking module in the Regional Ocean Modeling System (ROMS) was converted into an Individual-Based model representing Eastern oyster larvae that has growth and vertical migration. Exchange of larvae between natural oyster reefs was estimated and used in an Individual-Based genetic model that simulates the genetic structure of eastern oysters. Particles were released from a number of reefs at several times and tracked until they reached a competent settlement size (330 μm). The simulated dispersal patterns showed that oyster larvae tend to drift down-estuary during the spawning season. The net result is that mixing of oyster larvae throughout Delaware Bay is extensive. Larval success is strongly affected by variability of temperature and salinity. Low temperature and salinity increases development times, which decreases the larval success. A stronger influence in the larval success is driven by salinity. The permanent salinity gradient in the estuary maintains an along estuary gradient in larval success. Larvae released in the upper bay populations encounter lower salinity than larvae release in the middle-lower bay populations. River discharge and spring-neap tides are the main forcing of the residual circulation, salinity and stratification in

the Delaware estuary, playing an important role in the larval success and dispersion. Years with low success are related to large events of river discharge within the spawning season. Large river discharge also enhances the down-estuary dispersal pattern. Larvae released during spring tides are transported down-estuary to high salinity areas increasing the larval success of upper and middle bay reefs. The dominant inflows in the subsurface layer and over the shoals during neap tides reduced the larval success by transporting larvae to low salinity areas. Thus, neap tides could be important in sustaining upper bay populations by increasing the export of larvae from middle to upper estuary populations. Nevertheless, the low exchange rates suggest that this mechanism by itself can not completely explain the survival of upper estuary populations. The well-mixed conditions over most of the estuary maintain larvae distributed throughout the water column and overcome the effects of larval swimming behavior. The genetics simulations show larval dispersal might be important in the movement of disease-resistant genes from high (middle-lower bay) to low (upper bay) disease-resistant populations. The transference of the resistant trait will occur in periods of 5 to 100 years. The results of this research confirm that biophysical processes influence the dispersion pattern of oyster larvae, and thereby, the pattern of recruitment and genetic dispersal throughout Delaware Bay.

To my wife Andrea and my dog Luna...thanks for the happy times!

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To my family, who don't speak any English, here are a few words in Spanish for them. Familia, sé que me perdí muchos momentos de alegría y por suerte solo

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CHAPTER 1

INTRODUCTION AND RESEARCH QUESTIONS

Many early life stages of fish and marine invertebrates have a pelagic larval phase before becoming part of the adult population [*Roughgarden et al.*, 1988]. For benthic populations, with near-sessile adults (e.g., barnacles, mussels, oysters) and for fish larvae and juveniles that need to return to their natal population, the pelagic larval phase plays an important role in the exchange of individuals, the survival of the adult population and the overall population connectivity [*Cowen et al.*, 2000; *Palumbi*, 2003; *Cowen et al.*, 2007; *Marinone et al.*, 2008]. Different approaches are used to estimate larval dispersion [e.g., *Botsford*, 2001; *Hedgecock et al.*, 2007; *Hitchcock et al.*, 2008; *Pineda*, 1991; *Shanks*, 1985; *Sotka and Palumbi*, 2006; *Wing et al.*, 1998; *Zacherl et al.*, 2009]. Yet, questions remain unanswered due to the numerous biological and physical processes involved in larval dispersion and to the broad spatial (1-10^5 m) and temporal (1-10^9 s) scales of these processes, which make them difficult to measure using conventional sampling methods [*Largier*, 2003].

In order to understand how larval dispersion is influenced by the interaction between larval biology and the changing environment, a good understanding of the targeted marine population is required. One of the most studied marine invertebrates in North America is the eastern oyster (*Crassostrea virginica*), which has received considerable attention because of its commercial value. A long-term record for oysters from 1953 to the present [*Powell et al.*, 2008] makes Delaware estuary unique in having the longest observed record available of any oyster population and one of the longest time series for any marine invertebrate worldwide. This information has been used to examine temporal changes in oyster population dynamics, including regime shifts [*Powell et al.*, 2009a,b] and basic biological relationships, such as the

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relationship between disease and mortality and between broodstock abundance and recruitment [*Hofmann et al.*, 1992; *Powell et al.*, 2008, 2009a]. Additionally, the biology of eastern oyster larvae is relatively well understood [*Kennedy*, 1996a], which has allowed the creation of larval models to study the connection of the larvae to the environment [e.g. *Dekshenieks et al.*, 1993, 1996; *North et al.*, 2008; *Kim et al.*, 2010].

Despite a wealth of studies on oyster gametogenesis, spawning and larval biology, the spatial and temporal trends in recruitment and their relationship to the adult population are still poorly understood. In the Delaware Bay estuary, for example, a down-estuary gradient exists in recruitment potential with up-estuary reefs recruiting sporadically and at a lower level relative to the adult population [*Powell et al.*, 2008]. The recruitment potential has large interannual variations which also differ between up-estuary and down-estuary reefs [*Powell et al.*, 2008]. These spatial and temporal trends impact oyster population dynamics, population resiliency, and management. Considering that larval dispersion of many marine invertebrates includes spawning time and location, larval development, behavior, mortality, transport and availability of suitable habitat to settle [*Largier*, 2003], the recruitment potential would depend mostly on larval dispersion. Thus, understanding the variability and interactions between the biophysical processes involved in dispersion can provide insights into oyster recruitment and their relationship to the adult population. The degree of interaction among these many factors underlies the significant seasonal and interannual variations observed in recruitment to Delaware Bay oyster populations.

Because of the sessile nature of adult oyster, the genetic exchange also occurs during the pelagic larval phase. For oyster populations affected by diseases, such as eastern oyster, the exchange is particularly important in the transference of genes associated to disease-resistant traits. In Delaware Bay, Dermo and MSX diseases mostly affect oyster beds in high salinity areas in the middle and lower estuary. The high disease pressure in the middle-lower bay beds has allowed the development

of disease-resistant genes. High oyster mortality in the Bay has been associated frequently to diseases epizootics. However, an MSX epizootic occurring during 1984-1986 produced a significant decrease in the prevalence of MSX disease in the entire Delaware Bay in only 5-6 years. The decrease in MSX prevalence has been explained in terms of gene flow from high to low disease-resistant populations [*Hofmann et al.*, 2009]. The gene flow is driven by the amount of larvae moving among the oysters population, i.e., the exchange rates among populations. Thus, larval dispersion in the Delaware Bay might also be important in propagating resistant genes within the Bay.

In this study the dispersion of oyster larvae in Delaware Bay and its impact on the transference of disease-resistant genes was investigated using a series of numerical models that simulate larval growth and behavior, Bay circulation and physical properties, and genetic structure of oyster populations. These models were used to address two primary research questions. The first provides insights on the effects of the environment on larval biology and dispersion: How does the interaction of larval biology and environmental variability determine the spatial distribution of oyster larvae in Delaware Bay? In Chapter 3 specific research questions are addressed to determine the larval dispersal pathways and the effects of interannual variability in the along-bay gradients of temperature and salinity in larval growth and development. In Chapter 4 the specific research questions focus on the effects of of intraseasonal variability in larval growth and development and in the relative importance of Bay circulation and larval behavior in determining larval pathways and potential settlement location. The second research question provides insights on the processes affecting the genetic structure of a population: What is the role of larval dispersion in the transference of disease-resistant genes? In Chapter 5 specific research question are addressed to explore how the genetic structure of a population is changed by immigration or transplantation, how many immigrants would be required to produce a genetic shift and

accumulation of disease-resistant genes and how long the immigrations must last.

This dissertation is organized as follows: a background section with a description of general physical characteristics of the Delaware Bay and the biological components of the oyster life cycle is presented in Chapter 2. Chapter 3 address the interannual variability in larval dispersion and presents details of the circulation and larval model and how the coupling was performed. Validation of the modeling approach using recruitment and settlement time series also is shown. A description of the sensitivity of the model to some of the selected parameters is given. Chapter 4 focuses on the intraseasonal variability of larval dispersion and presents more details of the relative importance of larval biology and physical processes such as river discharge and tides in the dispersion of oyster larvae. A description of the genetic model is presented in Chapter 5, followed by a description of the role of larval dispersion on the movement of disease resistant genes. Chapter 6 summarizes the previous chapters with respect to the research questions and presents the conclusions of this research.

CHAPTER 2

BACKGROUND

2.1 PHYSICAL ENVIRONMENT

2.1.1 General Features of the Study Area

One of largest estuaries in North America, the Delaware Bay estuary system, is located in the Middle Atlantic Bight in the eastern coast of the U.S.A. (Figure 1). This coastal plain estuary includes the Delaware River and Bay and has a surface area of around 1840 km^2. The axial distance from the entrance at Cape Henlopen/Cape May to the head at Trenton, New Jersey is about 210 km, with a drainage basin of 35,000 km^2 that extends into 5 states (Delaware, Pennsylvania, New Jersey, New York and Maryland). The estuary has a funnel shape, with a width of 18 km at the Capes and 0.3 km at Trenton, NJ. However its widest cross section is 43 km about 20 km upstream of the bay mouth. The bathymetry of the estuary presents a main narrow channel that extends along the estuary, with an average depth of 12 m, flanked by shoals with depths of 2-5 m. In the lower estuary, a more irregular bathymetry shows two more channels of shorter length. The channels are located in the southern part of the lower-middle bay, leading to a large shallow plain area in the middle-northern area (Figure 1).

The Delaware estuary has been classified as a weakly stratified estuary using the ratio between tidal and fresh water volume [*Garvine*, 1991]. The main tidal constituent in the estuary is the semidiurnal lunar tide (M_2), with an amplitude ranging from 0.7 m at the mouth [*Wong and Muenchow*, 1995] to 2.7 m at the head of the estuary [*Parker*, 1991]. According to *Whitney and Garvine* [2008], the largest tidal current amplitudes, 0.8 m s^{-1}, occur along the main axis of the estuary and in the Delaware River. Tidal currents of 0.2-0.3 m s^{-1} are observed mostly on the

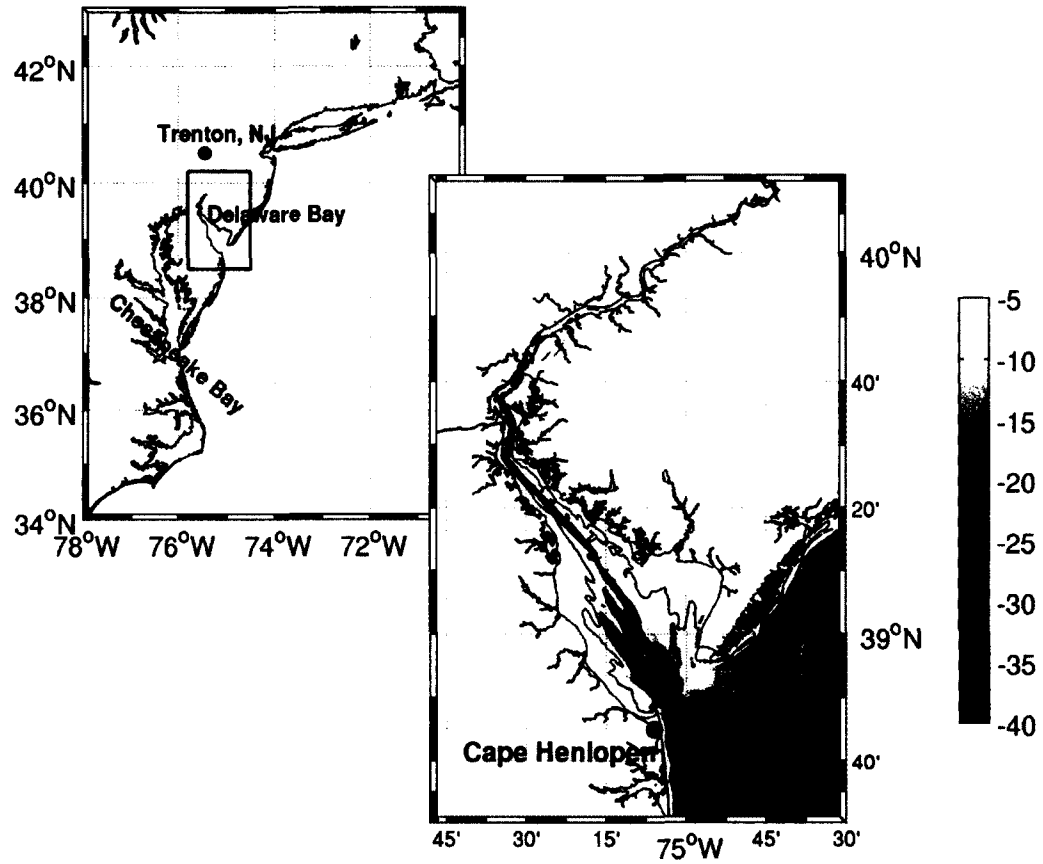

Figure 1. Map and bathymetry of the Delaware Bay estuary system in U.S.A.

shoals of the Delaware Bay, close to the shore. The lowest tidal current amplitudes (0.1 m s^{-1}) occur in the northern section of the widest part of the lower estuary. The Delaware estuary receives on average 1.3×10^9 kg $year^{-1}$ of suspended sediment from its river tributaries [*Cook et al.*, 2007]. Most of these tributaries are up-estuary; therefore, the turbidity in the Delaware estuary decreases downstream with maximum turbidity concentrations of 60-200 mg l^{-1} occurring 75-110 km up-estuary from the mouth of the Delaware Bay [*Pennock*, 1985]. In the shallow areas in the lower estuary, concentrations can reach 180 mg l^{-1}.

The Delaware River is the major contributor of freshwater to the estuary (58%), with an average discharge of 330 m^3 s^{-1} [*Sharp et al.*, 1986a], followed by the Schuylkill

River (15%). Others freshwater sources do not account for more than 1% of the total discharge. The last 96 years of monthly mean discharge shows a seasonal cycle with maximum values of 580-630 $m^3\ s^{-1}$ during early spring (March and April) and minimum discharges of 170-175 $m^3\ s^{-1}$ during late summer and early autumn (August and September) (U.S. Geological Survey, Hydrologic Unit Code 01463500, Delaware River at Trenton New Jersey). Overall, the salinity decreases linearly up-estuary [*Garvine et al.*, 1992], from 30-32 in the lower estuary to 0 in the upper-most part of the estuary. However, seasonal to interannual variations in salinity are associated with the freshwater input from the Delaware River; thus, increases/decreases in river discharge, decrease/increase the salinity [*Wong and Muenchow*, 1995]. The water temperature also presents seasonal cycles, which is influenced directly by the solar heating cycle, with a surface maximum in summer of 24°C and a surface minimum in winter of 5°C [*Keiner and Yan*, 1997]. On the Middle Atlantic Bight, southerly winds are predominant during spring-summer months, with a marked synoptic (2-10 days) variability caused by tropical storms. In the estuary synoptic temporal scales are also predominant. In terms of magnitude, wind in the estuary tends to be weaker than wind on the shelf, mostly because of the frictional effects of the land, yet a strong correlation has been observed between shelf and lower-estuary winds [*Moses-Hall*, 1992, cited by *Wong and Moses-Hall,* 1998].

2.1.2 Circulation and Hydrography

The subtidal dynamics of the Delaware estuary has been described by several studies [*Wong*, 1994; *Wong and Muenchow*, 1995; *Pape and Garvine*, 1982; *Garvine*, 1991; *Wong*, 1998]. The early studies of *Pape and Garvine* [1982], show the classical two-layer estuarine circulation in the deepest sections of the bay, i.e., seaward flows (outflows) in the surface layer and landward flows (inflows) in the deep layer

[*Pritchard*, 1956]. Following studies have shown that the transverse structure of currents and hydrography is dominated by strong lateral gradients [*Wong*, 1994]. While barotropic outflows of low salinity water are observed on the shoals at both sides of the estuary, barotropic inflows of high salinity occur mainly in the channels. Salinity intrusions can reach 90-100 km up-estuary [*Garvine et al.*, 1992]. *Wong* [1994], using an analytical model, suggests that this transverse partition is driven by the laterally varying bathymetry combined with gravitational and wind forcing. Under moderate and low wind forcing, the lateral partition of the flow and salinity is dominated by gravitational effects and changes in bathymetry, producing outflows over the shoals and inflow in the channel. Strong winds might overcome the gravitational force in determining the transverse structure of currents and hydrography.

Winds have a local and a remote effect on the estuarine circulation variability [e.g., *Garvine*, 1985; *Wong*, 1998, 2002]. Local winds might produce downwind flows along the shores and upwind flows in the channel [*Wong*, 1994; *Winant*, 2004; *Sanay and Valle-Levinson*, 2005]. Thus, under particular circumstances, local wind and gravitational forcing in Delaware estuary might reinforce or oppose each other, depending on the direction of the wind [*Wong*, 1994]. Wind blowing outside the estuary, on the continental shelf can have a remote effect on estuarine circulation. Ekman dynamics in the northern hemisphere cause an alongshelf northward wind to set down the sea level in the mouth of the estuary, while an alongshelf southward wind will set up the sea level just outside the estuary [*Garvine*, 1985]. In both cases the sea level perturbation propagates inside the estuary affecting the circulation. If a sea level set up occurs, a unidirectional barotropic inflow is expected, while a set down can produce a barotropic outflow [*Wong*, 1994]. *Wong* [1998] studied the importance of local and remote wind effects in the Delaware estuary suggesting that for any particular point inside the estuary, local wind is likely to be more important than remote wind in driving the subtidal circulation. On the other hand, remote winds are important to

the laterally averaged subtidal transport into or out of the estuary, and in driving sea level fluctuations. The synoptic variability of winds during the spring-summer season drives currents and hydrography at the same temporal scale [*Wong*, 2002]. Just outside of the estuary entrance a buoyancy driven coastal current is formed by the exiting estuary plume. Due to the effects of Coriolis, the plume is deflected to the south, forming a coastal current in the same direction of the Kelvin wave propagation [*Garvine*, 1991; *Muenchow et al.*, 1992; *Wong and Muenchow*, 1995]. The coastal current extends 80 km along the shelf, with speeds of 0.2 m s^{-1} [*Wong and Muenchow*, 1995]. This current is faster than the flow in the northern side of the mouth [*Muenchow and Garvine*, 1993], creating a null zone in this area.

2.2 BIOLOGICAL ENVIRONMENT

2.2.1 Oyster Habitat

Eastern oyster populations are distributed from Nova Scotia, Canada to the Yucatan Peninsula, Mexico [*King and Gray*, 1989]. In the Delaware estuary, natural oyster beds are located mostly in the middle estuary in the New Jersey waters of the estuary (Figure 2), while smaller populations exist in the Delaware waters of the estuary. The distribution of natural oyster beds has been obtained from annual stocks surveys of oysters performed since 1953. These long-term records make Delaware estuary unique in having the longest database available of any oyster population [see *Powell et al.*, 2008, and references therein for survey details]. The available information has been used to study oyster population dynamics and basic relationships, such as disease-mortality and broodstock-recruitment.

2.2.2 Oyster life history

As with many marine invertebrates, oysters have a complex life cycle which includes a pelagic and a benthic phase. Egg fertilization and larval growth occur in

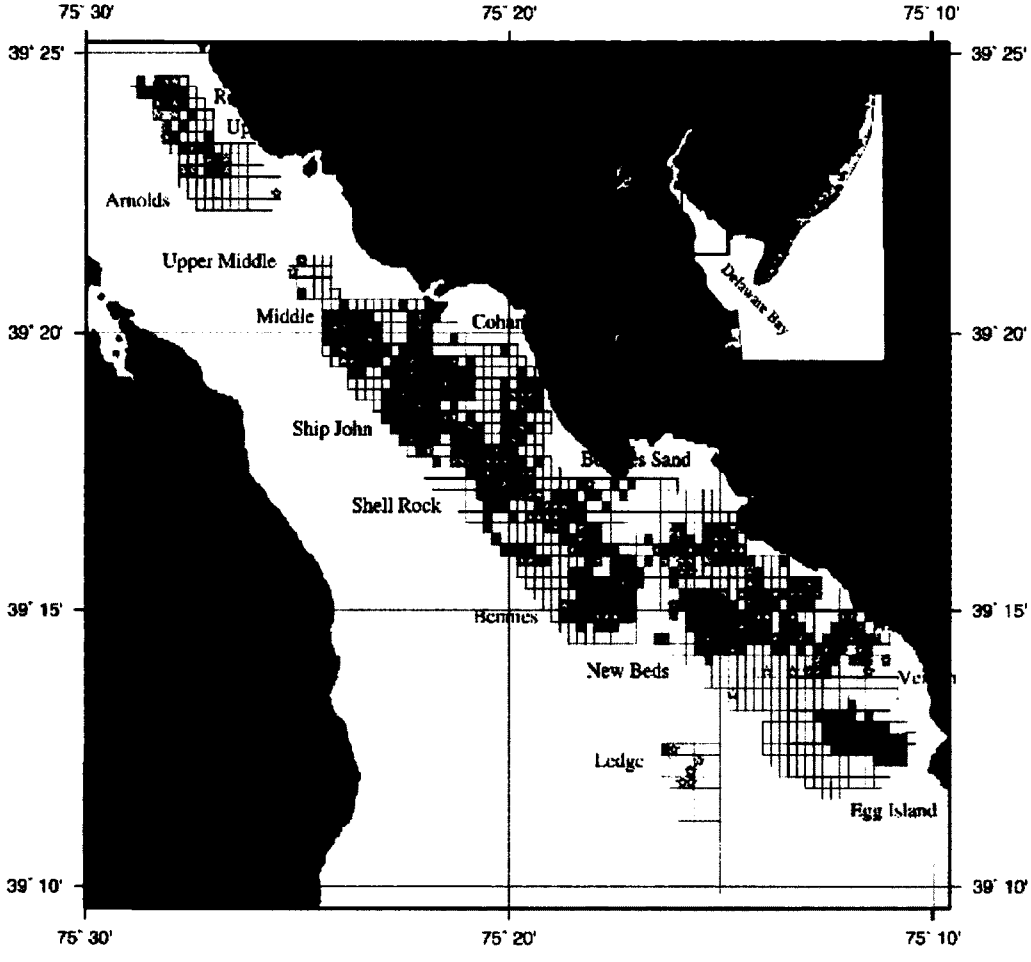

Figure 2. Natural oyster bed distribution in the New Jersey waters of the Delaware Bay estuary (from *Powell et al.*, 2008).

the water column. Once larvae settle and recruit into the population, juvenile and adult development occurs on the sea bed. Oysters are sessile organisms, once the larva settles and attaches to the bottom, the adult become permanently part of that population. Adult oysters have a life span of around 10-20 years for *Ostreas* [*Comfort*, 1957; *Heller*, 1990] and greater than 6 yr for *Crassostrea* [*Comfort*, 1957; *Kirby*, 2000]. Factors such as temperature, salinity, food supply and diseases influence the growth, reproduction and mortality of the populations [*Hofmann et al.*, 1994; *Kennedy*, 1996b] affecting oysters populations abundances. The life cycle begins with the reproduction

in which oysters release eggs and sperm into the water column (spawning) when temperatures are greater than 20°C. Spawning can also be stimulated by chemical stimuli [*Yonge*, 1960]. The spawning is intermittent at intervals of several days [*Korringa*, 1952], with averages of 28×10^6 eggs per spawn [*Davis and Chanley*, 1956]. Once the egg has been fertilized, it develops into a free-swimming veliger larva in less than 24 hours [*Kennedy*, 1996a].

The survival of larvae depends on several factors, such as fertilization success, the effects of siltation on eggs and the earliest larval stages, inherent genetic variability of the larvae, loss from the estuarine system by advection and predation, extremes in environmental conditions, the inability to find a suitable habitat at the time of metamorphosis, and loss during metamorphosis [*Dekshenieks et al.*, 1996; *Kennedy*, 1996a]. The larval development time varies among oyster species, but usually is about 3-4 weeks [*Kennedy*, 1996a]. The development time is also influenced by environmental factors that the larva is exposed to during its planktonic stage [*Dekshenieks et al.*, 1993]. A series of studies have demonstrated that temperature and food [*Loosanoff and Davis*, 1963; *Loosanoff*, 1965; *Laing*, 1995], salinity [*Butler*, 1949; *Davis and Calabrese*, 1964; *Ulanowicz et al.*, 1980], turbidity [*Davis*, 1960; *Huntington and Miller*, 1989] and oxygen [*Widdows et al.*, 1989] are the main environmental conditions affecting oyster larvae development and survival.

Toward the end of the development period, the larva moves downward and seeks a suitable habitat to settle. According to *Galtsoff* [1964] settlement occurs when larvae reach 300 to 350 μm. In the settlement process, cues to initiate and encourage larval settlement are crucial [*Bonar et al.*, 1990]. These cues could include: the presence of adult oysters, clean substrate and adequate current flow [*Crisp*, 1976]. When the larva finds this habitat and cements itself to the oyster bed, it metamorphoses to the adult form. Then, the newly attached oyster (spat) is recruited to the sessile adult population.

2.3 ENVIRONMENTAL EFFECTS ON OYSTER POPULATION DYNAMICS

2.3.1 Reproduction and Spawning

Reproduction and spawning occur during early spring and late summer and is controlled by a combination of factors, such as temperature, salinity and food availability [*Kennedy*, 1996a]. Salinity and food influence directly the adult growth and fecundity and will be discussed in the Adult Growth and Mortality section (see section 2.3.3). The water temperature produces latitudinal differences between estuaries located at the north and south of the population distribution ranges. In the northern estuaries, the reproductive season is shorter than that in most southern estuaries with discrete spawning pulses [*Hofmann et al.*, 1992]. Furthermore, temperature differences seem to affect the number of oyster generations produced every year. In northern estuaries, like Delaware estuary, the reproductive season occurs once per year [e.g., *Barber et al.*, 1991], while, in southern estuaries, like Galveston Bay, oysters may produce multiple spawns each year [*Hayes and Menzel*, 1981]. *C. virginica* spawning time is larger, and more frequent for estuaries in the south (e.g., Galveston Bay) than northern estuaries like Chesapeake Bay [*Dekshenieks et al.*, 1993]. The latter has great implications for the overall survival of the populations, since more spawning produce more larvae in the water column and consequently an increase in the chances of high recruitment.

2.3.2 Larval Development, Mortality, Behavior and Dispersion

Temperature, salinity, food and turbidity play an important role in the development, survival and behavior of oyster larvae (see references above). For organisms with sessile adult life, the fate of the larvae will impact the recruitment rates and populations distributions. Larval models show that the duration of the planktonic larval phase of *C. virginica* is temperature-dependent with warmer water increasing

larval growth rates and decreasing the development time [*Dekshenieks et al.*, 1993]. If warmer waters coincide with periods of high food supply the development time is reduced even more [*Loosanoff and Davis*, 1963; *Loosanoff*, 1965]. Using a numerical model, *Dekshenieks et al.* [1993] estimated that for optimal conditions of temperature, salinity and food (24°C, 25 and 2.0 mg C l^{-1}, respectively) the larval development is between 14 to 25 days. The same study suggests that low salinity increases the development time by 38% in Galveston Bay.

Larval mortality is affected by growth, advection and predation [*Mann and Evans*, 1998]. None of these factors is well understood for marine organisms, especially for the eastern oyster. If larval growth is slow, the larva might never reach a competent size to settle, and then it will die. The same might occur if the larva is advected outside the estuary to cold waters or where no suitable habitat to settle exists. Predation on larvae was studied using a numerical model by *Dekshenieks et al.* [1997] using predation as a closure term. Their study suggests that larval survival depends on the position in the water column where predation occurs. More larval survival is expected if predation occurs in surface waters than if it occurs near the bottom.

Vertical movement of the larva is controlled by the swimming behavior. In the case of oyster larvae, the swimming behavior changes as larval development occurs. Early larval stages have been found to be randomly distributed in the water column and older larval stages appear more frequently near the bottom [*Carriker*, 1951; *Andrews*, 1983a]. Laboratory experiments have also associated swimming rate as a function of temperature and larval size [*Hidu and Haskin*, 1978]. The relationship is linear only for larval sizes less than 115 μm, i.e., swimming speeds increase with the increase in temperature and size. For sizes greater than 115 μm the relationship becomes non-linear. The same experiments show that sinking rates increase exponentially with the increase of larval size. Vertical swimming behavior also depends on the oyster species. For instance, *C. virginica* tends to swim up in the presence of a salinity

gradient whereas *C. ariakensis* tends to swim down [*Newell et al.* 2005, cited by *North et al.* 2008]. Different patterns in the vertical distribution of oyster larvae have been associated with tidal phase and stratification [*Carriker*, 1951; *Kennedy*, 1996a]. In well mixed waters, older larval stages (greater than 2 days) of *C. virginica*, move deeper with increase in age and size [*Andrews*, 1983a]. *Dekshenieks et al.* [1996], using a larval behavior model, suggest that the vertical distribution of larvae is strongly influenced by the vertical structure of the water column, especially for small sized larvae. Oyster larvae are not constantly in motion in the water column [*Hidu and Haskin*, 1978]; they vary the time that they spend swimming in response to variations in the salinity gradient [*Kennedy and Heukelem*, 1986]. Since salinity gradient changes with tides, river discharge and winds, temporal fluctuations of these processes will have an impact on the swimming behavior, vertical distribution, and therefore on the larval dispersion.

The dispersal of oyster larvae is not very well known, but understanding its spatial scales, variability, etc, is fundamental to the dynamics and distribution of the populations. In Chesapeake Bay, *North et al.* [2008], using a coupled larval-physical model, found that in most cases, eastern oyster larvae disperse away from their release location, and do not return to their original population. The success of larvae to encounter a suitable settlement habitat was attributed to river runoff, with high transport success related to low river discharge [*North et al.*, 2008]. The same study shows that larval swimming behavior had a great influence on the dispersal distance and the overall connectivity among the oyster subpopulations. In contrast, in a modeling study in Mobile Bay, *Kim et al.* [2010] suggest that although behavior is important in retaining larvae near the spawning area, the spatial distribution of oyster recruitment might be explained only by physical transport. Especially in the Delaware estuary there is no information about oyster larval dispersion. Most of the attention has been focused on processes affecting the dispersion of Blue crab [e.g., *Garvine et al.*,

1997; *Petrone et al.*, 2005; *Tilburg et al.*, 2005, 2007; *Epifanio and Garvine*, 2001]. A review by *Epifanio and Garvine* [2001] suggests that crab larvae are exported to the continental shelf by the permanent river outflow that occurs in the southern part of the estuary mouth. Many of the larvae are not able to return to the estuary since they are driven southward by the coastal Delaware current. Larvae that escape from this current are retained in the Middle Atlantic Bight by subtidal currents and then are transported back to the estuary by wind-driven events. A retention area with weak currents outside the estuary is an important area to concentrate and retain crab larvae [*Tilburg et al.*, 2007].

2.3.3 Adult Growth and Mortality

As in the other phases of the oyster life-history, temperature, food and salinity are environmental factors affecting growth and mortality of the adult populations. Nevertheless, salinity is one of the most important in determining oyster distributions and reproduction within estuarine regions [*Galtsoff*, 1964; *Dekshenieks et al.*, 2000]. For estuarine species, such as oysters, salinity variations affect respiration and filtration rates [*Loosanoff*, 1953; *Shumway and Koehn*, 1982] causing fluctuations in growth rate and adult mortality. Salinity lower than 10 decreases filtration rates, which determines the amount of food that an oyster ingests, thus decreasing growth and fecundity of the oyster.

The effects of salinity on growth rates have been observed in many estuaries, using numerical models and observations. In the Delaware estuary, growth rates of oysters living in high salinity areas are greater than those living in low salinity regions [*Kraeuter et al.*, 2007]. According to *Wang et al.* [2008], fluctuations between spring and summer oyster growth rates in the Apalachicola Bay are related to salinity. The lowest growth rates occur at the time of lowest salinity, which is induced by maximum river discharge in mid-spring, whereas the maximum growth rates occur

in mid-summer because of high temperature and food supply [*Wang et al.*, 2008]. Modeling studies for post-settlement oysters show an increase in mortality of oysters exposed to low salinity for long periods of time [*Hofmann et al.*, 1992; *Powell et al.*, 1996]. *Powell et al.* [1996] suggest that the effects of salinity on mortality might be higher than those caused by competition, reduced food supply, turbidity and disease. In Galveston Bay, these periods of low salinity are associated with high freshwater inputs in the Bay. *Hofmann and Powell* [1998] present information that suggests that oyster commercial landings decrease as a result of large river discharge in previous year. High salinity also has been related to an increase in oyster mortality in the Apalachicola estuary [*Livingston et al.*, 2000]; therefore, a decrease in the river discharge might have adverse consequences for the oyster populations. This discrepancy might be explained by separating the direct and indirect influences of salinity over the population. Salinity influences directly the filtration rates, and therefore the physiologically associated functions. Indirectly, high salinity is beneficial for organisms that prey upon oysters, and also for the parasites that cause disease in the adult populations.

Adult mortality is influenced by predation, overfishing and diseases. Predation, especially in juvenile oysters, is caused by crabs, oyster drills, starfish and boring sponges. Oysters might use high turbidity waters to escape predation; thus, increases in river discharge are not only important in lowering the salinity, but also in increasing water turbidity. Overfishing has been one factor responsible for the decline of the oyster population [*Rothschild et al.*, 1994]. With the collapse of the oyster fisheries in Chesapeake Bay, problems such as eutrophication begin to occur [*Jackson*, 2001]. Many studies have evaluated and proposed management strategies to recover these fisheries [e.g., *Andrews and Ray*, 1988; *Jordan et al.*, 2002; *Jordan and Coakley*, 2004], yet restoration has not been completely successful.

One of the causes of populations stocks still being low is disease that strongly

influences population abundance of Eastern oyster [*Council*, 2004]. Eastern oyster populations are affected by two diseases: Multinucleated Spore Unknown (MSX) and Dermo, caused by the protozoans, *Haplosporidium nelsoni* and *Perkinsus marinus*, respectively [*Ford and Tripp*, 1996]. Both diseases are affected by temperature and salinity. High temperature and salinity can initiate disease epizootics [*Soniat*, 1996], thus climatic variability is likely to drive variability in the propagation and outbreaks of the diseases [e.g., *Powell et al.*, 1996; *Soniat et al.*, 2005]. For instance, not until 1990 did Dermo disease appear in Delaware Bay, but mortality of Eastern oyster by Dermo had a long record in Chesapeake Bay and estuaries in the Gulf of Mexico [*Ford*, 1996; *Ray*, 1996]. In 1995 Dermo was reported in Maine [*Kleinschuster and Parent*, 1995] and lately in Canada [*Stephenson et al.*, 2003]. According to *Cook et al.* [1998], the northward propagation of Dermo along the US eastern coast, is due to an increase in the winter temperatures. *Ford and Chintala* [2006] show that *P. Marinus* does not adapt to low temperatures, thus the northward propagation of the disease is driven by the recent warming trend in the northeastern US. ENSO cycles also have been associated with Dermo epizootics in the northern Gulf of Mexico estuaries. The decrease in rainfall during La Niña events reduces freshwater input to the estuaries, increasing the salinity which initiates and intensifies Dermo disease in the area [*Soniat et al.*, 2005].

In both Chesapeake and Delaware Bay estuaries, MSX was first observed in the late 1950s [e.g., *Andrews*, 1968; *Haskin and Ford*, 1982; *Ford*, 1996]. Disease epizootics associated with Dermo and MSX have occurred periodically during the last 60 years in the Delaware estuary [*Lafferty et al.*, 2004; *Powell et al.*, 2008]. The largest event occurred in 1985, when an MSX epizootic killed around 47% of the oyster stock. Sudden increases in mortality were observed again with the appearance of Dermo in 1990 [*Powell et al.*, 2008]. The sudden onset of disease in 1985 was caused by a drought that allowed MSX to move upbay killing 70% of the oyster in the low salinity areas.

Low salinity areas have been proposed as refugia for oysters since the parasites causing diseases require high salinity to survive. In the Delaware estuary, the locations of the oyster seed beds are defined by salinity regimes of 0-15 (upper), 10-20 (middle), 15-30 (lower). Population characteristics generally increase or decrease along this gradient with salinity and food as the dominant controls. Thus, the upper estuary and rivers are considered refugia areas for oysters. The prevalence of MSX decreased after the 1985 epizootic, suggesting that the oysters that repopulated the estuary were mostly lower bay populations that had developed disease resistant genes.

CHAPTER 3

MODELING THE DISPERSAL OF EASTERN OYSTER (*CRASSOSTREA VIRGINICA*) LARVAE IN DELAWARE BAY

3.1 INTRODUCTION

The pelagic phase of the life cycle of the Eastern oyster (*Crassostrea virginica*) typically lasts from 15 to 25 days [*Kennedy*, 1996b], during which time the larvae are part of the plankton. Oyster larvae have an ontogentic behavior in which older larvae swim upwards on the flood tide in response to increased salinity and sink downwards on the ebb tide in response to decreased salinity [*Carriker*, 1951]. The nonuniform vertical distribution resulting from this behavior interacts with the estuarine circulation to disperse oyster larvae throughout the estuary. As a result, at metamorphosis when the larvae set and become part of the sessile population, they may recruit to areas that differ from their spawning location. The final location of oyster larvae is then the result of circulation (passive) and larval growth and behavior (active migration) processes, both of which are modified by local environmental conditions.

The oyster population in Delaware Bay is distributed in reefs that cover a salinity gradient that ranges from about 5-10 in the upper bay to 25-30 in the lower reaches of the bay (Figure 1). As a result larvae spawned from these reefs will experience a gradient in salinity and also food concentration, both of which are important factors regulating the growth and development of Eastern oyster larvae [*Dekshenieks et al.*, 1993]. Thus, an along-Bay gradient in growth and behavioral responses of oyster larvae will contribute to variability in dispersion and ultimate settlement locations.

The comprehensive study of Eastern oyster larvae presented in *Carriker* [1951] was developed around the premise that the horizontal distribution of the larvae directly affects the location of natural oyster beds and the extent to which setting of

oyster juveniles occurred on these beds. Quantitative surveys of Delaware Bay oyster populations have been ongoing since 1953, which has allowed relationships between broodstock abundance and recruitment to be examined [*Powell et al.*, 2008]. This analysis showed variability in recruitment to different parts of Delaware Bay and suggested that the frequency of good recruitment events increased down-bay and that sporadic recruitment occurred on the Delaware side of the bay. Thus, the larval source regions, the conditions that allow larvae to arrive at particular locations, and the controls exerted on larval growth and development at local as well as Bay-wide scales interact to determine where and when larvae set. The degree of interaction among these many factors underlies the significant seasonal and interannual variations observed in recruitment to Delaware Bay oyster populations.

In this study the interactions of circulation and growth processes in determining the horizontal distribution of oyster larvae in Delaware Bay were investigated with a coupled circulation-oyster larvae model. Specific research objectives focused on understanding variability in larval growth and development in response to along-bay gradients in temperature and salinity, the dominant transport pathways for larvae, and the exchange of larvae between reef areas of Delaware Bay. These objectives are integral to the science goals of the Delaware Bay Ecology of Infectious Diseases initiative which is focused on understanding how oyster populations in Delaware Bay respond to diseases, climate, and environmental and biological variability [*Hofmann et al.*, 2009].

The next section provides a description of Delaware Bay and the models used in this study. This is followed by descriptions of the simulations and results. The discussion section places the simulation in the context of what is known about oyster distributions in Delaware Bay.

3.2 METHODS

3.2.1 Circulation and Larval Models

In this study, a coupled circulation-oyster larvae model provided the framework for determining the relative effects of circulation (advection and diffusion), environmental conditions (temperature, salinity, food and turbidity), and biological processes (growth, development and swimming behavior) on oyster larvae dispersal pattern and primary transport pathways. The circulation model is described in detail by *Wang et al.* [2012], and only a general description is presented here. The oyster larvae growth and behavior model is described in *Dekshenieks et al.* [1993, 1996] and a brief summary is given below to indicate the connections to the circulation and environmental conditions.

3.2.1.1 Circulation Model

The hydrodynamic circulation model is based on the Regional Ocean Model System (ROMS) version 3.4 (www.myroms.org). This model is a free-surface, hydrostatic, primitive equation model that uses terrain-following coordinates [*Shchepetkin and McWilliams*, 2005]. The model was configured and calibrated for the Delaware estuary and its adjacent continental shelf [*Wang et al.*, 2012]. The domain consists of a curvilinear grid with horizontal resolution ranging from 0.2 km in the small areas (e.g. rivers) to 2.1 km in the shelf. Vertical processes are represented using sigma coordinates with 20 vertical levels with resolution of ~0.03 m in the shallow areas and ~6.2 m in the deep areas.

Model forcing includes freshwater input from six major tributaries of Delaware estuary that was obtained from USGS gauge measurements. The air-sea fluxes estimated from distributions obtained from the North America Regional Reanalysis [*Mesinger et al.*, 2006]. Open ocean tides are taken from a regional tidal model

[*Mukai et al.*, 2001]. Initial conditions consist of a flat sea surface, vertically uniform salinity with an along-estuary gradient, and constant temperature. Validation of the circulation model against water level, temperature and salinity observations was done using observations from 1984/1985/1986, 2000/2001, and 2005, and is described in [*Wang et al.*, 2012].

3.2.1.2 Larval Growth-Behavior Model

The larval model was developed by *Dekshenieks et al.* [1993, 1996] to estimate the vertical and time-dependent distribution of a cluster of oyster larvae of a given size. For this research, this cluster-based model was adapted to an individual-based model to simulate development and vertical behavior of each larva released in the circulation field. The larval model is composed of 2 sub-models to simulate larval growth and the behavior of larvae.

The larval growth sub-model estimates the time rate of change of larval size (dS/dt) for each oyster larva based on temperature, salinity, food supply and turbidity, following the relationship:

$$\frac{dS}{dt} = growth(food, size) \times tsfactor \times turbeff, \tag{1}$$

where *growth(food,size)* corresponds to the growth rate calculated for different larval sizes and under variable concentrations of food and *ts factor* and *turbeff* correspond to the effects of temperature and salinity, and turbidity, respectively. These effects have been parameterized using laboratory experiments and observations summarized in lookup tables [*Dekshenieks et al.*, 1993]. Minimal larval growth occurs at low temperature, salinity, and food supply. Growth increases with high temperatures, salinities of 17.5-25, and food concentrations >3.0 mg C l^{-1}. The parameters and relationship to estimate the effect of turbidity are given in Table 1.

Table 1. Relationships used to estimate the effect of turbidity on oyster larval growth.

Equation	Condition	Parameters
$turbeff = m\ turb + c$	< 0.1 g l^{-1}	m= 0.542 $(g\ l^{-1})^{-1}$ c= 1.0 $(g\ l^{-1})^{-1}$ $turb$ (ambient turbidity)
$turbeff = be^{-\beta(turb-turb\theta)}$	$> 0.1g\ l^{-1}$	$b = 0.375\ (g\ l^{-1})^{-1}$ $\beta = 0.5\ (g\ l^{-1})^{-1}$ $turb\theta = 2.0\ g\ l^{-1}$

The larval behavior sub-model [*Dekshenieks et al.*, 1996] calculates the vertical velocity of oyster larvae as a function of swimming rate (SW), sinking rate (SR), and the fraction of activity of the larvae (TS) using,

$$W_{bio} = TS \times SW - (1 - TS) \times SR \tag{2}$$

The swimming rate has been calculated from laboratory experiments showing a non-linear dependency on temperature and larval size. Larval sinking rate ($mm\ s^{-1}$) is directly proportional to larval size, and it is prescribed as $SR = 2.665e^{0.0058(SZ-220)}$, where SZ is the larval size in microns (μm). Oyster larvae combine periods of upward motion with periods of rest based on the changes of salinity gradient. The relationships to estimate the fraction of activity of the oyster larvae are presented in Table 2. According to laboratory experiments, the fraction of swimming time varied between 0.83 and 0.64 [see *Dekshenieks et al.*, 1996, for more details].

Table 2. Relationships used to estimate the effect of salinity changes on oyster larval behavior.

Equation	Condition	Parameters
$TS = c\Delta S + d$	Increasing salinity	c= 0.0622 $\frac{fraction\ active}{time \times \Delta S}$ d = 0.3801 % *activity* ΔS (Salinity gradient)
$TS = -e\Delta S + f$	Decreasing salinity	e = 0.0668 $\frac{fraction\ active}{time \times \Delta S}$ f = 0.7515 % *activity*

3.2.1.3 Coupled circulation-larval model

A particle tracking module is available in ROMS in which the trajectory of the particles ($\vec{X}$) is related to the velocity of the particle ($\vec{U}$) for each time step (dt) following,

$$\frac{d\vec{X}}{dt} = \vec{U}(\vec{X}, t). \tag{3}$$

Additionally, the ROMS lagrangian module interpolates variables such as temperature and salinity to the location of each particle at each model time step (30s) in these simulations.

The larval behavior sub-model is coupled with the vertical displacement of the particle by adding W_{bio} (eq. 4) to the vertical component of eq. 3,

$$\frac{dz}{dt} = w(z,t) + W_{bio}(z,t) \tag{4}$$

Horizontal larval swimming velocities are neglected because they are several orders of magnitude slower than horizontal currents [*Gaylord and Gaines*, 2000; *Pfeiffer-Hoyt*

and McManus, 2005, e.g.]. Since swimming and sinking rate depend on the larval size (see section 3.2.1.2), eqs. 1 and 4 are solved simultaneously at each circulation model time-step. Optionally, the vertical mixing due to sub-grid-scale turbulence is also included in the vertical displacement by the particle tracking module in ROMS as a random vertical walk ($Vwalk$) [*Hunter et al.*, 1993; *Visser*, 1997]. A fourth-order Milne predictor and a fourth-order Hamming corrector scheme are used to solve eqs. 1 and 4. When $Vwalk$ is activated, eq. 4 also can be solved using the predictor-corrector scheme only in the horizontals components of eq. 3 and a simple forward scheme in the vertical component.

A settlement condition was added to the model, such that the larva stops moving and attaches to the bottom when its size reaches 330 microns [*Dekshenieks et al.*, 1993]. Space and time variable food and turbidity for Delaware estuary are inadequatelu known to support model simulations; so, a constant food concentration of 4 mg C l^{-1} and turbidity of 0 g l^{-1} were imposed.

3.2.2 Simulations

3.2.2.1 Simulation design

Particles were released in the simulated flow fields at locations that correspond to the primary oyster reefs in the upper and middle portions of Delaware Bay (areas 2 to 7 in Figure 3). Additional release sites were included in lower Delaware Bay (area 1 in Figure 3) and along the Delaware side of the Bay (area 8 in Figure 3) where less extensive oyster reefs exist. Spawning of Eastern oysters in mid-latitude bays such as Delaware Bay occurs from mid-June to mid-September [*Thompson et al.*, 1996]. Particles were released at five-day intervals during this time to simulate a total of 18 spawning events. For each event, 200 particles were released near the bottom at each site, resulting in a total of 36,000 particles released over the entire season. The particle release numerical experiments were done for each of the five years for which

the Delaware Bay circulation model has been validated [*Wang et al.*, 2012]. The Bay was sub-divided into fifteen regions (areas 1 to 15 in Figure 3) for analysis of patterns of larval settlement based on the Lagrangian trajectories.

The sensitivity of the simulation results to a constant food value of 4 mg C l^{-1} was tested by reducing the food by half (2 mg C l^{-1}) and repeating the simulation that used conditions from 2000 (Table 3). The effect of turbidity was examined by increasing the turbidity to 0.2 g l^{-1}, which is an average value measured for the upper-middle estuary [*Cook et al.*, 2007], and repeating the simulation with conditions from 2000. Finally, the settlement condition was tested by using a smaller size of 270 and 300 μm. For each perturbation simulation, the average larval success for each release location was estimated and connectivity matrices were computed and both were compared to previous results to determine changes in success and exchange rates.

Table 3. Simulations performed to test sensitivity of the model to changes in some of the parameters used.

Food mg C l^{-1}	Settlement Size μm	Turbidity g l^{-1}	Simulation Code
2	330	0	f2,s330,t0
4*	330	0	f4,s330,t0
4	270	0	f4,s270,t0
4	300	0	f4,s300,t0
4	330	0.2	f4,s330,t0.2

*Reference simulation

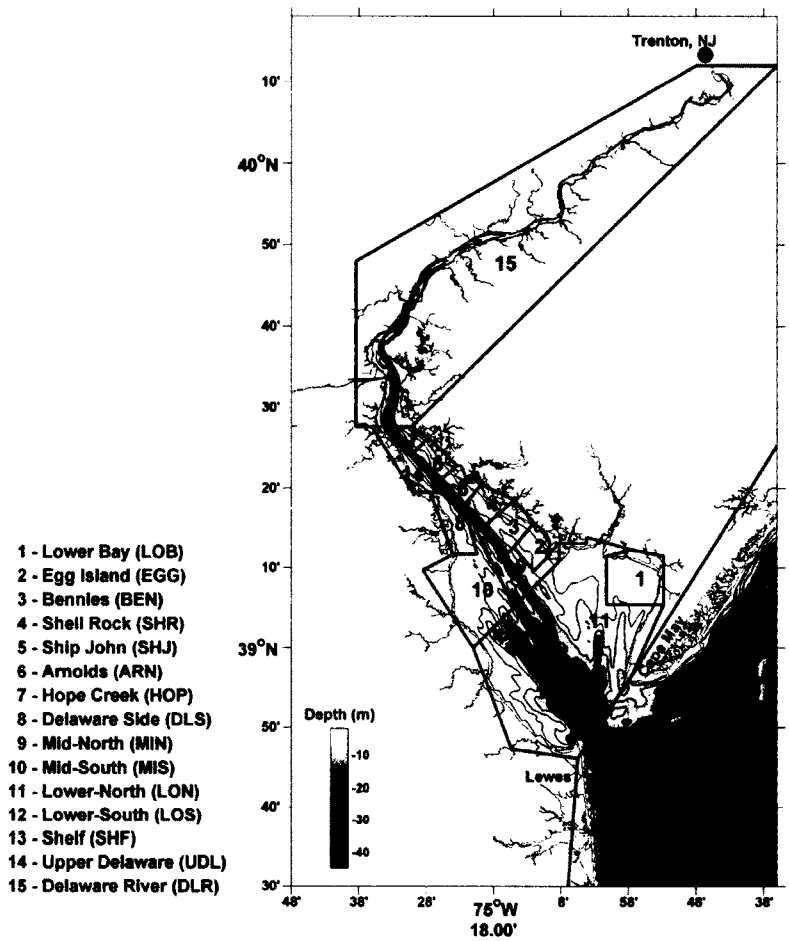

Figure 3. Study area showing the release and settlement locations used in the simulations. The sites used to release particles in the simulated flow fields (regions 1-8) generally correspond to the locations of natural oyster reefs in Delaware Bay (see listing). These release sites and an additional seven regions (regions 9-15) were used to analyze the settlement patterns obtained from the Lagrangian particle tracking simulations. River discharge measurements were obtained from USGS gauges at Trenton, NJ. The air temperature 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.

3.2.2.2 Lagrangian trajectory analysis

In mid-latitude systems, such as the Delaware estuary, Eastern oyster larvae usually reach a settlement size within 30 days [*Kennedy*, 1996b]. Thus, larval success was defined as the percent of the total released larvae that developed to settlement size within 30 days and was calculated for each release location and spawning event (release time). The percent success values obtained for each release time and location for an individual year were averaged to obtain a single metric of success and these were then compared across the five years using a one-way ANOVA to assess inter-annual differences in larval success. All possible pairs of means were then compared with a Tukey's honest significance test to determine which years were significantly different.

The dispersion and exchange of oyster larvae among the different regions of Delaware Bay was examined using connectivity matrices. The connectivity matrix shows the percent of larvae arriving at a particular location in terms of the total larvae that were released at another location. Only the larvae that reached settlement size within 30 days were included in these calculations.

3.2.2.3 Delaware Bay oyster data and model evaluation

Measurements of oyster larvae settlement and recruitment have been made at 30-35 sites distributed throughout the New Jersey and Delaware portions of Delaware Bay at yearly intervals from 1954 to 1986 [see details in *Fegley et al.*, 2003; *Powell et al.*, 2008]. Settlement counts were collected for the spawning season in each year using wire mesh bags, suspended just above the bottom, which contained clean oyster shells. The shell bags were replaced every week between late June and the end of August and every two weeks until early October. Each shell was examined under a microscope to count the newly settled oyster (spat) and age estimates of the spat were used to determine settlement time. The mean number of spat per shell was

calculated for each station; the means of each shell bag replaced for each station were summed and expressed as the mean cumulative spat count per shell for each station during each spawning season. The means from the sampling sites for all years were used to obtain a long-term pattern of the oyster larvae settlement in Delaware Bay. A similar mean was calculated for equivalent regions of Delaware Bay from the simulated particle settlement locations.

Oyster surveys in the New Jersey waters of Delaware estuary have been ongoing at yearly intervals from 1953 to present [*Powell et al.*, 2008]. These data have been used to provide an estimate of oyster recruitment. For this study, recruitment data from 1983 to 1989 and from 1996 to 2009, which correspond to the simulation time periods, were used to estimate the ratio of spat to adult (oysters $>$ 1-yr) for four sites in Delaware Bay: Arnolds, Ship John, Shell Rock and Bennies (site locations on Figure 3). For each region, a mean and probability of the spat abundance exceeding 50% of the total adult oyster abundance were estimated (Table 4). Similar statistics were computed from the simulated particles.

Table 4. Ratio of spat to adult oyster, a measure of recruitment, obtained from measurements made at four sites in Delaware Bay (locations are shown on Figure 3). The mean recruitment ratio was calculated from the measurements at the four sites for each year. The equivalent ratio was calculated from the same four sites for the five years used in the simulations. The total mean for each year and the mean obtained using only the five years (5-yr values) that correspond to the simulation times are shown.

Year	Arnolds	Ship John	Shell Rock	Bennies	Observed Mean	Simulated Mean
1983	0.12	0.26	0.53	0.53	0.36	
1984	0.002	0.03	0.04	0.08	0.04	4.0
1985	0.09	0.69	1.21	1.30	0.82	4.5
1986	1.16	5.08	10.73	2.33	4.83	4.7
1987	0.51	1.42	2.23	2.29	1.61	
1988	0.27	0.24	0.34	1.09	0.49	
1989	0.16	0.33	0.21	0.90	0.40	
1996	0.19	0.08	0.09	0.12	0.12	
1997	0.2	0.73	0.92	3.06	1.23	
1998	0.92	2.13	1.64	2.03	1.68	
1999	0.59	2.17	4.04	4.54	2.84	
2000	0.15	0.2	0.79	1.08	0.56	4.6
2001	0.05	0.09	0.22	0.44	0.20	4.1
2002	0.2	0.54	4.59	0.86	1.55	
2003	0.05	0.17	0.38	1.28	0.47	
2004	0.05	0.28	1.85	2.07	1.06	
2005	0.31	0.2	0.46	0.54	0.38	
2006	0.14	0.32	0.32	0.42	0.30	
2007	0.18	1.63	1.53	2.54	1.47	
2008	0.22	0.11	0.5	0.89	0.43	
2009	0.15	0.82	1.89	2.53	1.35	
Total Mean	0.27	0.83	1.64	1.47		
Total # >0.5	4	9	12	17		
5-yr Mean	0.29	1.22	2.59	1.05		

3.3 RESULTS

3.3.1 Environmental effects on larval development and success

Particles, representing oyster larvae, were released in three regions of the Delaware estuary that span the observed salinity range and summer temperature gradient for this system (Figure 4). Ten days after release, larvae released from the low salinity region (Hope Creek) were half the size of those released in the higher salinity Lower Bay region (Figure 4a and c). Larvae released in the mesohaline central portion of the Bay (Shell Rock) were of intermediate size (Figure 4b). After 20 days, differences in larval size in the three salinity zones were more pronounced (Figure 4d-f). Larvae that remained in the upper-most part of the estuary were $\sim$100 μm smaller than those just a few kilometers down estuary (Figure 4d and e). Larvae released in the Lower Bay that remained in the warmer and higher salinity waters along New Jersey were larger than those that moved to the center of the lower estuary (Figure 4f) and were considerably larger than those in the upper estuary regions. At 30 days, the larvae released in the upper Bay remained small (Figure 4g) and had not reached settlement size. Most of the larvae released in the mid and lower regions reached settlement size (Figure 4h and i). The differences in larval size, and hence growth, affected larval dispersion. The larvae released at Shell Rock in the mid-reaches of Delaware Bay (Figure 4b) were broadly dispersed; whereas, those released at the Hope Creek and Lower Bay sites were less dispersed (Figure 4a and c).

To further analyze the effect of temperature and salinity on oyster larvae, the averages of the temperature and salinity values encountered by successful larvae during their trajectory were calculated for each release time at each release site from the simulations done for each of the five years (Figure 5a and b). These averaged environmental conditions were then compared to the percentage of larvae that were successful (Figure 5c). On average, larvae experienced similar along-estuary temperatures for

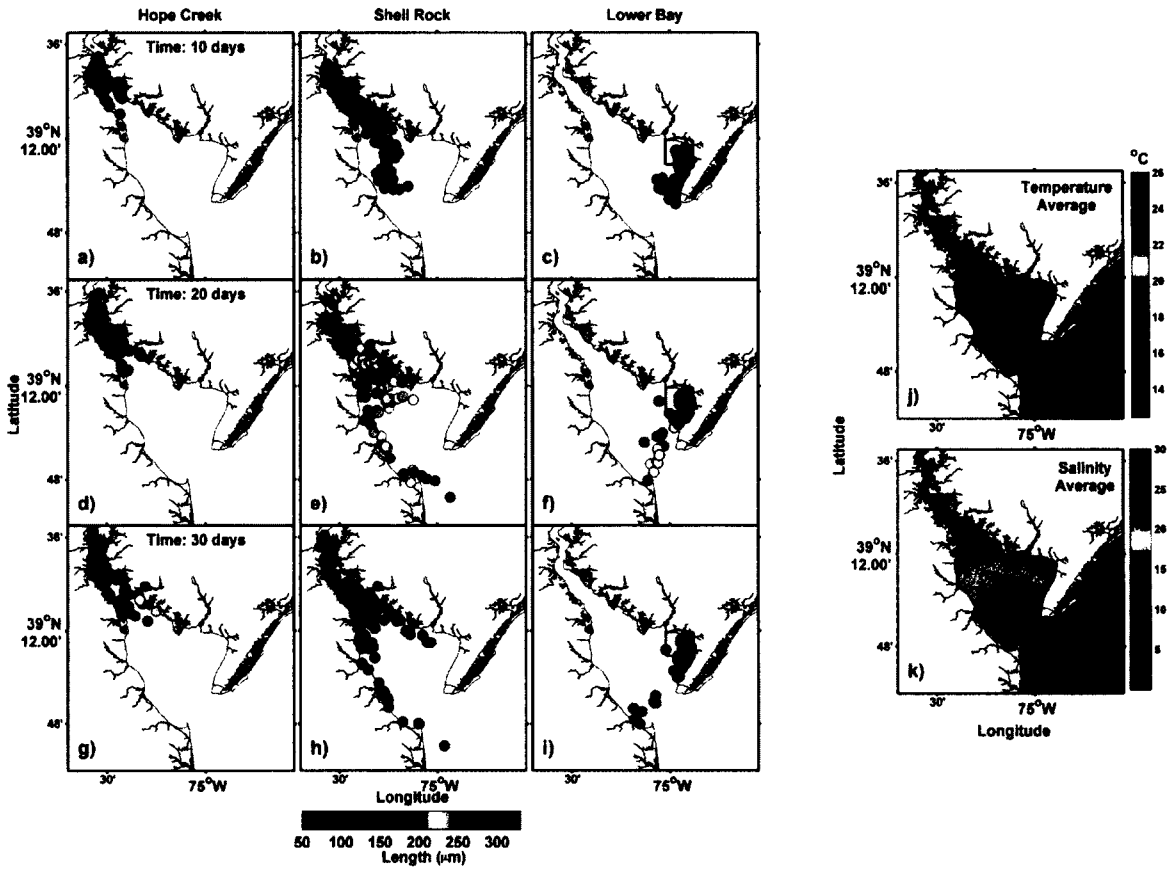

Figure 4. Dispersion and development, indicated as length, distribution for larval particles at 10 days (a-c), 20 days (d-f), and 30 days (g-i) post release on 15 June 2000. Particle release locations (red outlined area) correspond to low (Hope Creek, a, d, g), moderate (Shell Rock, b, e, f) and high (Lower Bay, c,f, i) salinity conditions. The 30-day depth-averaged temperature and salinity corresponding to the release date are shown (panels to right).

the same release time (Figure 5a), suggesting that vertical and horizontal temperature variability along the estuary is small. Larvae released from the Lower Bay and Egg Island regions (locations on Figure 3) had success rates greater than 80%, independent of the release time (Figure 5c). Larval success rates decreased toward the upper estuary, with less than 20% of the larvae released from Hope Creek reaching

settlement size in any year. The percentage success was higher during mid-July and mid-August, when maximum temperatures occurred (Figure 5a and c). Spearman correlations between the bay-wide average temperature and percentage larval success were low, but statistically significant, for all years (Table 5). Thus, larvae exposed to warm temperature had higher success rates and vice versa.

Salinity in Delaware Bay has a clear along-estuary gradient which is generally low in the upper estuary and high in the lower estuary (Figure 5b). Superimposed on this spatial gradient is a temporal variation with higher salinity occurring later in the summer (Figure 5b). The percentage of larval success increased down-estuary in association with this salinity gradient (Figure 5c). The Spearman correlations gave high correlations between salinity and percentage of larval success (Table 5), suggesting that salinity is more important than temperature in determining larval success in Delaware Bay.

Table 5. Spearman's correlations calculated between percentage larval success and the average temperature and average salinity encountered along the particle trajectories for each simulation year. All correlations are significant ($p < 0.05$).

	1984	1985	1986	2000	2001
Success vs. Encountered salinity	0.68	0.84	0.85	0.74	0.80
Success vs. Encountered temperature	0.24	0.21	0.21	0.20	0.27

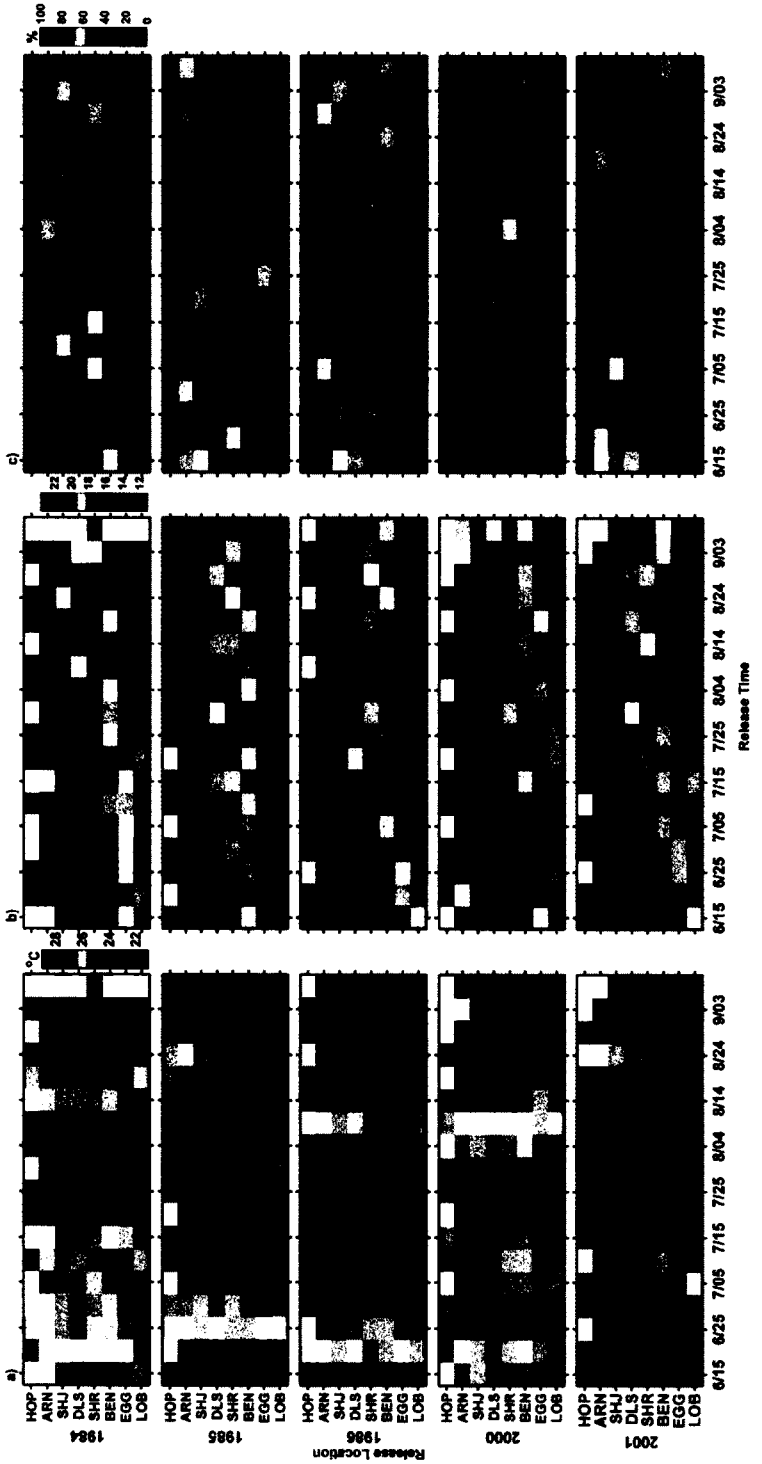

Figure 5. The distribution of the average a) temperature, b) salinity encountered by successful larvae along the particle trajectories and c) larval success for each release site and release time for each of the simulation years. Average temperature and salinity could not be calculated for locations and time when larval success was zero (white regions in a) and b).

Environmental conditions varied between the simulation years. Temperature was typically above 18°C throughout the spawning season in all years, but periods with temperature above 20°C varied between the years (Figure 5a). In 1984, water temperatures remained cool until mid July and cooled again in late August. The spawning season in 1986 was characterized by a short period of temperatures above 22°C that extended throughout the Bay. During 2000 and 2001 water temperatures warmed above 18°C early in the spawning season and remained consistently warm throughout the Bay until mid to late August. The overall temperature means showed that larvae encountered cooler waters during 1984 and 2000 than in other years (Table 6).

Table 6. Means and standard deviations calculated from the simulated values encountered along the simulated trajectories averaged over all sites in Delaware Bay between mid-June and mid-September for each simulation year. Larval success is determined by the number of larvae reaching 330 μm in 30 days relative to the total number released. Temperature and salinity averages are based on those encountered by a particle along its trajectory. River discharge is based on that for the Delaware River. Air temperature was obtained from the North American Regional Reanalysis (NARR) product for the Delaware Bay region.

	1984	1985	1986	2000	2001
Larval success	60.6±34.4	74.2±28.9	69.9±32.3	61.8±35.2	72.7±31.3
Salinity	17.6±2.6	18.2±2.7	17.8±2.5	16.6±2.6	17.6±2.6
Temperature	26.1±1.3	26.5±1.1	26.3±2.1	25.9±1.2	26.8±1.1
River discharge	239±136	144±70	170±45	221±58	120±31
Air temperature	21.8±1.5	22.6±1.2	22.7±2.1	21.5±1.2	22.3±1.3

The salinity encountered by larvae was high, greater than 20, in the lower reaches of Delaware Bay and decreased to values less than 12 in the upper Bay (Figure 5b). Over a spawning season, maximum salinity occurred in August and September in the lower to mid-regions of the Bay. Interannual differences in salinity were most pronounced in June and early July at the beginning of the spawning season. In the early part of the spawning season for 1984, 1986 and 2000, larvae released at Shell Rock, Bennies and Egg Island encountered salinities less than 20 (Figure 5b), which is below the value for optimal growth [*Dekshenieks et al.*, 1993]. The mean of the encountered salinity was highest for the larvae released in 1985 and lowest for those released in 2000 (Table 6).

The percent larval success rate showed along-Bay and temporal variability, with higher success occurring in the lower reaches of the Bay and later in the spawning season (Figure 5c). Overall success in 1984 and 2000 was about 10% lower than that obtained for 1985, 1986 and 2001 (Table 6). Testing with a one-way ANOVA showed that the interannual differences in temperature, salinity and success rate means were statistically significant (Table 7). A multiple comparison test, using the Tukey's honestly significant difference criterion, showed that the mean temperature and salinity encountered along a trajectory during 2000 was statistically different from that encountered in 1985 and 2001 (Figure 6a and b). The larval success means for 1984 and 2000 were statistically lower than the means for 1985 and 2001, at 95% of significance (Figure 6c).

Time series of measured air temperature and Delaware River discharge averaged at 30-day intervals (Figure 7) were compared with the average temperature and salinity encountered by the larvae for each year. The air temperature showed increasing values from June until early August, after which temperature decreased (Figure 7a). The timing and duration of the maximum temperature varied from year-to-year (Figure 7a). River discharge showed considerable year-to-year variation in magnitude and

Table 7. Results from the one-way ANOVA used to test the significance of temperature and salinity encountered along a particle trajectory, air temperature and river discharge on the percentage of larval success. The total number of data points used in the analysis was 144.

	Sum of Squares	Degrees of Fredoom	Computed F	Significance level (p)
Larval success	1055.8	715	5.4	10^{-5}
Encountered salinity	6.8	580	5.7	10^{-5}
Encountered temperature	2.0	580	7.8	10^{-6}
River discharge	5.9×10^{3}	85	7.6	10^{-6}
Air temperature	2.2	85	2.2	0.07

timing (Figure 7b). The lowest mean air temperature occurred in 2000, which coincided with the lowest encountered temperatures (Table 6). Comparisons of the air and water means using Spearman correlations showed these to be statistically significant in all years at all the release sites (Table 8). However, there were no significant interannual differences in mean air temperature (Figure 6d).

The relationship between river discharge and encountered salinity was less clear (Table 8). Lower salinity was encountered early in the 1984, 1986 and 2000 spawning seasons (Figures 5b and 6b). The mean river discharges were highest during the early summer of 1984 and 2000, but normal in 1986 (Figure 7b). Spearman correlations between encountered salinity and river discharge were not significant for most years and release locations, with exception of some release locations during 1984, 1986, 2000 and 2001 (Table 8). The lack of correlation may result from the low variability and small discharge during the summer in most years (Figure 7b), suggesting that differences were driven for only a few events of high river discharge during 1984 and

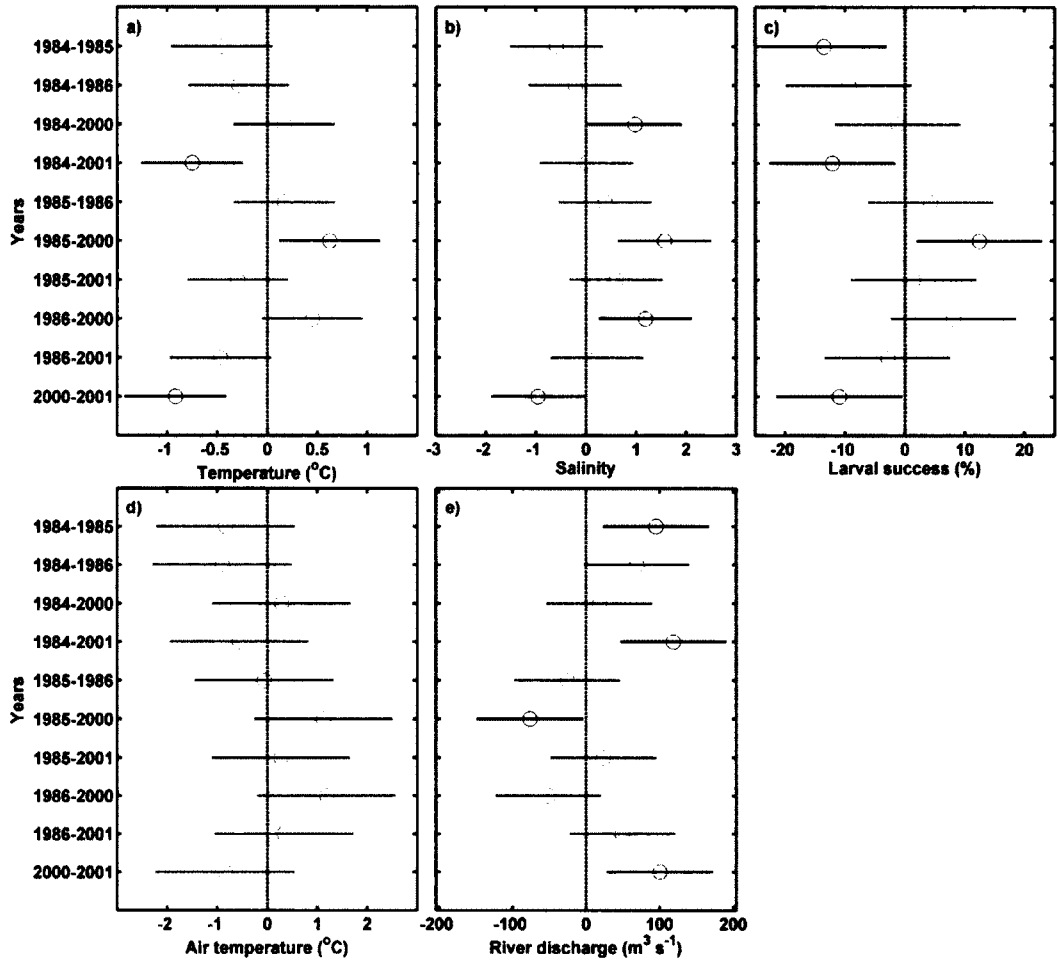

Figure 6. Comparison of the difference between means (o) of different year-pairs (Table 7) for a) average temperature encountered along the particle trajectories, b) average salinity encountered along the particle trajectories, c) larval success, d) air temperature and e) river discharge obtained from the Tukey's honest significance test. The 95% confidence interval is shown and comparisons for which the confidence interval does not include zero are statistically significant (denoted by heavier lines).

2000. Significant interannual differences in river discharge were found for 1984 and 1985, 2000, and 2001 (Figure 6e). These times correspond to significant interannual differences in the percentage larval of success (Figure 6c), suggesting that the lower percentage larval success in 1984 and 2000 may be related to high river discharge. The

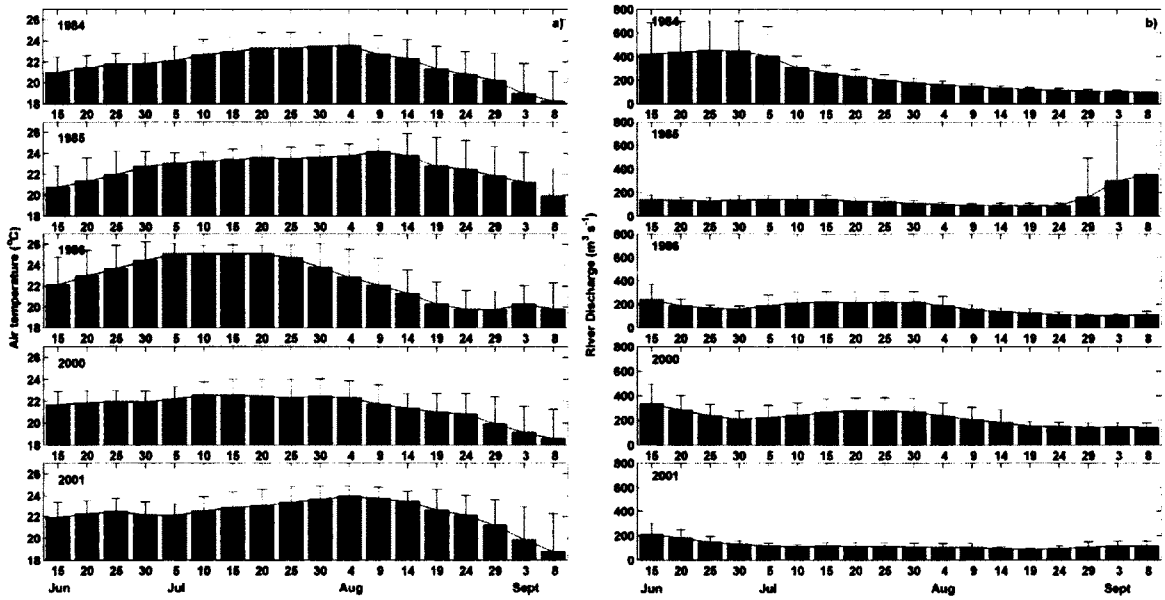

Figure 7. The 30-day averages of a) air temperature and b) river discharge during the oyster spawning season for the five years used in this study. The error bar associated with the averages is shown.

increase in percentage larval success in 1985 and 2001 corresponds to times of low river discharge (Figure 6c and e). An increase in river discharge did not necessarily indicate that successful larvae encountered low salinities. For example, the differences between 1984-2000 and 1986-2000 seemed not to be related to the corresponding increase in river discharge (Figure 6b and e).

3.3.2 Larval dispersion and exchange

For the years included in this study, the simulated larvae typically reached a competent size to settle over the shoals and in the upper and the north region of the lower estuary (Figure 8). Few of the simulated larvae settled in the center of the lower estuary, and almost no larvae were exported from the lower Bay to the adjacent continental shelf. This general pattern occurred in all simulation years, with little

Table 8. Spearman's correlations between air temperature and average temperature encountered along the particle trajectories and between river discharge and average salinity encountered along the particle trajectories for particles released from the indicated oyster reefs (locations shown on Figure 3) for each simulation year. Significant correlations are indicated by bold text.

	HOP	ARN	SHJ	DLS	SHR	BEN	EGG	LOB
Air temperature vs Encountered temperature average								
1984	**0.90**	**0.91**	**0.93**	**0.93**	**0.92**	**0.89**	**0.88**	**0.89**
1985	**0.83**	**0.85**	**0.84**	**0.79**	**0.86**	**0.84**	**0.84**	**0.83**
1986	**0.96**	**0.94**	**0.94**	**0.95**	**0.93**	**0.91**	**0.93**	**0.91**
2000	**0.70**	**0.88**	**0.91**	**0.74**	**0.84**	**0.87**	**0.84**	**0.73**
2001	**0.95**	**0.92**	**0.91**	**0.89**	**0.89**	**0.83**	**0.81**	**0.82**
River discharge vs Encountered salinity average								
1984	-0.15	-0.40	**-0.76**	**-0.83**	**-0.86**	**-0.83**	**-0.85**	**-0.74**
1985	0.39	0.34	0.33	0.10	0.23	-0.03	0.34	-0.08
1986	-0.05	-0.36	-0.23	-0.09	-0.16	-0.24	-0.26	**-0.56**
2000	0.47	-0.31	-0.36	**-0.69**	-0.41	-0.26	-0.25	-0.40
2001	-0.08	-0.30	-0.30	**-0.62**	**-0.48**	**-0.55**	**-0.50**	-0.32

interannual variability.

The dispersal of oyster larvae between areas of Delaware Bay was determined using connectivity matrices that were calculated as the percent of successful larvae released during the spawning season from specific points in the estuary that settled in the release region or in different locations (Figure 9). The connectivity matrices provide estimates of exchange rates of individuals between different regions of Delaware Bay. The general pattern of exchange rates was similar for the simulation years, but the

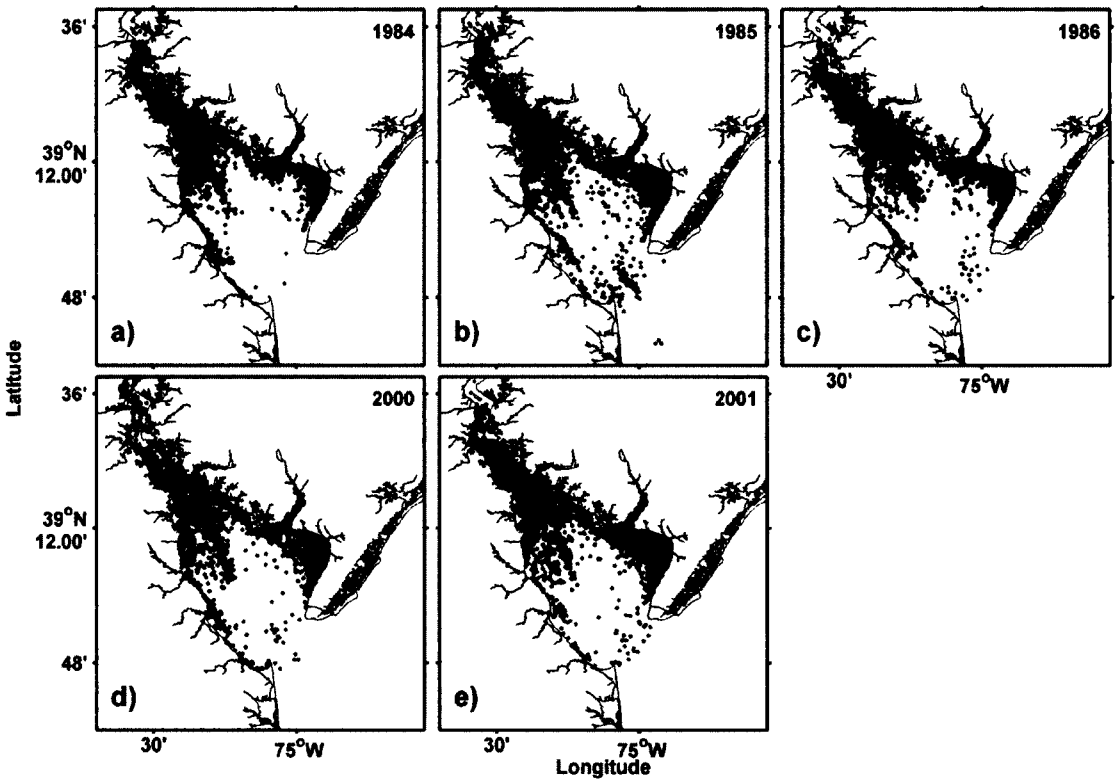

Figure 8. Distribution of settlement locations for all successful larvae released in the spawning seasons of a) 1984, b) 1985, c) 1986, d) 2000 and e) 2001.

magnitude of the exchanges varied from year-to-year (Figure 9). The lowest exchange rates occurred in the upper reaches of Delaware Bay (e.g., Hope Creek) where fewer than 5% of all larvae reached settlement size within 30 days. The small number of successful larvae originating in this region were transported down-Bay and contributed to populations at Ship John and Arnolds in the central Bay. Larvae originating at Arnolds and Ship John tended to remain in the region and settle at their origination site. These sites also exported a large percentage of larvae down-Bay as far as Egg Island, and also exported a small percentage of larvae up-Bay. For larvae originating in the Egg Island region, fewer than 10% settled at this site or at adjacent oyster reef sites. The majority of the larvae were exported down-estuary, with more than 50% of the initial larval pool reaching settlement size in the Lower-North and Lower Bay regions (Figure 9). The Lower Bay region received small inputs of larvae from the upper and middle portions of Delaware Bay. Larvae released in the Lower Bay mostly remained in the region. Less than 1% of the larvae originating in this region had the potential to settle in the upper estuary regions. Of the natural oyster reefs, Hope Creek and Egg Island have low rates of self recruitment and receive small inputs from other regions of Delaware Bay. Larvae originating in these regions tend to be exported. The reef areas along the Delaware side of the Bay and Lower Bay regions showed high rates of self recruitment. However, the magnitude of this recruitment is partially determined by the size of the regions used in the analysis (Figure 3). For example, a large percentage of the larvae released between Bennies and Ship John reached settlement size in the larger regions used for assessing transport to the Delaware Side and Lower Bay regions. The percent exchange calculated from the total larvae released at the different sites showed that rates for 1984 and 2000 were lower than for the others years (lower right panel in Figure 9), particularly for the Upper Delaware, Ship John, Delaware Side, Bennies, Egg Island and Lower Bay regions. These years also had lower larval success.

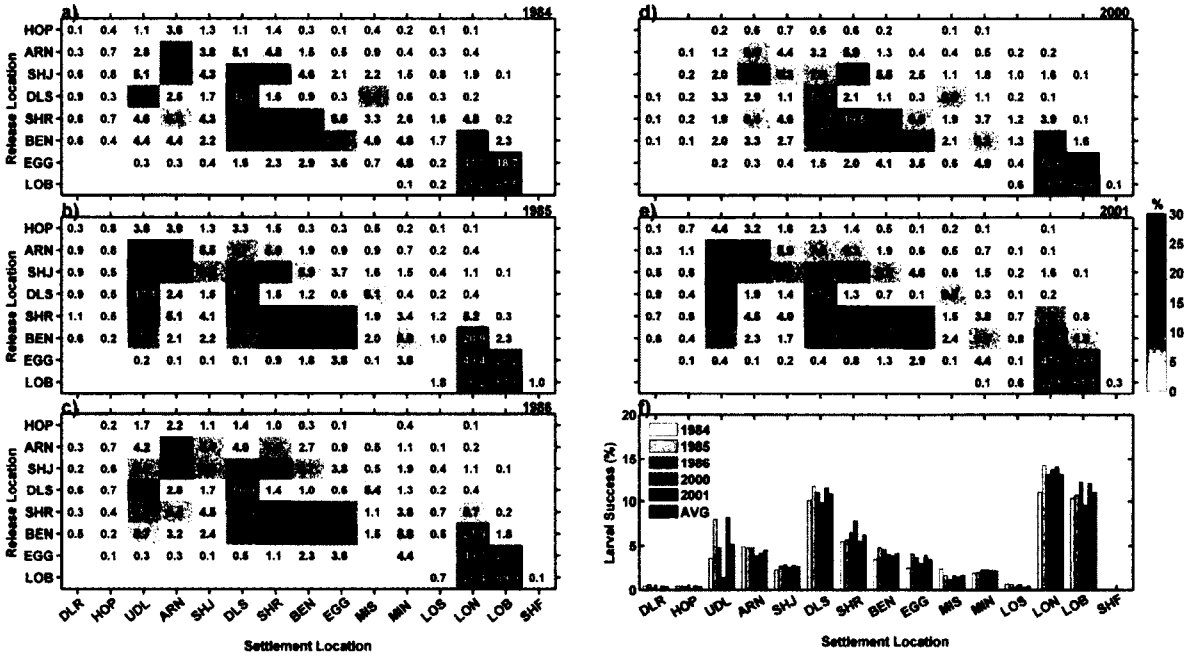

Figure 9. The percent of successful larvae released at a particular location (y axis) that set in the same or another location (x axis) calculated from simulations done for a) 1984, b) 1985, c) 1986, d) 2000, and e) 2001. Values greater than 0% are shown and the degree of connectivity is indicated by the shading. f) The percent of the total larval particles that were released that settle in each location in each year is compared to the five-year average (AVG) for each region.

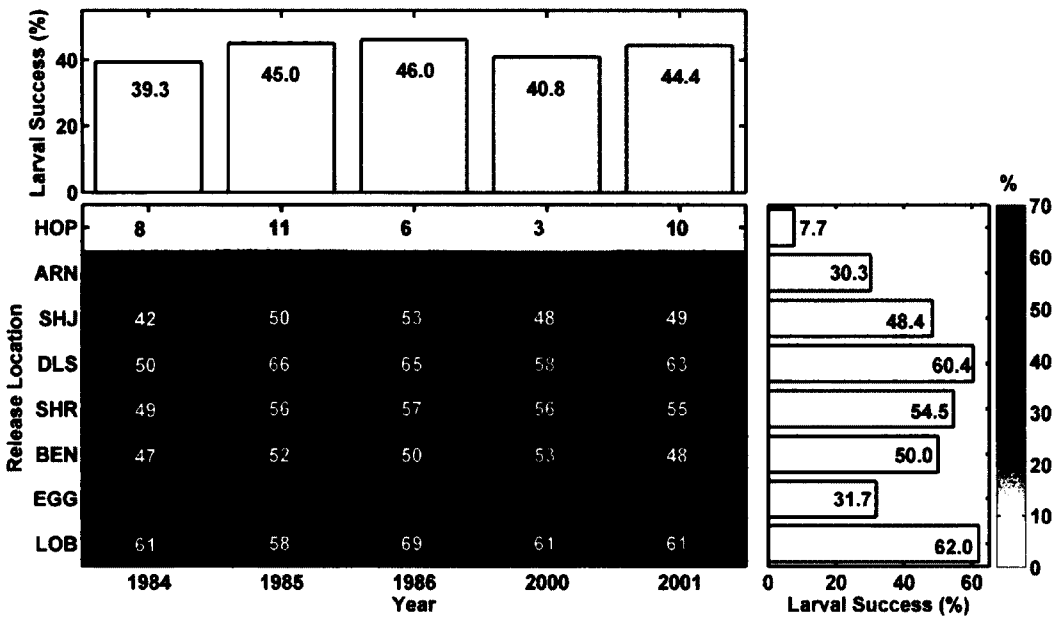

Figure 10. Percent of successful larvae that set on the natural oyster reefs in each year (upper panel) and the five-year average success for each location (right panel).

The relative contribution of larvae to the natural oyster reefs, Hope Creek to Lower Bay regions (areas 1-7, Figure 3) was estimated by the percent of successful larvae that settled in one of these locations (Figure 10). In general, 40-45% of the oyster larvae spawned in Delaware Bay survived their pelagic phase to set on a natural reef (Figure 10). Some interannual variability occurred, with 1984 having the lowest success rate. The Hope Creek reef region had the lowest success rate, 8-11%, in all years (Figure 10). The reef areas between Ship John and Bennies had the highest success rates of 50-65% (Figure 10). The Egg Island reef area is noticeable because it had larval success rates that were about one-half of those of the reef areas to the north and south. Larval success was highest at all of the natural reef sites in 1986.

The fate of larvae released at sites along Delaware Bay was used to extract general patterns of larval dispersal (Figure 11). The upper Bay region had low larval success

rates and a small percentage of larvae were exported up and down-estuary from this region. Larvae spawned in the mid-Bay region along the New Jersey side remained in the area (self-recruit) or were exported down-estuary or across the Bay to the Delaware side. Larvae spawned along the Delaware side of the Bay had a higher rate of self recruitment. The Egg Island region exported over half of its larvae to down-Bay regions. In the Lower Bay essentially all of the successful larvae recruited to the local region. High (1984) and low (2001) river discharge years showed essentially the same general dispersion patterns (Figure 11).

3.3.3 Larval model validation

Evaluation of the robustness of the simulated exchange rates (Figure 9) was done by comparisons with the measured 30-year average oyster spat settlement and recruitment rate estimated for 1983-89 and 1996-2009 (Table 4). The oyster spat settlement sites were primarily in the New Jersey waters of the estuary, so comparisons were made for only this area. The observed settlement patterns (Figure 12) showed low settlement in the upper estuary region around Arnolds oyster reef. Settlement increased down-estuary with the highest settlement occurring in the eastern-most part of the lower estuary adjacent to the Cape May Peninsula (Lower-North and Lower Bay regions in the simulations). The same pattern is seen in the connectivity matrices (Figure 9) and in the overall average settlement (Figure 10). The highest settlement rates are in the central and lower Bay reef regions, with maximum settlement in the Lower Bay region (Figure 10).

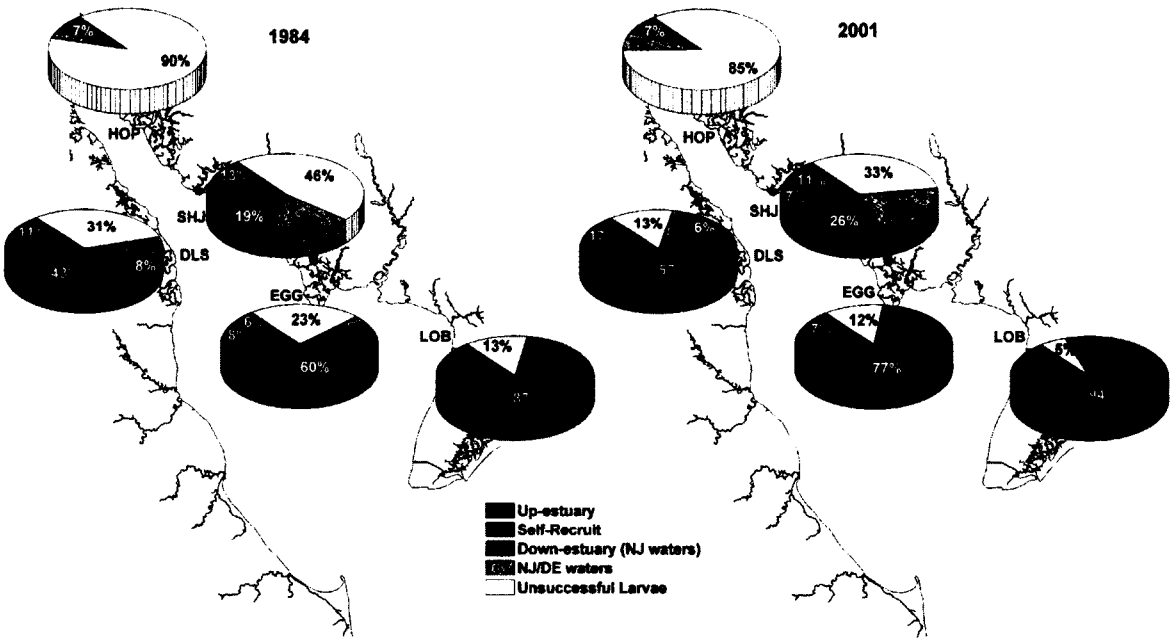

Figure 11. Fate of larvae released at Hope Creek (HOP), Ship John (SHJ), Egg Island (EGG), the Delaware side of the Bay (DLS), and the Lower Bay (LOB) during high (1984) and low (2001) river discharge conditions expressed as percent that are exported up-estuary, down-estuary, or settle locally. The across-estuary flux is estimated by the percent of particles that move from New Jersey to Delaware waters and vice versa (NJ/DE waters). The percent of unsuccessful larvae at each location is shown as a comparison. The percent contribution is given for those that are greater than 5%.

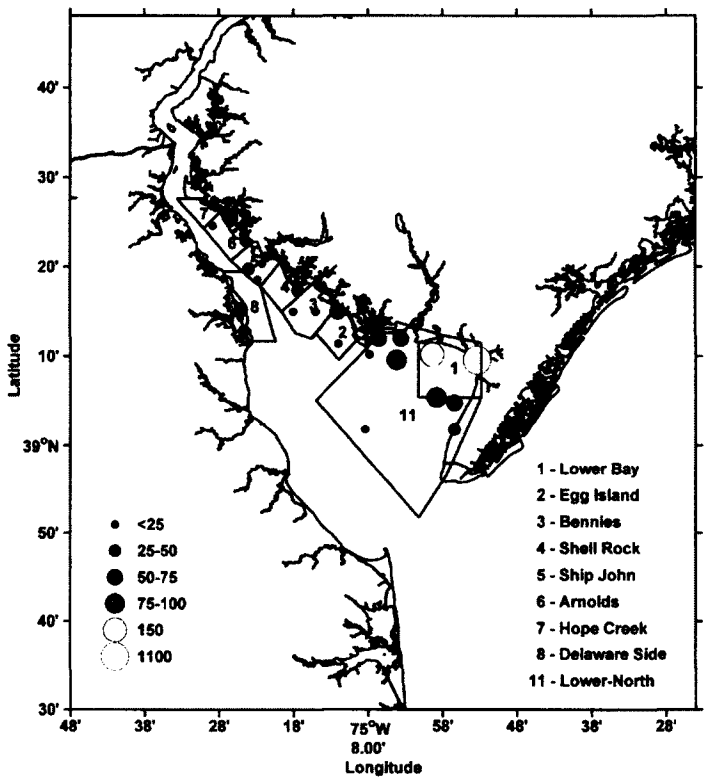

Figure 12. Oyster larvae settlement pattern obtained from spat set measurements made in Delaware Bay during the spawning season (June-October) from 1954-1986. The average mean cumulative spat per shell obtained from the measurements is indicated (dot size and color).

The observed ratio of spat to adult oysters, the recruitment rate, was low in the upper estuary in the vicinity of Arnolds and increased down-Bay towards Bennies oyster reef (Table 4). In most years, the recruitment ratio increased down-estuary, suggesting that the reefs in this region have a higher probability of successful recruitment. The simulated larval success rates showed this same general pattern. The interannual variability in the measured recruitment rates differed from the observed. Recruitment in 1986 was the highest at all sites for all of the years (Table 4). The

simulated average recruitment is similar to that estimated from the measurements (Table 4), but this was not the result of a larger than normal recruitment event relative to other years (Figure 9f). The interannual recruitment variability seen in the measured values is not reproduced in the simulated values (Table 4). In general, the simulations tended to reproduce the long-term spatial patterns in larval settlement and recruitment, but not the observed temporal variations. Part of the discrepancy may be the result of different areas that are represented by the measured and simulated values. The model regions used for the analysis have regular shapes, unlike the irregular shapes of the natural reefs, and do not include the small reefs that surround the larger reefs. For example the measurements at Arnolds include some upper estuary populations that have lower recruitment rates [*Powell et al.*, 2008] which would enhance the differences with the simulated values.

3.3.4 Model Sensitivity

Larval development time, success, and exchange rates are dependent on food and turbidity concentrations and the choice made for the size at which a larva is competent to set. A reduction in food concentration from 4 to 2 mg C l^{-1} decreased the larval success in most of the release regions (Figure 13a). From Hope Creek to Shell Rock, larval success was reduced to less than 20%, well below the success rates obtained with the higher food supply. Success rates at sites in the lower estuary were higher, but still less than those obtained with the higher food concentration. Even with the reduced food, an along-estuary gradient in larval success occurred. The percentage larval success was not significantly changed by the inclusion of a moderate turbidity concentration (Figure 13b). Success was reduced by 5-20%, with the largest reductions occurring at the upper Bay sites. Setting at smaller size increased larval success rates, especially in the upper and middle regions of the Bay (Figure 13c). The slower growing larvae in these regions have a higher survival with a smaller settlement size.

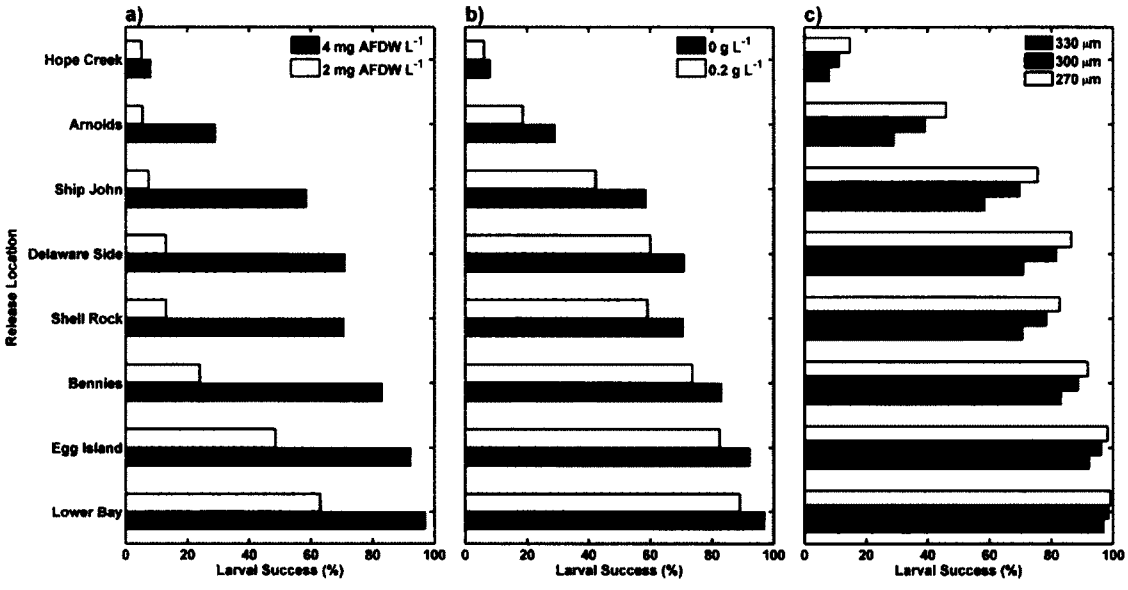

Figure 13. Percent of successful larvae for each release location that resulted from a) decreased food concentration, b) increased turbidity, and c) decreased size at which settlement can occur. The percent larval success at each location obtained for the conditions used in the basic model simulations (filled bar) are shown for comparison.

The benefit of smaller settlement size is lost in the lower Bay, where success rate is essentially independent of settlement size (Figure 13c).

3.4 DISCUSSION

3.4.1 Influence of environmental variability on larval development and success

The simulated success rates showed that between 35 to 40% of released larvae failed to reach settlement size within 30 days, independent of release site. For the simulated larvae that settled on natural oyster reefs, this percentage was increased by about 20%. These success rates are based on a maximum settlement time of 30 days; longer times are assumed to result in failure. The time in the plankton provides an

ever increasing chance of reduced settlement because of increased predation risk and the possibility of encountering adverse environmental conditions [e.g., *Dekshenieks et al.*, 1993; *Przeslawski and Webb*, 2009]. However, a 30-day limit to settlement resulted in a clear down-estuary trend in larval success. Larvae produced in the upper estuary had less than a 40% chance of settling compared to an 80% chance of success for the larvae produced in the lower estuary (Figure 5). For conditions when food supply is not limiting, larval development and success were dependent upon variations in temperature and salinity that the larva experienced during its pelagic phase. Reduced success rates occurred for larvae that were exposed to low-temperature and, particularly, low-salinity waters (see Tables 5 and 6). The responses to these general conditions were further modified by within-estuary gradients of environmental conditions. For the 5 simulation years, average temperatures varied from year-to-year but tended to be homogeneous across the Delaware estuary. Salinity had a pronounced down-estuary gradient and this was a primary determinant of the spatial structure of larval success.

The interannual differences in years of low (1984, 2000) and high (1985, 2001) larval success correspond to differences in the temperature and salinity encountered by larvae during transport. This is especially the case for the differences that occurred between the 1984 and 2000 spawning season and those in 1985 and 2001. Statistical analysis suggests that differences in encountered temperature in the different years were not related to air temperature differences (Figure 6), possibly because of the similar temperature ranges between the years. However, the amplitude and temporal occurrence of maximum and minimum temperatures, the seasonal cycle in air temperature, had clear differences between the years (Figure 7a), which was also apparent in the encountered temperature (Figure 5a). This, coupled with the high correlations between air and encountered temperature within each spawning season (Table 8), indicated that water temperature responds to the seasonal cycle in solar radiation,

which might account for the year-to-year differences in the encountered temperature.

Years of low (1984, 2000) and high (1985, 2001) larval success corresponded to years with high and low river discharge, respectively (Figure 6 and Table 8). Decreased larval success during 1984 and 2000 could be attributed to a few high river discharge events during the spawning season (Figure 7a). Comparisons of conditions from 2000 to those in 1985 and 2001 showed that differences in larval success in these years accrued from low salinity conditions resulting from high river discharge. For other times and specific locations in the Bay, correspondence between river discharge and larval success was not as strong. The salinity encountered by a larva is determined by the initial release location, timing of release, and dispersal scale. Thus, the conditions encountered by a larva along a trajectory reflect local conditions which may not be representative of the variability at the larger Bay-wide scale (Figure 4). Even with this caveat, the year-to-year variability in larval success and along-Bay gradient in success seemed to be largely defined by salinity variability for much of the spawning season. Reduction of overall Bay salinity by high river discharge effectively reduced larval growth and success throughout the estuary. Low dispersion rates in the upper and lower estuary (Figure 4) allowed larvae to be exposed for longer times to low and high salinity conditions, respectively, which ultimately affected their development and success. The effect of lowered salinity could be mitigated by increased food supply [*Dekshenieks et al.*, 1993], but the food concentration used for the simulations reflected optimal conditions. Reduced food supply and increased turbidity could likely be associated with increased river discharge, which would further reduce larval growth and success rate.

The mid-Atlantic portion of the United States is projected to experience warmer and wetter conditions and increased river discharge as a result of a warming climate [*Najjar et al.*, 2000; *IPCC*, 2007; *Najjar et al.*, 2010]. These climate-induced changes may produce conditions that are not favorable for maintaining the rate of larval

success that is needed to sustain the natural oyster reef systems in Delaware Bay and ensure connectivity between these populations.

3.4.2 Larval dispersion and exchange

The simulated particle trajectories showed that most larvae tend to remain in or be transported to certain areas, especially in the middle and lower regions of the Delaware estuary. The transport patterns showed that in general larvae drifted down-estuary. This transport removes larvae from the upper estuary reefs and contributes to the reduced larval recruitment rate that has been observed for the up-estuary regions of Delaware Bay. Down-estuary transport of larvae may be a basic pattern in estuarine systems. Modeling studies of oyster populations in Terrebonne Basin of south central Louisiana suggested that down-estuary transport occurred in this system [*Soniat et al.*, 1998].

The simulated settlement patterns showed consistently higher rates of larval set in the lower estuary which is in agreement with long-term observations from Delaware Bay. The particle trajectories showed that the high settlement that occurs in this area is supported by larvae that originate from the Lower Bay reef. The topography of the lower Bay forms a shallow semi-enclosed region behind the Cape May peninsula (Figure 3). This area is characterized by a recirculating flow and weak currents [*Wang et al.*, 2012]. Thus, the high rates of self-settlement and recruitment may be maintained by the circulation of the lower Delaware Bay. Recruitment to oyster reefs along the Delaware side of the estuary also showed the potential of being supported by self-settlement. The Delaware side of the Bay is strongly influenced by river discharge; the freshwater plume from the Delaware River exits along this side of the Bay [*Wang et al.*, 2012]. The consistent presence of an out-estuary flow would seem to favor horizontal dispersal, but the potentially high self-recruitment and low exchange rates with nearby regions suggest low across-estuary transport and low net dispersal.

Larval supply from the natural reefs on the New Jersey side of the Bay tends to be from the Shell Rock reef area, although this is a small contribution to the overall recruitment to reefs on the Delaware side of the Bay.

Low rates of across-estuary larval dispersal have been observed in other estuarine systems. Studies in Mobile Bay, Alabama suggested that the observed across-estuary gradient in oyster larvae settlement resulted from low larval supply from a high settlement in the western Bay and low settlement areas in the east [*Kim et al.*, 2010].

The physical and biological processes underlying differential larval supply and settlement rates in estuarine systems such as Mobile and Delaware Bays remain to be quantified. However, the results from this study clearly show that river discharge is important from both a circulation and biological perspective. The salinity environment produced by high or low river discharge directly modifies the larval growth rate [*Dekshenieks et al.*, 1993]. In the Delaware Bay simulations, years with high river discharge (1984 and 2000) resulted in reduced growth rate and failure to reach settlement size within 30 days. These were years when larval dispersion and transport within Delaware Bay were reduced relative to other years. This suggests that the effect of reduced salinity on larval growth may be more important than direct removal of larvae from the estuary by increased discharge rates. Variability in river discharge will also produce changes in food supply and turbidity which may further contribute to decreased larval growth rate. However, it is possible that periods of higher discharge may produce increased food supply that could mitigate the effect of low salinity on growth rate. The physical and biological mechanisms underlying across-estuary exchange and dispersal of oyster larvae within Delaware Bay as well as other estuarine systems require more study because these determine the connectivity of the oyster populations.

In a similar study modeling the oyster larval dispersal for Chesapeake Bay, *North et al.* [2008] found that oyster larvae disperse away from their natal populations with

very low self-recruitment. However, we emphasize that this conclusion depended upon the specification of the local scale. The success of the *C. virginica* larvae in encountering a settlement habitat was attributed by *North et al.* [2008] to river runoff; the same relationship was not evident for *C. ariakensis* larvae, which was explained by the different behavior of the two oyster species. *North et al.* [2008] suggested that higher rates of settlement success were associated with low river discharge; high river flow transported larvae away from good settlement habitat. The Delaware Bay simulations showed that periods of low river discharge were characterized by the availability of more larvae throughout the estuary, possibly increasing the probability of a larva encountering good habit for settlement. Thus, enhanced growth rate, shorter planktonic time, more overall larvae and reduced down-estuary transport, should result in increased larval success in years characterized by reduced river discharge. However, this prediction is independent of the post-settlement populations (the source of the larvae), which may experience increased disease mortality or lower growth and reproductive rates due to decreased food supply during periods of high salinity.

3.4.3 Model limitations

Settlement of the simulated larva particle was based on reaching a size that is representative of the average size of larvae that set. In nature, biological and physical cues, such as the presence of adult oysters and the availability of clean substrate are known to initiate and encourage larval settlement [e.g., *Butler*, 1955; *Osman et al.*, 1989; *Roegner and Mann*, 1990; *Fitt and Coon*, 1992]. The settlement criteria used in the model assumes that these cues, which vary in space and time, are equivalent throughout Delaware Bay. However, the good agreement between the simulated settlement patterns and the long-term observed along-estuary recruitment gradient suggest that these cues are not significant determinants of larval settlement patterns in Delaware Bay. Also, variations in the settlement size for the simulated larvae did

not significantly alter the overall recruitment patterns obtained from the simulations. Thus, the approach used for determining larval settlement is adequate for obtaining the basic recruitment patterns in Delaware Bay.

Predation mortality was not included as one of the factors affecting the simulated larvae during transport, although it is potentially an important process. Predation pressure depends on larval size and location in the water column [*Dekshenieks et al.*, 1997] and insufficient information is available from Delaware Bay to estimate the contribution of these losses. However, it might be expected that predation will operate similarly over Delaware Bay, in which case it would alter net exchange rates but not the general spatial transport and settlement patterns. The simulated larval success rates of about 55-60% were produced by mortality that was attributed to environmental conditions, such as low salinity and temperature. An additional predation mortality of 20-30% would still result in a larval supply that is sufficient to maintain the oyster populations in Delaware Bay. This provides an indirect estimate of the predation or natural mortality that oyster larvae may experience.

The particles released in Delaware Bay represent a small fraction of the real cohort size that is released by the post-settlement oyster population during the spawning season. Simulations in which particles were released in proportion to the estimated oyster population at individual reefs [*Powell et al.*, 2008] using conditions from 1985 and 2000 (results not shown) showed larval success and dispersion patterns that were similar to those obtained with a constant particles simulations.

CHAPTER 4

CIRCULATION AND BEHAVIOR CONTROLS ON DISPERSAL OF EASTERN OYSTER (*CRASSOSTREA VIRGINICA*) LARVAE IN DELAWARE BAY

4.1 INTRODUCTION

The horizontal dispersion and subsequent recruitment of Eastern oyster (*Crassostrea virginica*) larvae are integral to the location and productivity of natural oyster beds [*Carriker*, 1951]. The extensive natural oyster beds in Delaware Bay tend to be aggregated along the New Jersey side and to be concentrated in the mid-reaches of the Bay (Figure 2). These beds are maintained by oyster larvae recruitment that is characterized by large intra- and interannual variability [e.g., *Kennedy*, 1996a; *Powell et al.*, 2008]. Lagrangian particle tracking simulations showed that the natural oyster beds in mid-bay on the New Jersey side (regions 2-5, Figure 3) are generally maintained by larval inputs from up and down bay regions as well as local recruitment (see Chapter 3). Regions further down-bay tended to have higher rates of local recruitment but with small inputs from up-bay reefs (see Chapter 3). The general down-estuary transport of oyster larvae in Delaware Bay is consistent with observed and simulated patterns of oyster larvae recruitment [*Powell et al.*, 2008, Chapter 3]. The interannual variability in transport, larval success, and recruitment accrues primarily from variations in freshwater discharge (Chapter 3).

Intraseasonal variability in larval transport and success is partially attributable to changes in environmental conditions, such as freshwater discharge events. However, higher frequency processes such as tidal-induced salinity changes and the effects of these on vertical distributions of oyster larvae contribute to variability at these shorter scales. The younger stages of Eastern oyster larvae tend to be more concentrated in the upper water column; whereas, the older stages, which develop an outer shell, are

found near the bottom [*Carriker*, 1951; *Andrews*, 1983b; *Baker*, 1991]. Superimposed on this distribution is an ontogenetic vertical migration behavior in which the larval stages move up in response to increasing salinity gradients and downward in response to decreasing salinity gradients [*Carriker*, 1951; *Kennedy*, 1996a]. This migration behavior is pronounced for the early and intermediate sized larvae [*Dekshenieks et al.*, 1996].

An observational study that compared the distributions of passive coal particles in an estuary with that of oyster larvae showed that passive transport via the circulation was not adequate to explain the larval distributions [*Wood and Hargis*, 1971]. Rather, active transport via selective swimming was needed to account for the up-estuary movement of the larvae, leading to the suggestion that vertical movement in response to tidal-induced salinity changes provided a mechanism to move larvae up-estuary, thereby facilitating return to spawning grounds or to areas beyond the spawning grounds [*Wood and Hargis*, 1971]. Simulations of oyster larvae movement in response to a semi-diurnally varying salinity field, as would occur during a tidal cycle, showed that the intermediate-sized larvae were retained higher in the water column thereby increasing the horizontal dispersal potential and suggested that this behavior provided an important mechanism for retention in the estuary and in potentially in areas favorable for growth and recruitment [*Dekshenieks et al.*, 1996]. In contrast, a recent modeling study in Mobile Bay suggested that although behavior is important in retaining larvae near spawning areas, the spatial distribution of oyster recruitment might be explained only by physical transport [*Kim et al.*, 2010]. Similar dominance of physical over biological transport was also proposed for the James River estuary [*Andrews*, 1983b].

This study extends the results presented in Chapter 3 to investigate the biological and physical processes that lead to intraseasonal variability in oyster larvae success and recruitment for Delaware Bay oyster reefs. Specifically, the effect of the

spring-neap tidal cycle on larval dispersal and recruitment was investigated. The approximate one-month frequency associated with this tidal cycle is of the same order as the larval planktonic time and as a result may be more important to larval dispersal than the general down-estuary advective flow. Thus, the objective of this study is to investigate the relative contributions of this high frequency flow and tidally-induced vertical migration on larval dispersal and subsequent success in Delaware Bay.

The modeling framework and analysis methods used to evaluate the relative effects of passive versus active larvae on transport pathways and retention are given in the following section. This is followed by a description of simulation results that focus on the effects of tidal forcing, episodic increases in river discharge, and behavior in regulating the transport of oyster larvae in Delaware Bay. These results are discussed in the context of what is known about oyster larvae recruitment in Delaware Bay and other systems.

4.2 METHODS

4.2.1 Coupled Circulation-Larvae Model

The circulation model used in this study is based on the Regional Ocean Model System (ROMS) that was configured for Delaware Bay and its adjacent continental shelf. Details on the model configuration and validation are in [*Wang et al.*, 2012]. The oyster larvae model is based on the models described in *Dekshenieks et al.* [1993, 1996], which simulate larval growth in response to environmental conditions of temperature, salinity, food supply and turbidity. The ontogenetic vertical swimming and sinking behavior is dependent on changes in salinity, larval size, and temperature.

Details of the models and the implementation of the coupled modeling framework are described in the method section in Chapter 3. The oyster larvae are represented as particles that are tracked in the simulated circulation distribution. As the particle moves, it encounters changing salinity and temperature conditions, which alter larval

growth and vertical behavior. Food supply and turbidity, which regulate growth, were held at a constant value along the particle trajectory.

The particle location was modified by the three-dimensional advective velocity, vertical diffusion, and the larval displacement due to its swimming and sinking behavior. The vertical advective velocity was obtained from the circulation model. Vertical diffusion 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 vertical swimming behavior determined the biological contribution to the particle vertical displacement. The particle trajectories were ended when a larva reached settlement size of 330 μm [*Dekshenieks et al.*, 1993] or failed to reach this settlement size within 30 days after release.

4.2.2 Simulation design and analysis

Particles were released at 8 locations in the Delaware estuary (Areas 1-8, Figure 14, which correspond to the areas of the natural oyster beds. Two hundred particles were released at each location at five-day intervals throughout the oyster spawning season, mid-June to mid-September, which represents 18 spawning events in each of the five simulation years (1984, 1985, 1986, 2000, and 2001). The velocity, temperature, and salinity conditions encountered by a particle along its trajectory were tracked, as were larval size, swimming/sinking speed, and swimming time. The time history of the conditions encountered by particles contributed to larval success, transport, and exchange rates between release and settlement locations.

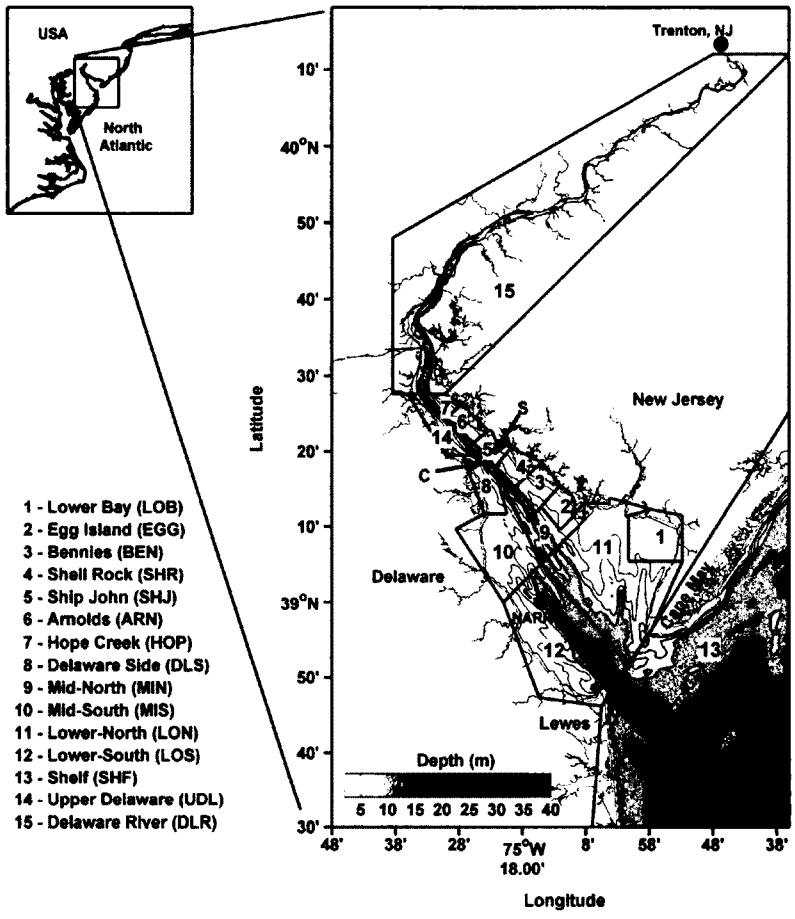

Figure 14. Map and bathymetry of the Delaware Bay system. The sites used to release particles in the simulated flow fields (regions 1-8) generally correspond to the locations of natural oyster reefs in Delaware Bay (see listing). These release sites and an additional seven regions (regions 9-15) were used to analyze the settlement patterns obtained from the Lagrangian particle tracking simulations. River discharge measurements were obtained from 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).

Larval success was estimated for each release location and spawning event (release time) by the number of particles that reached settlement size within 30 days. Larval transport was 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 was used to construct frequency histograms that showed the transport length scales and orientation. Larval dispersion was obtained from connectivity matrices that relate the percent of the total larvae released at a location that successfully set in the same region or other regions. The resulting percentages provide estimates of exchange rates among regions.

The relative contribution of circulation and biological behavior in affecting larval dispersion was determined by comparing results of simulations with passive particles (no larval growth and behavior) to those with particles that had growth and behavior (larval biology). To address the effects of vertical mixing, the simulations with larval biology were also compared to simulations that did not include the vertical random walk term. Comparisons of flow conditions in different years were made 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 (Figure 14). Spectral and cross-correlation analysis of these time series provided the dominant variability periods for different environmental conditions, which were then related to the simulated larval transport and retention patterns.

The transport patterns from the larval particle simulations were used to estimate spatial and temporal variability in larval retention in four representative regions in the estuary. These regions were defined to include the low salinity regions in the upper Bay (Areas 6, 7, 14, 15, Figure 14), the high salinity oyster beds in the lower Bay (Area 1, Figure 14), the oyster beds on the Delaware side of the Bay (Area 8, Figure 14) and the natural oysters reefs in the mid reaches of the Bay (Areas 2 to 5,

Figure 14). For each region and release time, the daily number of particles remaining in the area from the release to the settlement time was determined. The daily number of particles in a region was 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.

4.3 RESULTS

4.3.1 Intraseasonal variability in residual circulation and salinity

Time series of simulated residual estuarine flow at locations in the channel and over the shoals in the mid-portion of Delaware Bay (Figure 14) showed combined periods of outflow velocities (negative, down-estuary) with periodic inflow currents (positive, up-estuary) that were associated with the spring-neap tidal cycle (Figure 15b, c, g and h). Both spring and neap tides were well resolved in the simulated flow distributions. Characteristics inflows in the deepest part of the channel and over the shoals occurred during neap tides. For spring tides the flow pattern consisted in barotropic outflow in the channel and over the shoals. The surface flows at the channel and shoals sites were significantly correlated with the surface elevation with a time lag of 3-5 days ($r=0.5$, $p<0.05$), but had no significant correlation 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 respond to the same forcing.

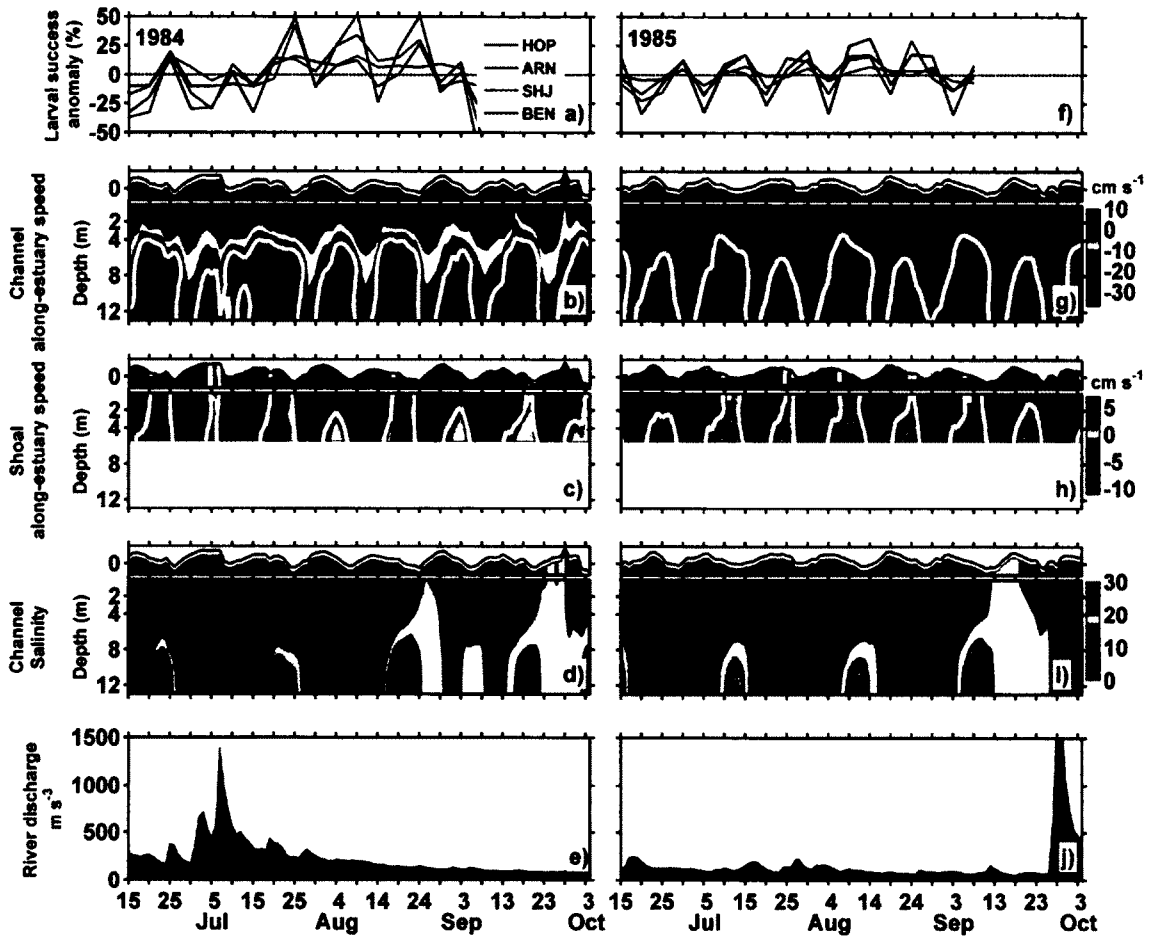

Figure 15. Time series for the spawning season of 1984 and 1985 showing larval success anomaly for four oyster reefs (a, f) identified as: HOP-Hope Creek, ARN-Arnolds, SHJ-Ship John, and BEN-Bennies. Reef locations are shown on Figure 14. The larval success anomaly time series were constructed from the simulated Lagrangian trajectories as described in the text. The simulated depth-time distributions of along-estuary flow in the channel (b, g) and over the shoals (c, h), and the salinity in the channel (d, i) for the 1984 (left panel) and 1985 (right panel) spawning seasons are shown. Negative velocities indicate down-estuary flow; positive velocities are up-estuary flow. The transition between inflows and outflows (0 cm s^{-1}) is indicated by the white contour. The surface elevation is indicated in the panel above the flow and salinity depth-time distributions. Time series of river discharge (e, j) obtained from USGS gauges at Trenton, NJ.

The strongest up-estuary flows brought high salinity (>25) water into the upper estuary (e.g., 1984: 6/20, 7/20, 8/19, in Figure 15d and 1985: 7/10, 8/19, 9/8 in Figure 15i) with significant correlations between near bottom velocity and salinity ($r=0.6$, $p<0.05$ lag=0-2 days). These strongest flows are related to the neap tides driven by the third quarter moon cycle. During spring tides, salinity was 15-18 and was vertically homogenous (e.g., 6/27/84. 7/30/85). Disruptions to this pattern occurred during high river flows, such as occurred in early July of 1984 (Figure 15e). Low river discharge, such as occurred in 1985 (Figure 15j), resulted in overall higher salinity (Figure 15i). For all simulation years, the fortnightly variability driven by neap-spring tidal cycles dominated the currents and salinity (Figures 15, 16). However, large river discharge events, such as occurred in early July 1984 (Figure 15e), 1986 (Figure 16a, b, c) and August 2000 (Figure 16d, e, f), produced large salinity changes that overwhelmed the fortnightly salinity variability.

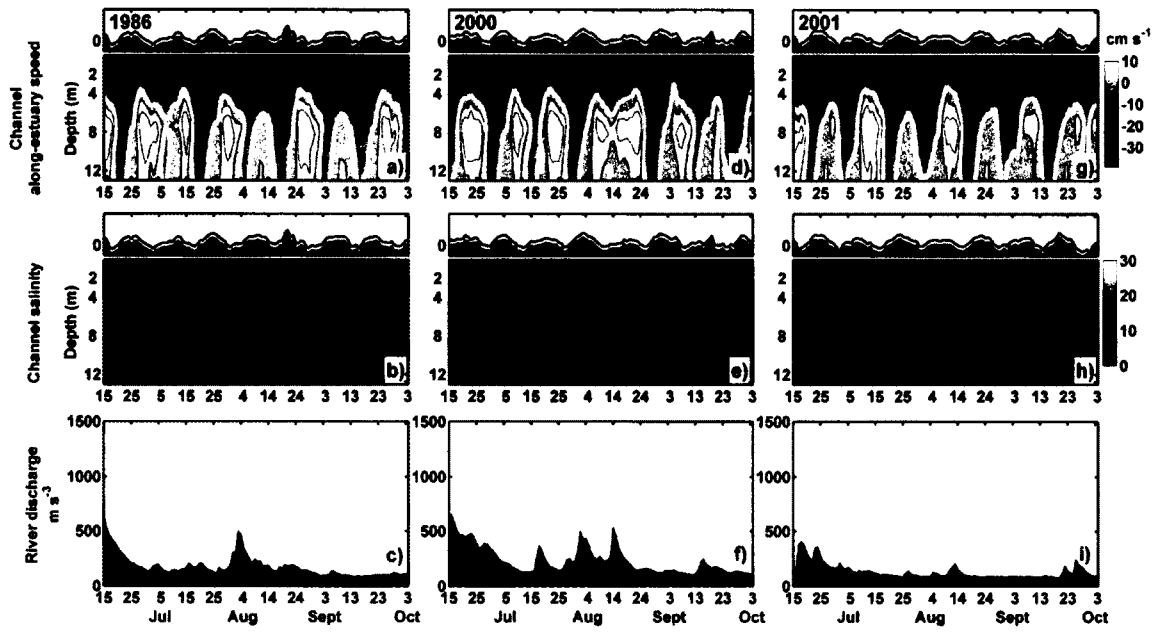

Figure 16. Time series for the spawning season of 1986, 2000 and 2001 showing the simulated depth-time distributions of along-estuary flow in the channel (a, d, g) and the salinity in the channel (b, e, h) obtained for the 1986, 2000 and 2001 spawning seasons. Negative velocities indicate down-estuary flow; positive velocities are up-estuary flow. The transition between inflows and outflows (0 cm s^{-1}) is indicated by the white contour. The surface elevation is indicated in the panel above the flow and salinity depth-time distributions. Time series of river discharge (c, f, i) obtained from USGS gauges at Trenton, NJ.

At the Bay-wide scale, the large river discharge in early July 1984 produced a low-salinity surface plume that extended along the main axis of the estuary (Figure 17a). The corresponding surface currents were predominately down-estuary, with the strongest flows occurring along the main channel (Figure 17b). Weak near-bottom currents were directed into the Bay and were slow (Figure 17c). The salinity difference between the surface and bottom waters was in excess of 10 along the main channel (Figure 17d), suggesting that this part of the Bay was strongly stratified. In

contrast, the shoal regions remained relatively well mixed (Figure 17d). During low river discharge, estuarine circulation, salinity and stratification are dominated by the spring-neap tides which are described next.

Spring tides produced a surface salinity distribution with less salty water on the north side of the Bay and more salty water on the south side where shelf water intrudes into the lower estuary (Figure 18a). Barotropic outflows occurred over most part of the Bay, with some regions in the lower Bay dominated by barotropic inflows (Figure 18b,c). The surface to bottom salinity difference was small (Figure 18d). The down-estuary movement of the surface isohalines during neap tides (Figure 18e) was comparable to that associated with high river discharge events. The surface and bottom flows were also similar, although reduced somewhat in magnitude (Figure 18f and g). The surface-bottom salinity difference was large along the main channel portion of the Bay and reduced over the shoals (Figure 18h).

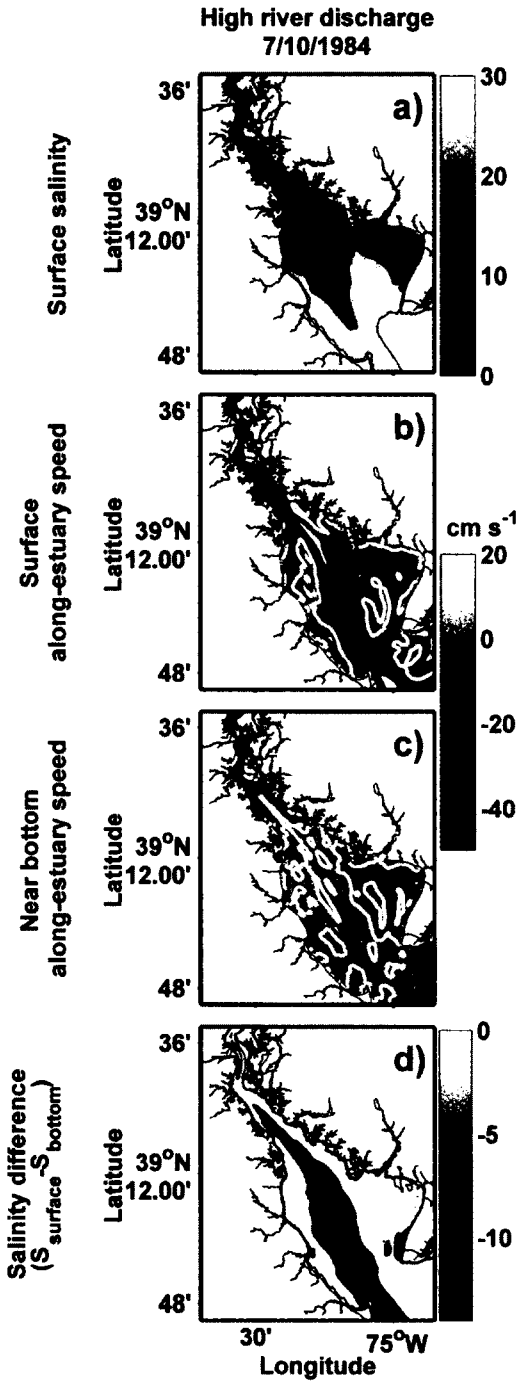

Figure 17. Distribution of simulated surface salinity (a), surface along-estuary speed (b), bottom along-channel speed (c), and the difference in surface and bottom salinity (a measure of stratification) (d) obtained for high river discharge conditions. The transition between inflows and outflows (0 cm s^{-1}) is indicated by the white contour in the currents distributions.

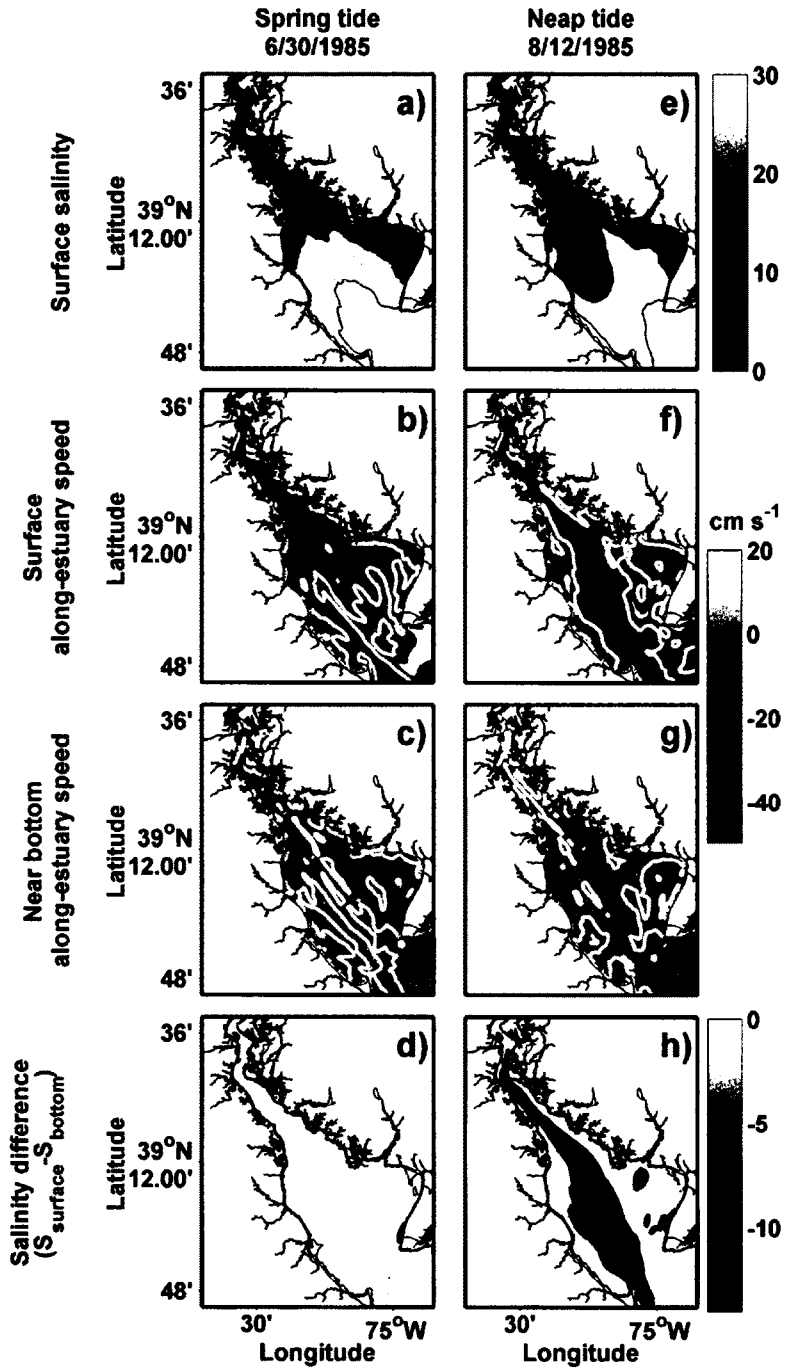

Figure 18. Distribution of simulated surface salinity (a, e), surface along-estuary speed (b, f), bottom along-channel speed (c, g), and the difference in surface and bottom salinity (a measure of stratification) (d, h) obtained for spring tide (left panel) and neap tide (right panel) conditions.

4.3.2 Intraseasonal variability in larval success

Spatial variability in larval success was associated with the along-estuary salinity gradient (Chapter 3), with larval success decreasing as salinity decreased. This spatial success gradient was removed from the simulation results by subtracting the average larval success estimated for each release location during a spawning season from each release time. The resulting anomaly time series then provides only the temporal changes in larval success.

The larval success time series obtained for 1984 and 1985 (Figure 15a and f) for locations in the upper and middle Delaware Bay showed two types of variations. The first consisted of two or more consecutive spawning events with low larval success, as occurred from mid June to late July in 1984 (Figure 15a). The second type of variability appeared as synchronized increases (e.g., 1984: 7/25, 8/24; 1985: 6/30, 8/24) and decreases (e.g., 1984: 7/30, 8/14; 1985: 7/5, 8/4) in larval success. High success anomaly, such as the ~50% observed on 25 July 1984 was followed by a period of low success anomaly centered on 30 July 1984 (Figure 15a). Similar synchronized high/low success variations occurred in the remainder of 1984, throughout the spawning period in 1985 (Figure 15f), and in the other years included in this study (1986, 2000 and 2001, not shown).

The prolonged period of decreased larval success in the early spawning season of 1984 (Figure 15a) was associated with large freshwater discharge events (Figure 15e), which produced low salinity conditions through Delaware Bay (Figure 17) for extended periods (Figures 15 and 16). Following 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 tended to be associated with periods of spring tide flows during which the general flow is directed out of Delaware Bay (Figure 15b, c, g and h).

The high survival events in the upper and middle estuary regions in 1984 and

1985 occurred during periods when outflow conditions prevailed in the channel and over the shoals in the 3-5 days following larval release (e.g., Figure 15b, c, g and h). These periods of outflow conditions occurred during spring tides. Decreased survival success occurred when larvae experienced predominant up-estuary flows following release, such as 30 July 1984 and 5 July 1985 (Figure 15), which tended to occur during neap tides. This general pattern was seen for the five years included in the analysis (Table 9). With few exceptions, increased larval success occurred during spring tides when barotrophic outflow were predominant and during transitions from neap to spring tides. Decreased larval success was associated with neap tides and transitions from spring to neap tides (Table 9). The exceptions to these general patterns occurred during periods of high river discharge (e.g., early July 1984 and 1986) and reduced temperature (e.g., August 1986). The effect of temperature on larval success is described in Chapter 3.

The fortnightly variability in the residual flow induced by spring and neap tides directly affects the transport direction of the larvae following their release. Larval success is related to transport direction, with low success events (e. g., 30 July and 29 August 1984 in Figure 15a and b, and 20 June and 7 July 1985 in Figure 15c and d) occurring during periods of up-estuary transport from the larva release point (Figure 19). High larval success events in 1984 and 1985 were associated with down-estuary transport from the release point (Figure 20). Similar results were obtained for the synchronized high/low larval success events in 1986, 2000 and 2001 (not shown).

Table 9. 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 beds (locations on Figure 14) 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 cooling (see Chapter 3) which is not considered in the analysis presented in this study. High or low success that occurred only at Arnolds is indicated as (ARN).

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

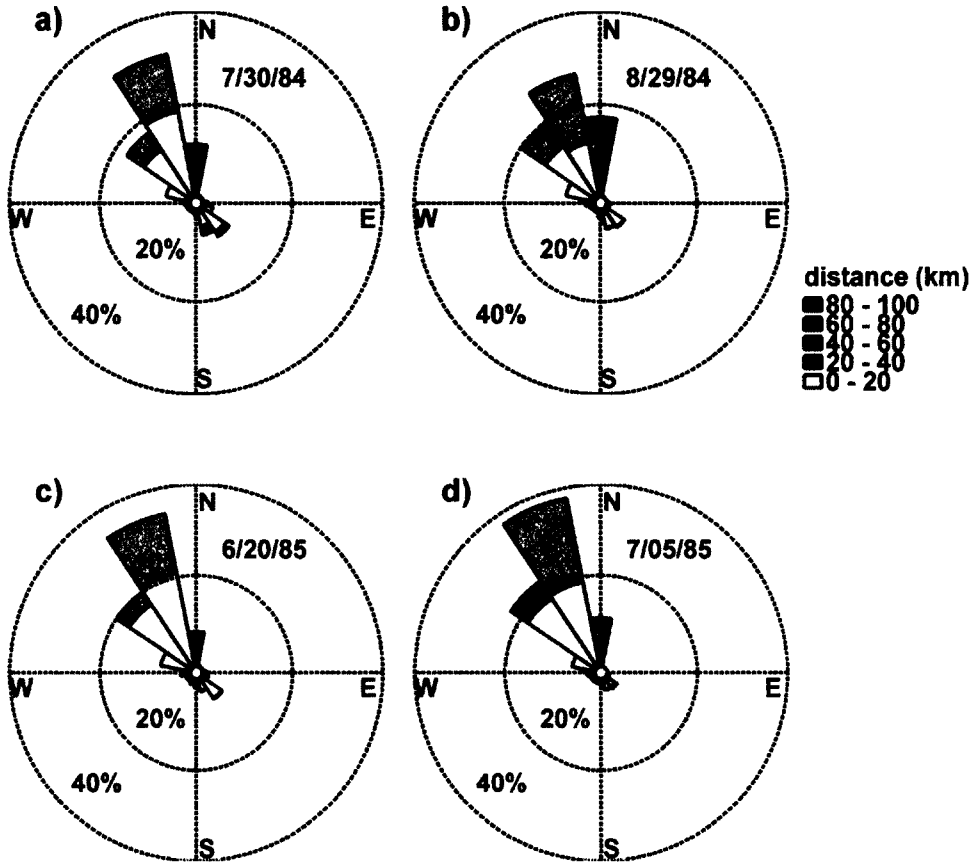

Figure 19. Histograms showing the transport direction, magnitude, and percentage of particles for particles released on a) 30 July 1984, b) 29 August 1984, c) 20 June 1985, and 7 July 1985.

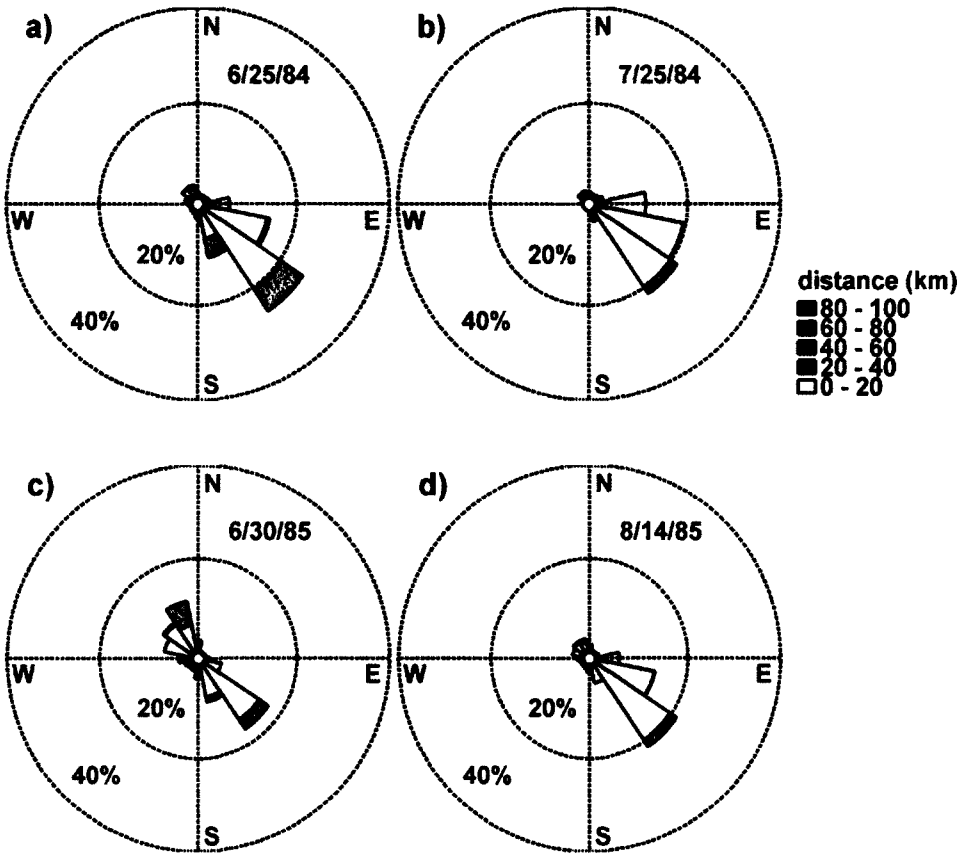

Figure 20. Histograms showing the transport direction, magnitude, and percentage of particles for particles released on a) 25 June 1984, b) 25 July 1984, c) 30 June 1985, and 14 August 1985.

The correspondence of larval success and timing of the spring-neap tidal cycle was investigated further by comparing larval success for releases from natural reef sites in the mid-reaches of Delaware Bay with along-estuary bottom speed in the channel (Figure 21). Bottom speed provided a reliable indicator of the occurrence of inflow and outflows (Figure 15). The mean speed used in the comparison was calculated for the first 5 days following a release, which provided independent estimates for larvae released at 5-day intervals. High success was determined by release events that

exceeded the mean success for an individual year.

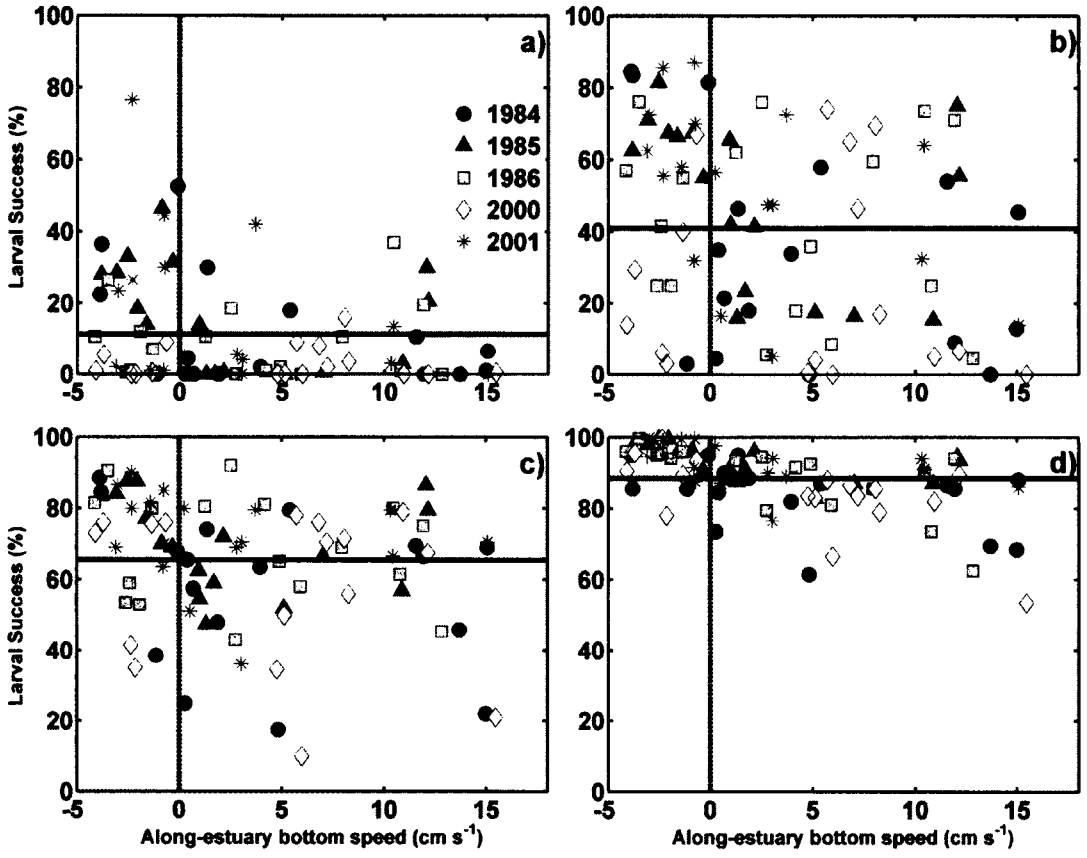

Figure 21. Relationship between along-estuary bottom speed and larval success for the 5 years included in this study for larvae released from a) Hope Creek, b) Arnolds, c) Ship John, and d) Bennies reefs. The five-year average success in each release location is indicated (horizontal lines) as is the zero velocity (vertical lines) which marks the shift from down-estuary flow (negative velocities) to up-estuary flow (positive velocities).

Larval success at Hope Creek, which is in the upper estuary, was generally less than the mean success in each year (Figure 21a). The salinity encountered by larva during transport to this part of the Bay was 14 or below (Figure 22a). At salinities below 15,

larval growth is reduced and below 12 is seriously compromised [*Dekshenieks et al.*, 1993]. Thus, larvae transported to Hope Creek via up-estuary transport were placed in a salinity environment that is not conductive to growth and development. At Arnolds, Ship John, and Bennies larval success was higher than the mean success during periods of outflow (down-estuary transport) during spring tides, especially for 1985 and 2001 (Figure 21b, c and d). At these sites, the enhanced success rates were associated with salinity in excess of 13 (Figure 22b, c and d). The Ship John and Bennies sites tended to have higher larval success rates (Chapter 3) but outflow circulation enhanced the larval success (Table 10). Reduced larval success at these three sites was associated with inflows (up-estuary transport) during neap tides, although this correspondence was not as strong as that for outflows (Table 10).

Table 10. Summary of the percentage of larval success events for larvae released at four natural oyster beds (locations in Figure 14) that exceeded the five-year average success that coincided with spring tides and the percentage of larval success events with below average success that coincided with neap tides (see Figure 21).

Release Location	Spring Tides	Neap Tides
Hope Creek	55	65
Arnolds	72	62
Ship John	66	55
Bennies	90	55

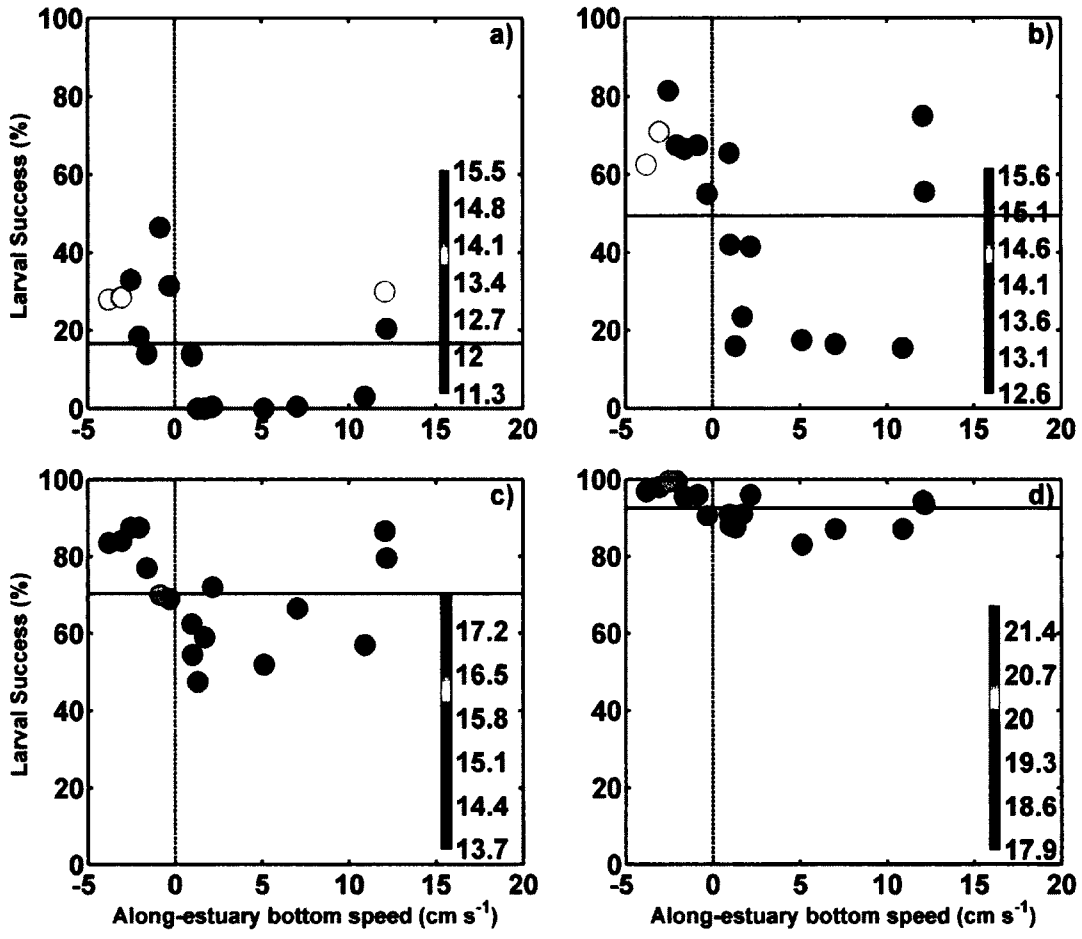

Figure 22. Relationship between along-estuary bottom speed, larval success, and salinity for 1985 for larvae released from a) Hope Creek, b) Arnolds, c) Ship John, and d) Bennies reefs. The average success at each release location is indicated (horizontal lines) as is the zero velocity (vertical lines) which marks the shift from down-estuary flow (negative velocities) to up-estuary flow (positive velocities).

The larval exchange rates in 1984, represented as connectivity matrices, showed significant reductions in larval settlement in the spawning regions (self recruitment) and in other natural reef areas in the upper and mid-bay during times of high river discharge (Figure 23). The reduction in successful settlement was largest for the reef sites in the upper Bay which have longer exposure to freshwater. By late July the

low salinity water was replaced with more typical salinity conditions (Figure 15) and larval success rates increased at the upper Bay sites (Figure 23a and b). Enhanced success occurred at all reef sites at the end of July, and was associated with the transition from a neap to a spring tide (Table 9). Subsequent periods of synchronized high larval success (9 August, 24 August, Figure 23) were associated with spring tide driving outflow conditions (Table 9). Periods with low river discharge (e.g., 8/4/1984) had increased exchange rates for the mid-Bay reef sites (Figure 23).

The fortnightly tidal variability also modified larval exchange rates (Figure 24). In general, larval releases during spring tides resulted in a higher percent exchange with downstream sites (Figure 24). For example, larvae released at Shelf Rock during predominant outflows (e.g., 6/30, 7/15, 8/14), produced increased exchanges with Bennies, Egg Island and the lower part of Delaware Bay (Figure 24). Larvae released during a neap tide provided increased inputs to sites upstream of the release location. Higher exchange rates at mid-Bay sites, such as Ship John and Shell Rock, occurred when larvae were released during neap tides (Figure 24).

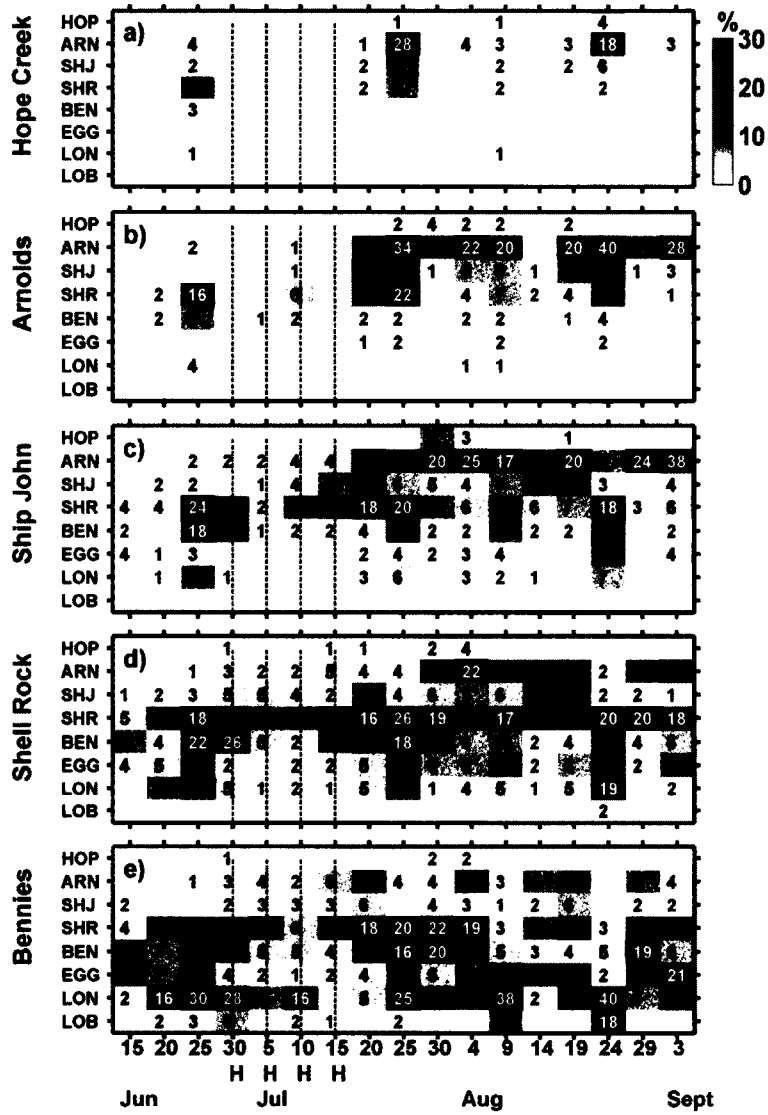

Figure 23. Time variability in the percent of successful larvae (x axis) released at a) Hope Creek, b) Arnolds, c) Ship John, d) Shell Rock and e) Bennies that set in the same or another location (y axis) for the spawning season of 1984. Periods of high river discharge (H) are indicated by the vertical dashed lines. The degree of connectivity is indicated by the shading, with darker shades associated with higher connectivity. The settlement locations 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.

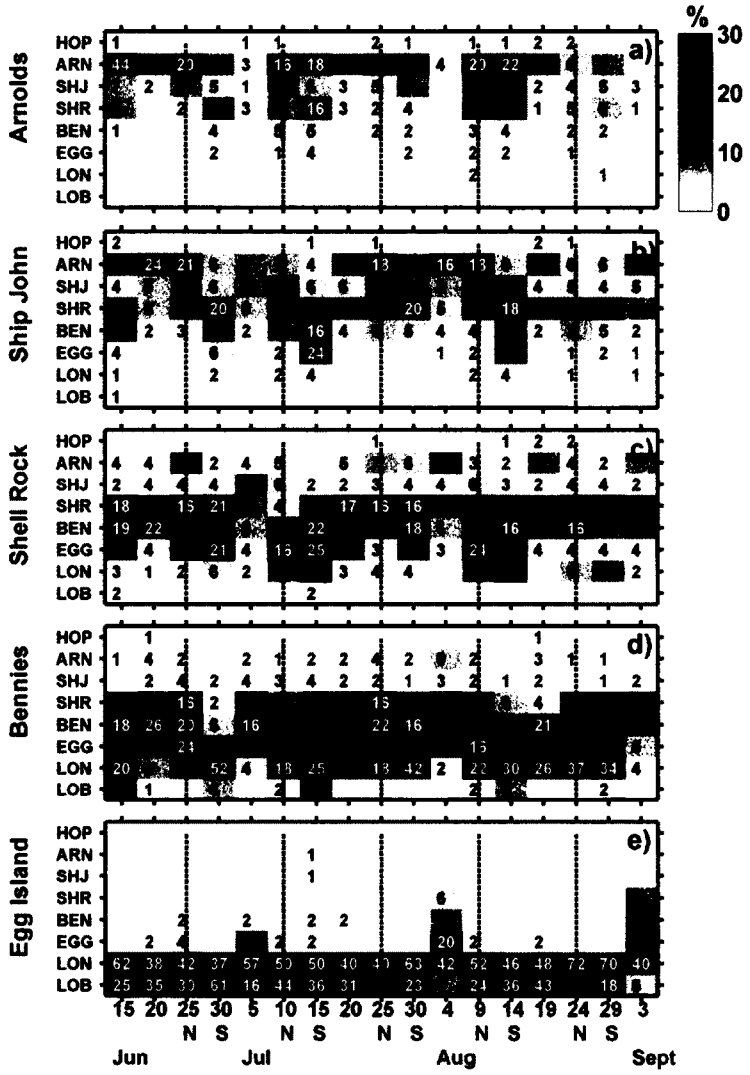

Figure 24. Time variability in the percent of successful larvae (x axis) released at a) Arnolds, b) Ship John, c) Shell Rock, d) Bennies, and e) Egg Island that set in the same or another location (y axis) for the spawning season of 1985. Periods of neap tides (N) are indicated by the vertical dashed lines, spring tides occurred following the neap tides. The degree of connectivity is indicated by the shading, with darker shades associated with higher connectivity. The settlement locations 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.

The exchange rates suggest that portions of Delaware Bay retain or export more larvae than others (Figures 23 and 24). The general pattern of larval export and retention was obtained by averaging over larger representative regions of Delaware Bay (see Methods section) for each release time and for the entire spawning season. In the upper Bay the general pattern was one of high particle retention (Figure 25a). The decrease in retention in 1984 and 2000 were associated with the high river discharge that occurred during these years. Particle transport into the upper Bay was enhanced during neap tides and particle export increased during spring tides (Figure 26a). Along the Delaware side of the Bay average particle retention was about 50% (Figure 25b) but considerable variability was introduced by the tidal cycle (Figure 26b). Neap tides tended to be associated with reduced larval retention and spring tides resulted in higher retention (Figure 26b). These counter-intuitive results arise because outflow conditions driven by spring tides provide larvae from upstream regions and the inflow during neap tides moves larvae through this part of the Bay to upper areas. Particle retention in the middle reaches of the Bay is relatively constant at about 30% (Figure 25c) and variability produced by the neap tides is small (Figure 26c). However, particle retention is enhanced during spring tides because of the inputs from upstream regions. Particle retention is uniformly high in the lower Bay (Figure 25d); the fortnightly variability had little effect on particle retention (Figure 26d).

4.3.3 Effects of biological behavior on larval dispersion

The effect of vertical migration behavior and vertical mixing on larval dispersion was assessed by comparing the results described above to those from simulations that used passive particles (i.e., without larval biology) and to results from simulations that included larval biology but no sub-grid vertical mixing (i.e., without the random walk term), respectively. For these simulations, particles were released at the same locations and times used for the year 2000 simulations. The final settlement location

for the passive particles simulations was taken as the position at the time when the larva reached settlement size in the simulations with behavior.

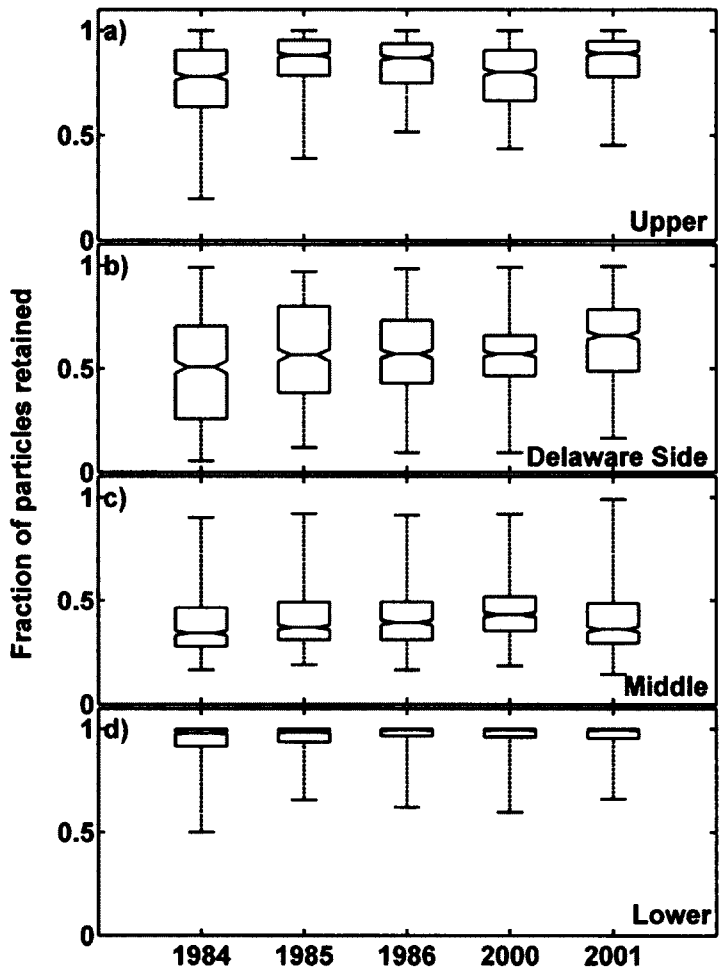

Figure 25. Interannual variability in larval retention calculated for the a) Upper, b) Delaware Side, c) Middle and d) Lower estuary regions of Delaware Bay from the simulated Lagrangian trajectories. The size of each box represents the 25^{th} and 75^{th} percentiles, the maximum and minimum values for each are represented by the vertical bars. The median of the estimates is given by the horizontal line and the degree of indentations 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.

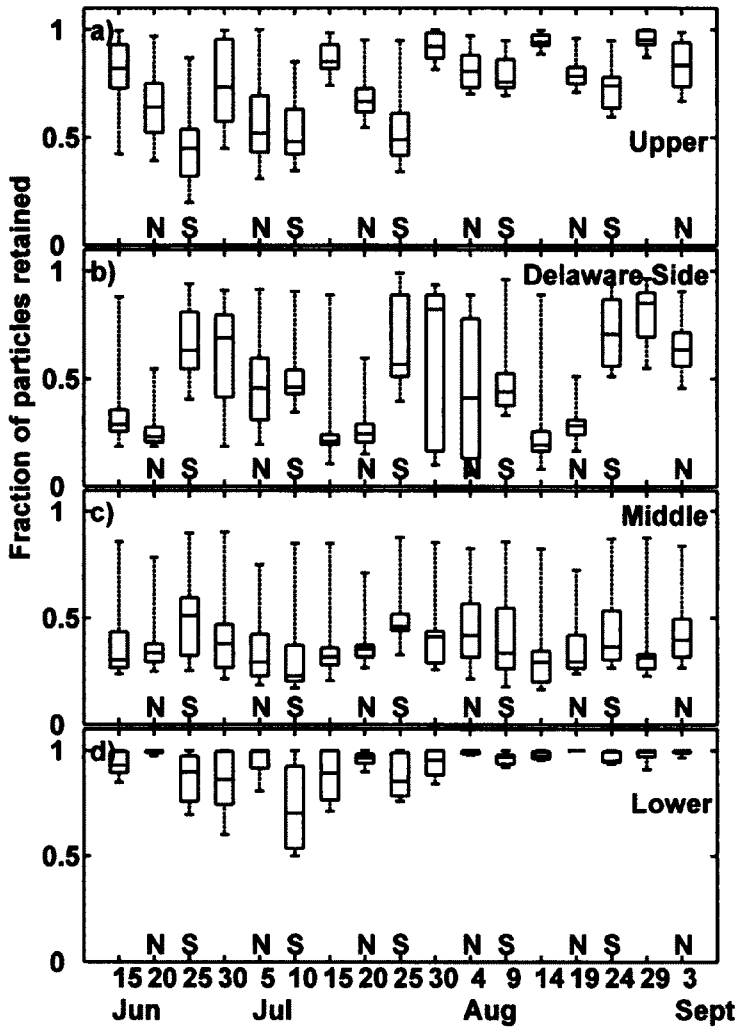

Figure 26. Intraseasonal variability in larval retention calculated for 1984 for the a) Upper, b) Delaware Side, c) Middle and d) Lower estuary regions of Delaware Bay from the simulated Lagrangian trajectories. The size of each box represents the 25^{th} and 75^{th} percentiles, the maximum and minimum values for each are represented by the vertical bars. The median of the estimates is given by the horizontal line and the degree of indentations 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.

Comparison of the simulated dispersion obtained for particles with and without larval biology that were released at Ship John on June 20, 2000 showed that those with larval behavior were mostly retained in the upper-middle estuary (Figure 27a). Passive particles tended to move down-estuary toward the southwestern side of the lower estuary (Figure 27b). The transport histograms showed that differences in distance for the two types of particles were about 5-10% (Figure 27c and d).

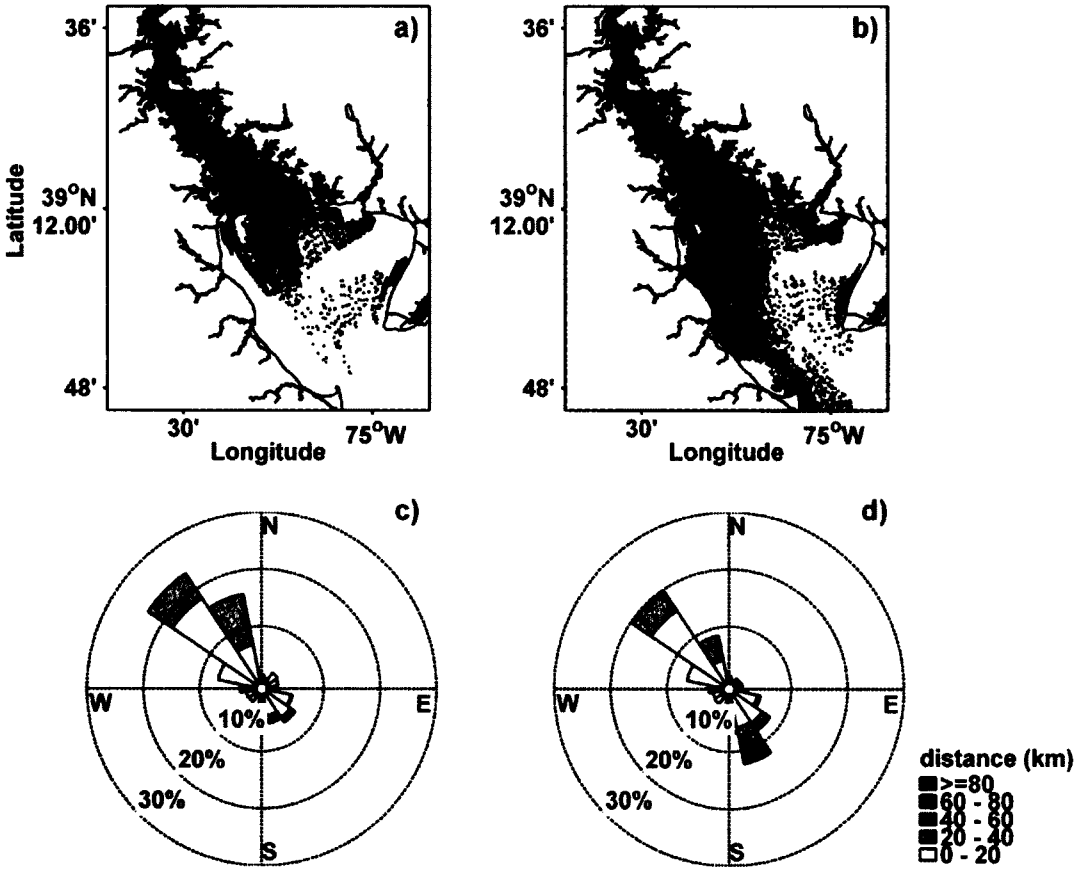

Figure 27. Distribution of particles released on 20 June 2000 from Ship John (black dots) a) with larval growth and behavior and b) without larval growth and behavior (passive particles). The larval transport histograms were estimated for particles c) with and d) without larval growth and behavior.

The connectivity matrix for the entire spawning season showed that the majority of the particles with vertical behavior reached settlement size mostly in region between Arnolds and Egg Island, and that most of the particles settled within the estuary (Figure 28a and b). Overall larval success was highest in the mid-reaches of the estuary (Figure 28c). The connectivity matrix for the passive particles had a similar pattern but with larger dispersal scales (Figure 28d and e). For example, more particles were transported to the upper estuary regions and to the continental shelf (Figure 28a and b versus 28d and e). The larger dispersal scales also resulted in a lower percent of settlement in the Bay region with natural oyster reefs (Figure 28e), which results in decreased larval success for these regions (Figure 28f).

The vertical distribution of particles with (Figure 29a) and without (Figure 29b) larval biology constructed for particles released from Shell Rock on 24 August 2000 showed that most were concentrated between the surface and 4 m. The Delaware estuary has large areas with depths <5m (Figure 14), so larvae have a high probability of encountering shallow areas than the deeper areas and channels. The particles with and without behavior had similar vertical distributions (Figure 29a and b), characterized by upward swimming following release, maintenance in surface waters during the intermediate portion of planktonic life, and descent until settlement. The removal of the vertical mixing produced larval distributions with larger vertical variations, suggesting that this process can cancel the effect of larval behavior, especially in a shallow system that is tidally mixed. This accounts for the small differences in dispersal patterns for the particles with and without behavior.

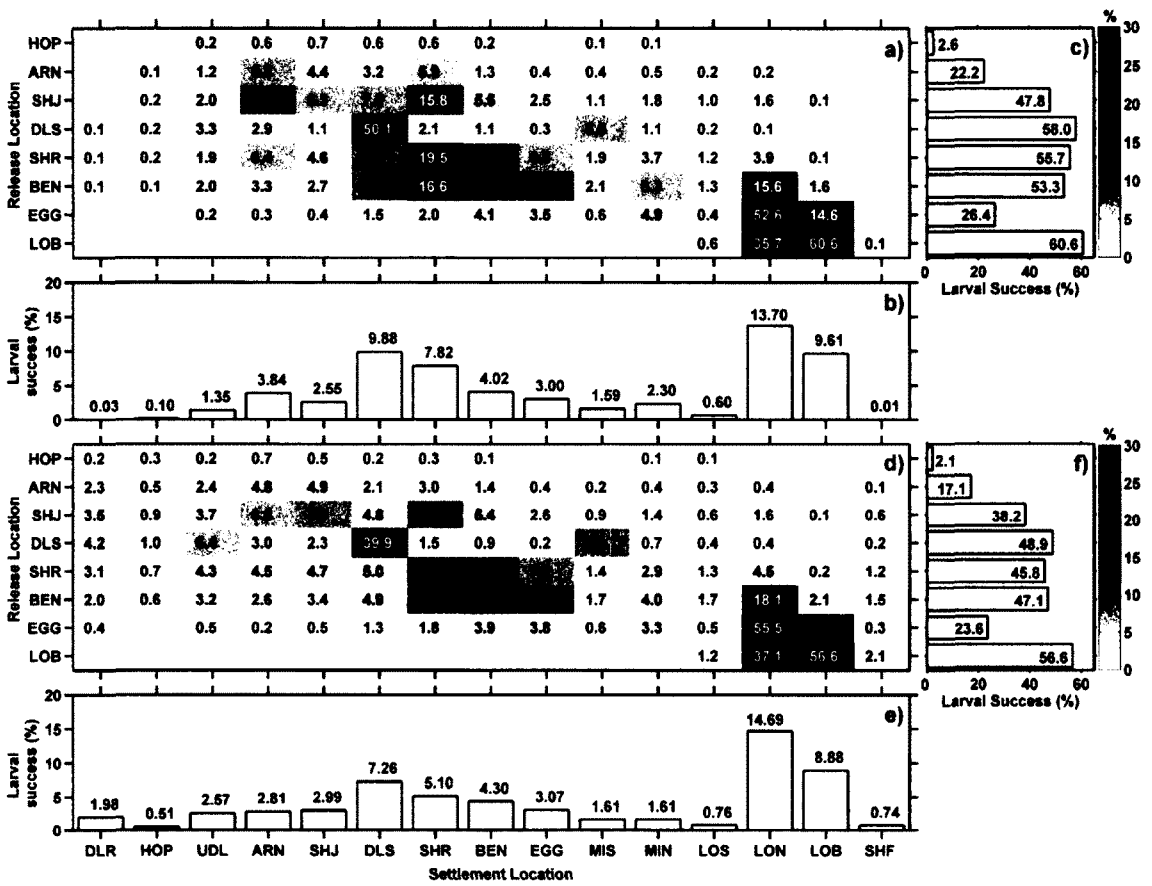

Figure 28. a) The percent of successful larvae released at a particular location (y axis) that set in the same or another location (x axis), b) the average percent of particles arriving at each settlement location, and c) the average percent of particles from the release location that arrived at the natural oyster reefs obtained from simulations done for 2000 that included larval growth and behavior. d) The percent of successful larvae released at a particular location (y axis) that set in the same or another location (x axis), e) the average percent of particles arriving at each settlement location, and f) the average percent of particles from the release location that arrived at the natural oyster reefs obtained from simulations done for 2000 that did not include larval growth and behavior. The degree of connectivity is indicated by the shading, with darker shades associated with higher connectivity. See Figure 14 for reef locations abbreviations.

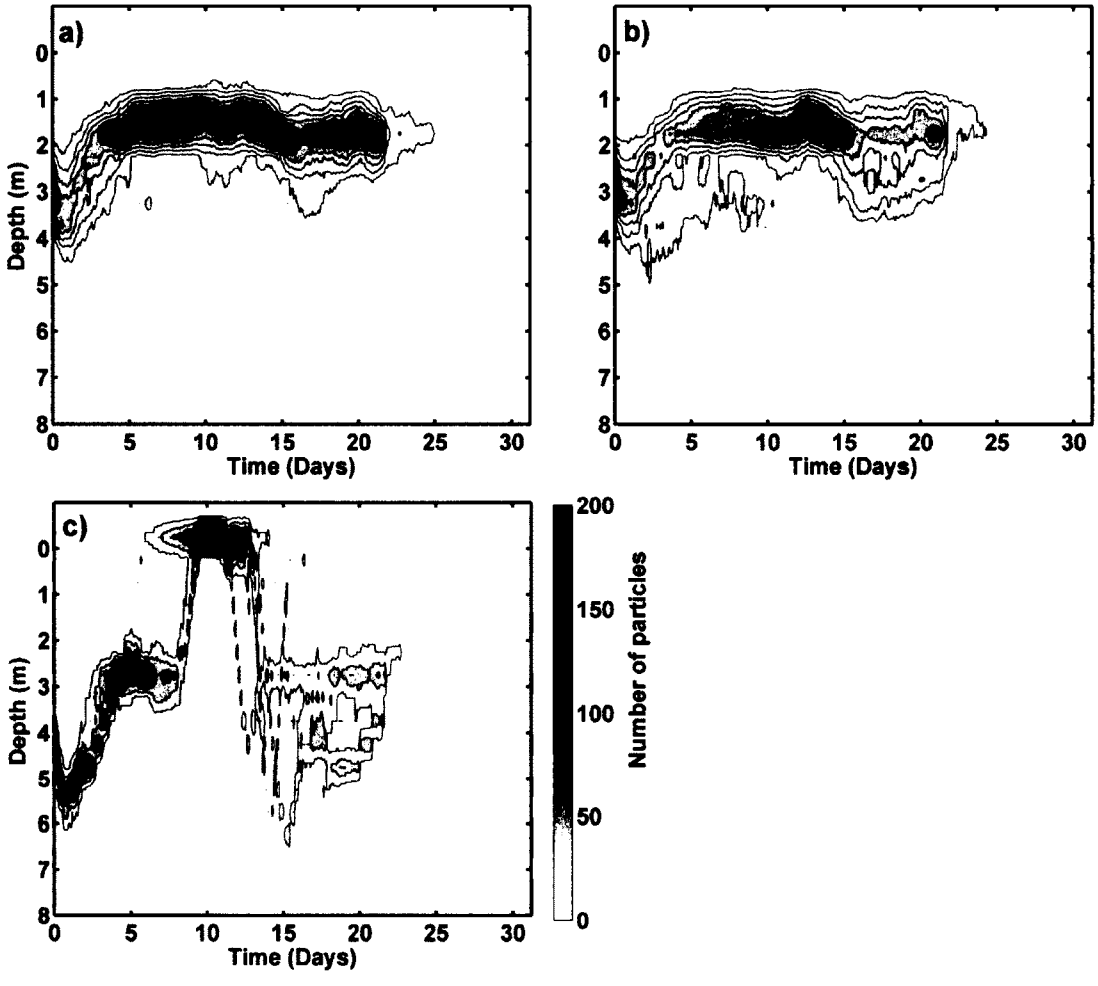

Figure 29. Vertical distribution of particles released from Shell Rock on August 24, 2000 obtained from simulations a) with biological growth and behavior, b) without growth and behavior and c) with growth and behavior but without sub-grid vertical mixing.

4.4 DISCUSSION

In this study, larval success (as a measure of survival) and larval transport (including physical transport and biological behavior) were used to determine relationships

between circulation, salinity and larval growth and behavior that control intraseasonal dispersion of oyster larvae in Delaware Bay. The two main relationships that were identified combine the effects of preferred transport pathways and salinity conditions that are conductive to larval growth and hence survival. Both spring and neap tides provide consistent changes in flow direction and salinity conditions and the fortnightly periodicity of these changes is within the 30-day life span of an oyster larva for Delaware Bay. The episodic increases in river discharge, and concurrent decrease in Bay salinity, are less regular events, but can persist for extended times and therefore affect larval growth and success.

4.4.1 Effect of spring-neap tides on larval dispersion

The subtidal circulation in the portion of Delaware Bay where natural oyster reefs are located was dominated by fortnightly variability associated with spring and neap tides. During neap tides outflows occurred in the surface layer and inflows in the deep channel and over the shoals. During spring tides barotropic outflows occurred in the upper-middle estuary region. The strong currents associated with spring tides increased tidal mixing, which in turn reduced vertical stratification and residual flow. The slower currents associated with neap tides reduced tidal mixing, enhancing stratification and the residual circulation [*Geyer et al.*, 2000; *Stacey et al.*, 2001].

The fortnightly circulation resulted in larval dispersion variability at the same frequency, which in turn provided a regular and repeating constraint on larval success. Larvae released during barotropic outflows (i.e., spring tides) were transported down-estuary, where high salinity favored larval success by decreasing the time needed to develop to settlement size. During neap tides, larvae were transported up-estuary in their early stages where low salinity waters increased development times, extending the planktonic time and hence decreasing the probability of success. Larvae entering

to the upper part of Delaware Bay are most likely to be retained in this region (Figure 25), providing a loss for the oyster population.

The effect of the fortnightly tides differed along the oyster reefs. The export of larvae from the middle to upper estuary reef sites was larger when releases occurred during neap tides (Figure 21). For upper estuary regions, where larval success is low, this could be an important mechanism that maintains a supply of larvae that is sufficient for survival of the adult population and also maintains connection of these populations with those in other regions of the Bay. The supply of new individuals to the upper-most reef site, Hope Creek, was very low, suggesting limited connection to the other Delaware estuary populations. *He et al.* [2012] showed that Arnolds and Egg Island oyster populations are genetically homogeneous in terms of disease resistant genes 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 likely contributes to maintenance of these genetic differences. However, *Munroe et al.* [2012] suggested that the characteristics of the adult oyster population are more effective at maintaining and transferring genetic characteristics than are larval exchanges. Thus, larval inputs may be more important for adult population maintenance.

In estuaries at the latitude of Delaware Bay, oyster spawning typically occurs 2-3 times during the spring-summer season [*Dekshenieks et al.*, 1993; *Kennedy*, 1996a]. 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 beds that span upper to lower Bay showed that peak spawning occurred in the lower Bay in June, proceeded up-Bay during the summer, and occurred at upper Bay sites in late July and early August [*Mesquita and Ford*, unpublished data]. This along-Bay gradient in peak spawning results in differential inputs of larvae in space and time that favors inputs from different reef areas as the spawning season progresses. Thus

depending on when and where peak spawning occurs, high frequency flows, such as the fortnightly tides, are important determinants of larval fate. In this regard the tidal flows mediate which reefs are sources of larvae for other areas and which are sinks. Reefs that more consistently provide sources of larvae are likely to have a larger impact on population genetic structure and contribute to the low effective population size determined for Delaware Bay oyster populations [*He et al.*, 2012].

The simulated particle trajectories showed the importance of high salinity in moderating larval growth and total planktonic time. Release from a particular location during the part of the tidal cycle that favors up-estuary transport may significantly reduce the potential set; whereas, release during down-estuary flow may enhance survival and hence potential recruitment. 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 [*Dekshenieks et al.*, 1993; *Kennedy*, 1996a]. Numerous studies have shown relationships between larvae transport and tides, internal waves, and bores [e.g., *Shanks*, 1986; *Shanks and Wright*, 1987; *Pineda*, 1994, 1999], and between the behavioral response of some larvae to the tides [e.g., *Hill*, 1991; *Thiebaut et al.*, 1992; *Forward and Tankersley*, 2001; *López-Duarte and Tankersley*, 2009]. This study extends these by showing that larval growth and potential success is affected by tidal variability.

4.4.2 Effects of river discharge on larval dispersion

The deleterious effect of low salinity on overall larval success in Delaware Bay is discussed in Chapter 3. This study showed that only a few events of high river discharge during the spawning season can decrease overall larval success (Figure 15). These results are based on the discharge of the Delaware River, which accounts for about 60% of the fresh water into the estuary [*Sharp et al.*, 1986a] and is responsible for most of the interannual and seasonal variability observed in the along-estuary

salinity gradient [*Garvine et al.*, 1992].

River discharge also affected the dispersion pattern causing a shift between upper and middle estuary regions in the percent of larvae that reached settlement size. More larvae were transported to the upper estuary during low river discharge conditions. The middle and lower estuary regions received more larval inputs when the river discharge was large. These changes in transport combine with salinity to produce a spatial gradient in success and settlement. However, increased down-estuary flow during high river discharge results in increased up-estuary subsurface flow. The larvae tended to well mixed throughout the water column, so the chances of up- or down-estuary transport are similar. Thus, larval success, which is largely determined by salinity, might be more important than transport patterns in determining exchange rates.

Larvae entrained in the high salinity water associated with the permanent recirculation and weak currents in the western part of the Cape May Peninsula in the lower Delaware Bay had higher rates of success. The circulation of this region supports local recruitment to populations in the lower estuary and allows this region to be a sink for larvae from the middle estuary populations. Retention areas in other estuaries systems have been proposed as control mechanisms of larval dispersal [*Sulkin*, 1981; *Shen et al.*, 1999]. The success of the oyster populations in the lower Delaware Bay may be attributable to the existence of a permanent recirculation in the lower Delaware Bay.

4.4.3 Importance of swimming behavior in larval dispersal

That retention of larvae within estuaries is maintained by vertical swimming behavior is a paradigm for marine systems. The simulated particles that included behavior tended to have higher rates of successful recruitment on the natural reefs in Delaware Bay, but the transport patterns of these particles relative to those without

behavior were not substantially different. Thus, the implication is that transport and larval success rather than vertical swimming behavior are the important determinants of oyster larvae dispersal in Delaware Bay. Vertical swimming behavior has been identified as a critical 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; *Largier*, 2003; *Pineda et al.*, 2007]. However, *Kim et al.* [2010] reported that although vertical behavior was important in retaining oyster larvae near spawning areas, physical transport alone can explain observed settlement patterns in Mobile Bay. This finding was attributed to the regular well-mixed conditions of Mobile Bay. The simulated circulation fields from Delaware Bay showed a well-mixed water column over the shallow areas of the estuary, where the oyster beds are located. The vertical larval distributions showed 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 oyster larvae is a result of the combined effects of behavior, advective flows and turbulent mixing, and all three need to be considered. 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 what maintains larvae around the natural oyster beds and within the estuary. Thus, all three must be represented in models that consider larval dispersal processes.

CHAPTER 5

THE EFFECT OF LARVAL DISPERSION AND ADULT TRANSPLANTATION ON THE MOVEMENT OF DISEASE-RESISTANT GENES BETWEEN OYSTER POPULATIONS

5.1 INTRODUCTION

Gene flow is a major evolutionary force acting upon genetic differentiation. It transfers alleles or genes among geographically separated populations allowing homogenization of the genetic structure of populations over large time scales [e.g., *Conner and Hartl*, 2004]. Gene flow or migration occurs primarily by the movement of individuals from one population to another only if the immigrants successfully reproduce in the new habitat [*Slatkin*, 1985, 1987]. Consequently, gene flow is critical to understanding the connectivity among populations and the evolution and adaptation of populations to fluctuations in the environment [*Hedgecock*, 1986; *Hedgecock et al.*, 2007].

For many benthic species with sessile adult life (e.g., mussels, clams, oysters) gene flow is mainly due to the dispersal of larvae from spawning grounds to settlement locations [*Palumbi*, 2003; *Cowen and Sponaugle*, 2009]. Thus, to understand how genetic adaptations are transferred from one population to another, a primary task is to identify source and sink populations, estimate the number of individuals (larvae) that are being exchanged among populations and determine how the environment affects the biological (e.g., growth, behavior) and physical (e.g., advection, diffusion) processes driving the dispersal of larvae. Furthermore, information on population mortality, abundance, effective population sizes (genetic drift) have to be combined with larval dispersal studies to determine the effectiveness of gene flow in evolutionary timescales [*Munroe et al.*, 2012].

The effects of gene flow on the changes of the genetic structure of marine organisms play an important role in the response of some species to factors causing populations decline (e.g., overfishing, habitat loss, pollution, diseases, etc). Especially important are the genes that contain alleles associated with some specific ecological traits related to fitness, such as reproduction and disease resistance. Diseases in marine ecosystems have been identified as a major cause of mortality of many marine animals [e.g., *Harvell et al.*, 2002; *Lafferty et al.*, 2004; *Powell et al.*, 2008]. However, in contrast to terrestrial ecosystems, information on marine ecosystems is still inadequate to understand some of the basics relationships causing diseases. Complex life histories of marine species, pathogens with greater numbers of intermediate hosts, and no barriers for disease transmissions, among others, make the knowledge of terrestrial diseases unsuitable to marine ecosystem [*McCallum et al.*, 2004].

The eastern oyster (*Crassostrea virginica*) is affected by two diseases that strongly influence its population abundances [*Council*, 2004]. Both diseases, the Multinucleated Spore Unknown (MSX) and Dermo are caused by the protozoans parasites *Haplosporidium nelsoni* and *Perkinsus marinus*, respectively [*Haskin and Andrews*, 1988; *Ford and Tripp*, 1996]. Selective breeding experiments have demonstrated that some oysters are genetically resistant to both MSX and Dermo diseases [e.g., *Ford and Haskin*, 1987]. Development of MSX disease-resistance has been reported for Delaware Bay since the 1970s [*Haskin and Ford.*, 1979], but only lately has it been shown that MSX disease-resistant genes are widespread in the Bay [*Ford and Bushek*, 2012]. Resistance to MSX has also been found in lower bay areas in the Chesapeake Bay, but localized in small areas and not widespread as in Delaware Bay [*Carnegie and Burreson*, 2011].

The development of disease resistance has been associated with the response of the disease-causing parasites to the environment. The MSX and Dermo pathogens are more tolerant of high salinity waters; as a result, oyster populations in these areas have

developed resistance by the continuous disease exposure. Oyster more susceptible to disease inhabit the low salinity areas, where the absence of the disease pathogens reduces the disease pressure [*Haskin and Ford.*, 1979; *Ford and Bushek*, 2012]. The differential in disease pressure produces variability in resistant individuals [*Carnegie and Burreson*, 2011] and creates disease refuges (i.e., zones with low infections) in the low salinity areas [*Hofmann et al.*, 2009]. These refuges are important as mortality by disease is not significant in these areas; however, they also might prevent or reduce the development of disease resistance the metapopulation level [*Ford et al.*, 2012].

To understand the adaptation of oyster populations to the selection of certain traits, an important factor in to determine the temporal scale involved in transference and development of disease resistance genes. For example, the transfer of MSX disease-resistant genes among the wild populations in Delaware Bay has been a result of only two large selection events occurring in the mid-1950's and 1980's [*Ford and Bushek*, 2012]. The 1984-1986 epizootic occurred after a drought that allow MSX disease move to the upper bay refuge area. The prevalence of MSX disease decreased considerably after this events which suggests that animals that repopulated the bay were dominated by MSX disease-resistant individuals [*Hofmann et al.*, 2009; *Ford and Bushek*, 2012]. In contrast to MSX disease, the development of Dermo resistance is not well known. Dermo has not reached the same high intensity levels; this can be explained by the higher tolerance of Dermo to lower salinities than MSX [*Powell et al.*, 2008]. Thus Dermo epizootics occur frequently in Delaware Bay suggesting little or no development of resistance. Another important aspect is to determine the number of immigrants required to produce a change in the genetic structure of the population. Large number of immigrants can transfer genes more rapidly among populations, favoring or decreasing the development of beneficial traits.

Although there are numerous methods to infer gene flow from genetic analysis [e.g., *Hedgecock*, 1986], these methods have a temporal constraint and it is difficult

to track the origin and number of immigrants. Thus, numerical models can be very useful to answer basic questions regarding gene flow. The available information of the relationships existent between oyster population dynamics and diseases has allowed the development of an individual-based model (DyPOGEn) that simulates the genetic structure of eastern oyster [*Powell et al.*, 2011a,b,c]. We use this model to investigate variability in the genetic structure of Delaware Bay oysters associated with the input of new alleles to the population. The new alleles represent immigrations of individuals with different genotypes, in this case coming from medium and high disease-resistant populations. Specifically we address questions such as, How many immigrants are required to produce an effect in the accumulation of an allele? How long must these immigrations be, and how does the age of the immigrants affect the allele's transfer? Addressing these research questions will allow us to better understand gene flow caused by natural (larval dispersion) and man-induced (transplantation) migrations as well as the temporal scales and immigrations sizes required to genetically change oyster populations. In the next section we describe the genetic model and the simulations performed to address the objectives. The results section shows the importance of larval dispersion over transplantation for the gene flow. These results are discussed in terms of the development of disease-resistant genes in Delaware Bay.

5.2 METHODS

This study uses the capabilities of an individual based genetic model developed under the NSF Biocomplexity in the Environment Program. The Dynamic Population Genetics Engine (DyPoGEn) model couples genetic structure to physiology of individual animals, and ultimately, population dynamics [*Powell et al.*, 2011a,b]. The model has been configured to simulate the genetic structure of *Crassostrea* oysters such as *C. gigas* and *C. virginica*. Oysters are diploid organisms with 10 pairs of chromosomes [*Wang et al.*, 1999, 2005]. The model allows each chromosome to

have multiple genes with multiple alleles. The population is described by the allelic structure of each individual.

The model framework follows a series of steps to determine the population characteristics, such as abundance, mortality, age, etc. [see *Powell et al.*, 2011a,b,c, for details of the equations and parameters]. Each year the population first suffers random adult mortality based on age. Then potential parents are chosen and reproduction occurs. Gametes are formed by meiosis and each set of haploid chromosomes have mixed allelic structure determined by random draw of chromosome strands from the parental genotype. Each offspring suffers random larval mortality. Finally each recruiting animal is assigned a birth date, a unique identifier, an age of zero and a functional sex based on its sex genes. The model allows crossover, random variation of number of offspring, fitness, among others processes [*Powell et al.*, 2011a,b,c].

5.2.1 Model Implementation

We used a chromosome configuration with four genes, with two alleles per gene. The model simulation was designed to add new individuals with specified genes to the population. One allele, in the first gene location (loci) of each chromosome on the second chromosome pair was marked with "0" or "1" to represent whether the disease resistant trait was present ("1") or not ("0"). To distinguish between initial animals and new immigrants, all initial animals were configured to be homozygotes, i.e., "00" animals. The new immigrants had at least one "1" alleles on the second chromosome pair (hereafter "01", "10" or "11" animals). No significant differences in the results occurred if other chromosome pairs were used.

The focus of these simulations was to study the rate of transference of beneficial (disease-resistant) or non-beneficial (neutral) genes. The beneficial effect of the imported alleles through fitness was implemented by setting a "00" animal to have fitness of 0, a "01" animal to have fitness of 0.5 and an "11" animal to have fitness of

1. This scheme provided an average benefit for the heterozygous individuals. The average age of mortality (5 years, from preliminary results) was increased by the fitness value for an animal to represent a form of disease resistance. Thus, an animal with a fitness of 1 lived on average one year longer than those with fitness of 0 (no benefit). This extension in the lifetime allowed the resistant animals to reproduce and retain the beneficial gene in the population.

5.2.2 Simulations

The experiments were performed for a range of model configurations to represent several features of the immigrants and immigrations (Tables 11 and 12). We set up simulations having the new immigrants being adults (2+ years old) which mimicked the effects of transplantation (T) of oysters and having new immigrants being 1 year old which mimicked the effects of larval dispersion (L). Each of these experiments was repeated with the new allele being neutral (N) (no benefit) or conferring a benefit (B). Additionally the effects of the selection of single or multi loci was examined with two sets of experiments where new immigrants were marked in the first position of the second chromosome pair (G1 or single-locus) or marked by all four genes of the second chromosome pair (G4 or multi-locus) (see Table 11 for all the models combinations)

Table 11. Genetics simulations varying the age and benefits of the new immigrants.

Immigration	Disease Resistance	Gene	Reference
Transplantation	Neutral	G1	TNG1
		G4	TNG4
	Benefit	G1	TBG1
		G4	TBG4
Larval Dispersion	Neutral	G1	LNG1
		G4	LNG4
	Benefit	G1	LBG1
		G4	LBG4

Table 12. Cases performed varying the number of immigrants and the time of the immigrations. For all the cases, the immigrations begin in generation 50.

Cases	% Immigrants	Type of Immigrations
Case0	0	
Case1	0.1	
Case2	0.5	Continuous immigrations
Case3	1.0	(Immigrants every generation)
Case4	5.0	
Case5	10.0	
Case6	0.1	
Case7	0.5	Episodic immigrations
Case8	1.0	(Immigrants for 10 generations)
Case9	5.0	
Case10	10.0	

A total of 10 cases were performed for each of the previous model setups, all the cases consisted of having a population that received a varying number of immigrants added through continuous (every generation) and episodic (for only 10 generations) immigrations (Table 12). The number of immigrants was estimated as a function of the average population size obtained from the reference case (Case0) and represent between 0.1 and 10% of the receiving population (Table 2). The model was allowed to adjust for 50 generations before any immigrants were added. All the simulations start with ~300,000 individuals and were run for 200 generations (200 years).

Simulations were run to identify the effects of immigrants from different populations based on the degree of disease resistance. Two cases were analyzed: (1)

Immigrants from population with high disease-resistant genes were marked as "11" animals, (2) immigrants with medium disease resistance were marked as "01" animals. Note that "01" and "10" animals had the same impact in the simulations. In both cases the initial animals in the base populations were marked as "00" animals. Therefore, a total of 160 simulations were performed which include the 8 model setups (Table 11), 10 cases for each model setup (Table 12) and 2 experiments with immigrants originating from high and medium disease resistance populations.

The frequency that the new allele appeared in the population (allele frequency) was calculated to estimate the transference of that particular allele among the individuals of the population. The allele frequency is calculated counting all the "0" alleles and "1" alleles and then dividing by the total number of alleles for the whole population. This information was used to calculate the elapsed time from the introduction of the new allele to the allelic frequency becoming common (reaching 25%) or dominant (reaching 50%).

5.3 RESULTS

The number of immigrants arriving in the population was estimated in terms of the temporal average of the population size estimated from the reference simulation (Case0 in Table 11). However, the modeled oyster population abundances were highly variable (Figure 30a), showing large changes in population size during the first 100 years, dominated by two large cycles of 40-60 year. After 100 years the population size varied mostly on shorter time scales (1-10 years) (Figure 30a). Additionally, each of the simulations in Tables 11 and 12 produces variability in the population size as well (Figure 30b). From the arrival of immigrants in generation 50, the abundances fluctuated between 400,000 and 1,400,000 individuals, with the median around 720,000 individual. The immigration rates were re-estimated to account for this variability (Table 13). Overall, the means were close to those initially used, especially for

smaller number of immigrants. Larger numbers of new immigrants tended to cause larger standard deviations but the means were of the same order of magnitude. For simplicity, hereafter we will refer to our preliminary immigration sizes, but taking in account the new estimates in the immigration sizes based on the variability in the modeled population abundances.

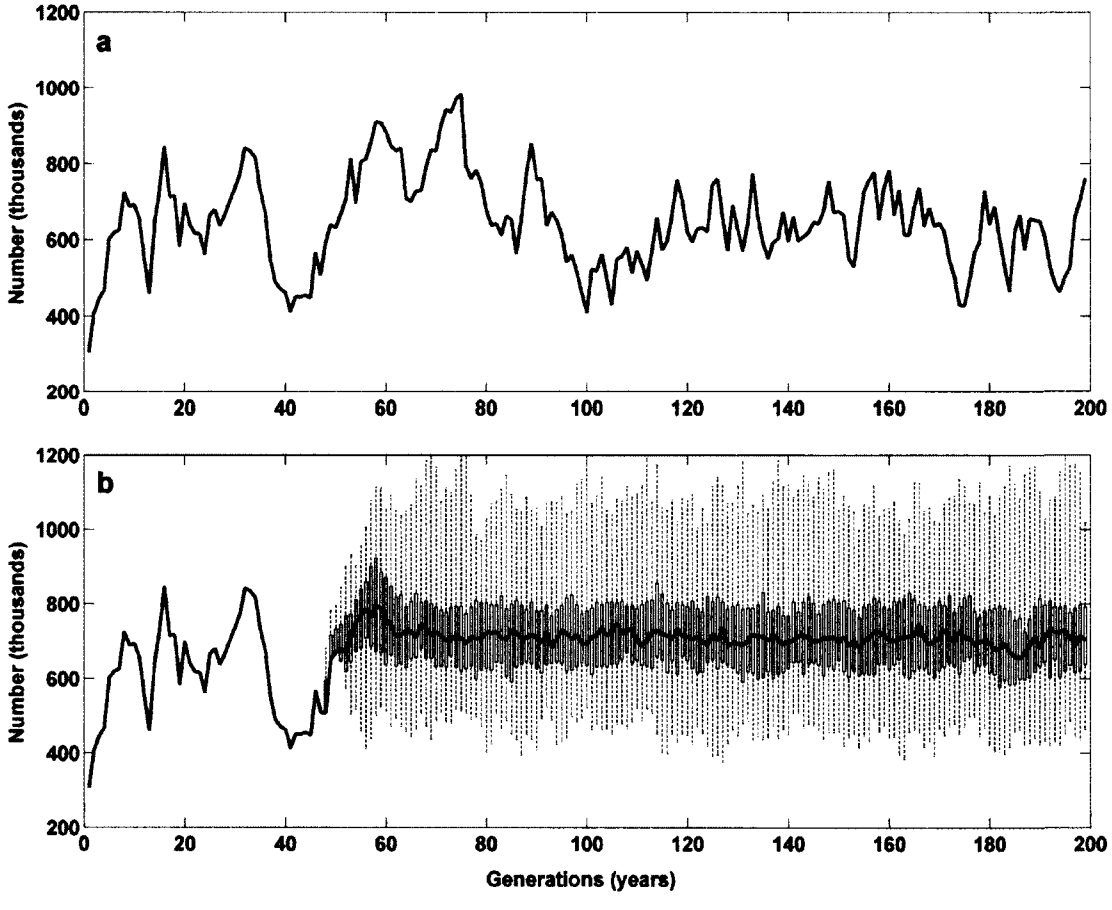

Figure 30. Populations abundance from the reference simulation (Case0) (a). Box plot using all 160 simulations (see Tables 11 and 12) (b), at each generation the median (black line), minimum and maximum range (dashed lines) and 25th and 75th percentile (blue box) of the abundance were estimated.

Table 13. Immigration rates based on the variability of the population abundance.

	Initial Immigrations rates (%)				
	0.1	0.5	1.0	5.0	10.0
Mean	0.14	0.72	1.43	7.17	14.35
MAX	0.27	1.35	2.69	13.46	26.93
MIN	0.08	0.41	0.82	4.10	8.20

The establishment of the introduced gene in the population was tracked by analyzing the changes in the allele frequency (Figure 31). Since there were no "1" alleles initially and no immigrants, the "1" allele is absent for the first 50 generations. For continuous immigration, adding ~700 immigrants (0.1% in Table 11, 0.08-0.27% in Table 13), resulted in a slow accumulation of the "1" allele. Even after adding immigrants for 150 generations, the average allele frequency in the population is around 25% (C1 in Figure 31). So, the allele accumulates in the population gene pool, but rather slowly. As expected, increasing the numbers of immigrants (Cases 2-5) causes the allele to accumulate faster and to be include in more of the population (upper panels Figure 31). For large immigration fraction (Cases 4-5), it was possible for the allele frequency to be ~1 at generation ~150, i.e, the immigrant allele became completely dominant. The small variability in allele frequency is due to genetic drift.

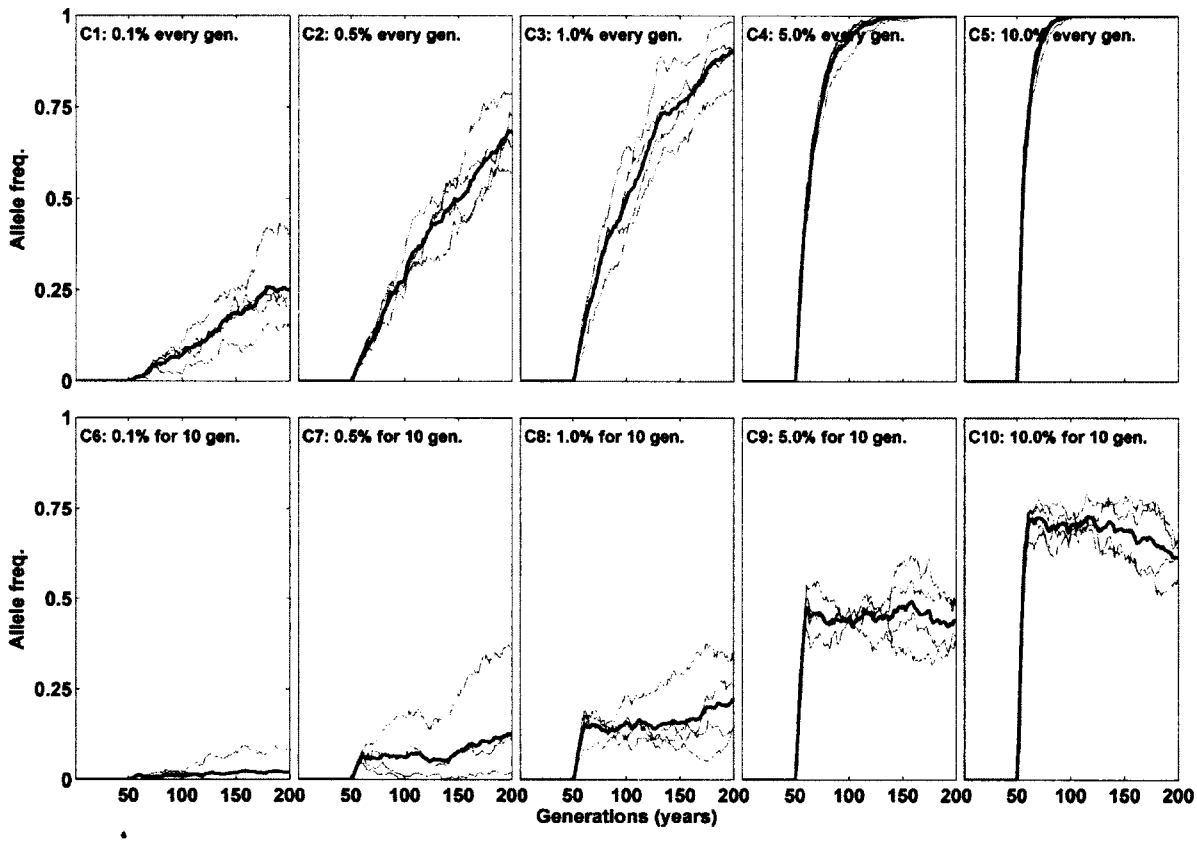

Figure 31. Allele frequencies from the simulations TNG1, TBG1, LNG1 and LBG1 (Table 11) where low disease-resistant populations ("00" individuals) received high disease-resistant immigrants ("11 individuals). Black lines represent the mean of the 4 simulations (gray lines) for each model configuration.

The simulations with episodic immigration also showed accumulations of the introduced allele, but at slower rates than with continuous inputs (lower panels Figure31). For example, with the smaller number of immigrants (Case6), there was a persistence of the "1" allele on average, even after immigration stops. During the episodic immigration with larger numbers of immigrants (Cases 7-10), the allele fraction increases. After immigration stops, the allele frequency does not change much but slowly drifts up or down for different simulations. Only for the highest number of immigrants

does the introduced allele become dominant (>50%) in the gene pool (C10 in Figure 31). For small immigrations, random drift allowed the neutral and beneficial allele to vanish in several of the simulations indicating the weak effect of small numbers of immigrants for only a few generations.

Although the character of the previous solutions look different, the only real issue is to determine how many generations it takes to have the "1" allele become common or dominant. Hence, the elapsed time from the introduction of the new alleles until the allele frequency reaches 0.25 (25%, i.e., common) and 0.5 (50%, i.e., dominant) was estimated for each simulation.

5.3.1 Immigrations of individuals from high disease-resistant populations

The single-locus simulations (G1) showed a decrease of the elapsed time with the increase of the number of immigrants for continuous (Figure 32a and c) and episodic (Figure 32b and d) immigrations. For very low continuous immigrations (0.1%), only larvae conferring a benefit to the population became common (>25%), with an elapsed time of 100 years. In contrast, for larger continuous immigrations (5-10%), the introduced allele became common in <5 years (Figure 32a) and dominant in about 10-15 years (Figure 32c). The episodic immigration with low immigrations rates showed only beneficial alleles becoming common in more than 80 years (Figure 32b). However, only large episodic immigrations seems to effectively transfer neutral and beneficial alleles (Figure 32b and d). Thus, for neutral cases with low input of immigrants (0.1-1%), continuous immigration may represent the only mechanism for the introduced allele to become common. Compared to continuous immigrations (Figure 32a and c), episodic immigration tended to establish more slowly the introduced allele in the populations.

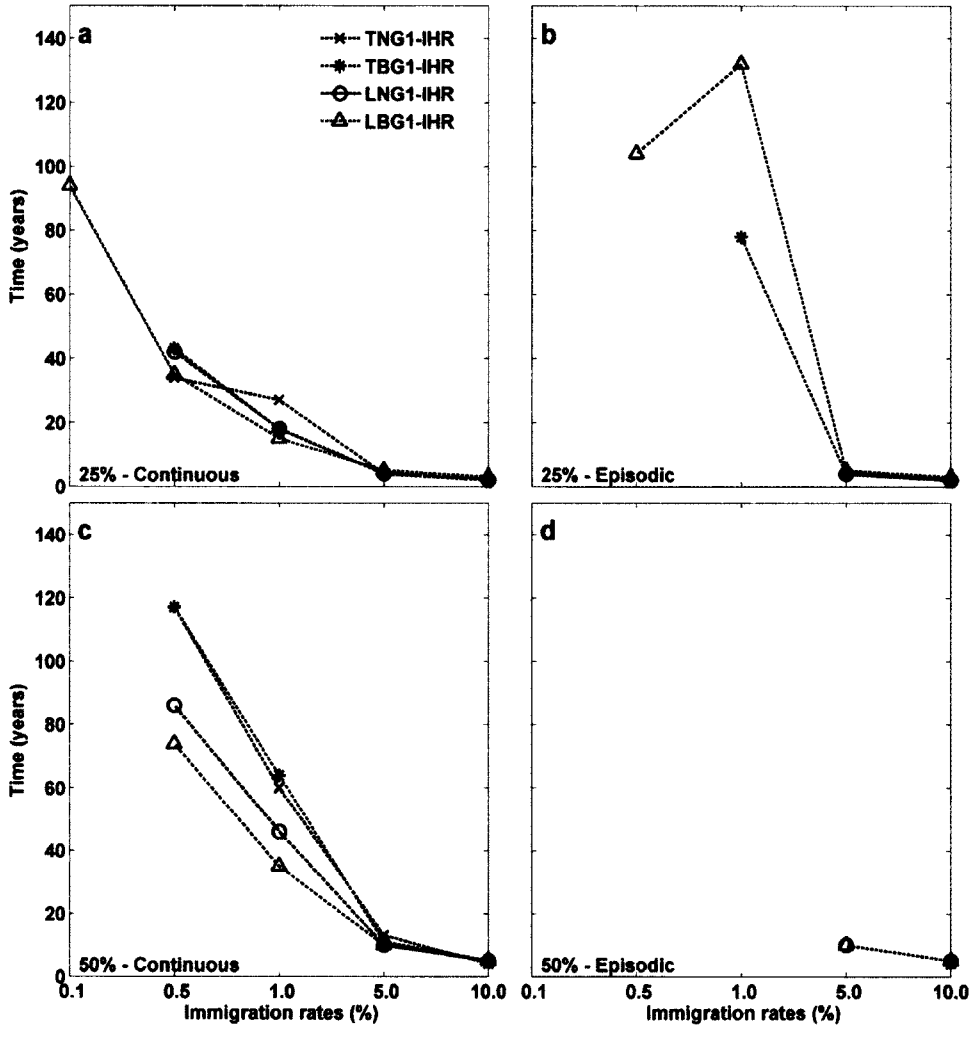

Figure 32. Elapsed times from the arrival of immigrants to the allele frequency reaching 25% and 50%. The simulations are shown for continuous and episodic immigrations for the single-locus configuration (TNG1, TBG1, LNG1 and LBG1).

Multi-locus simulations (G4 in Table 11) showed similarities with the single-locus results. Continuous immigration established the introduced allele faster than the episodic immigration, i.e., shorter elapsed time for the new allele become common (Figure 33) or dominant (Figure 34). Simulations conferring some benefit also improved the allele retention in the population, which seemed particularly important

for low episodic immigration simulations (Figures 33 and 34). The most noticeable differences between single- and multi-locus cases were that the elapsed time for the new allele to become common or dominant is larger in the multi-locus cases. The difference occurred because more alleles are involved in the disease resistance and it takes longer for multiple genes to become established in the population.

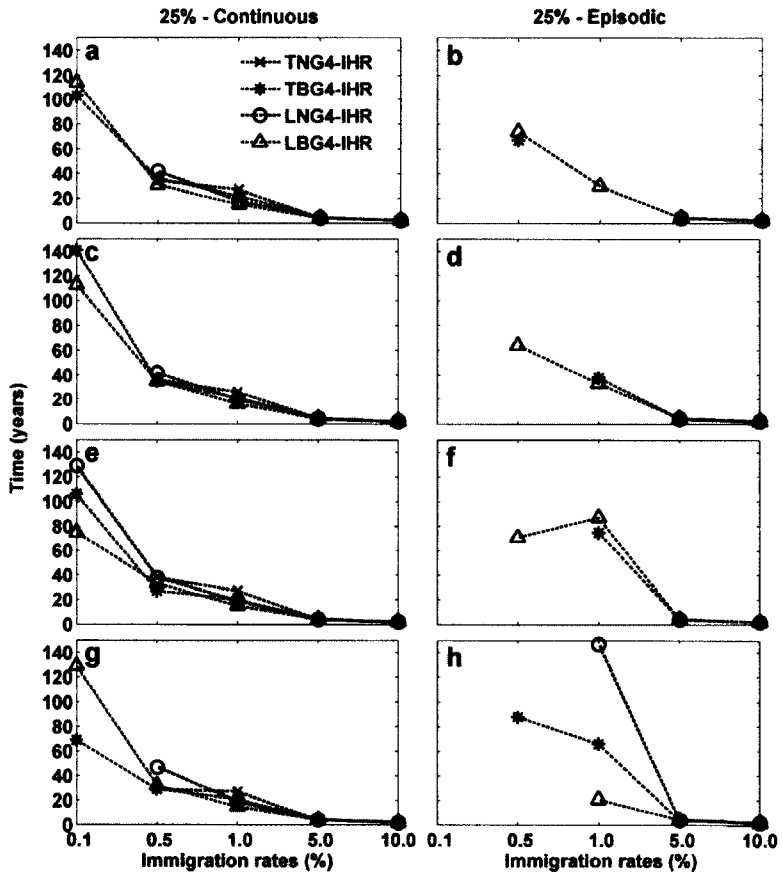

Figure 33. Elapsed times from the arrival of immigrants to the allele frequency reaching 25% for continuous and episodic immigrations for multi-locus simulations (TNG4, TBG4, LNG4 and LBG4). Simulations correspond to high disease-resistant immigrants ("11" individuals) arriving in low disease-resistant populations ("00" animals).

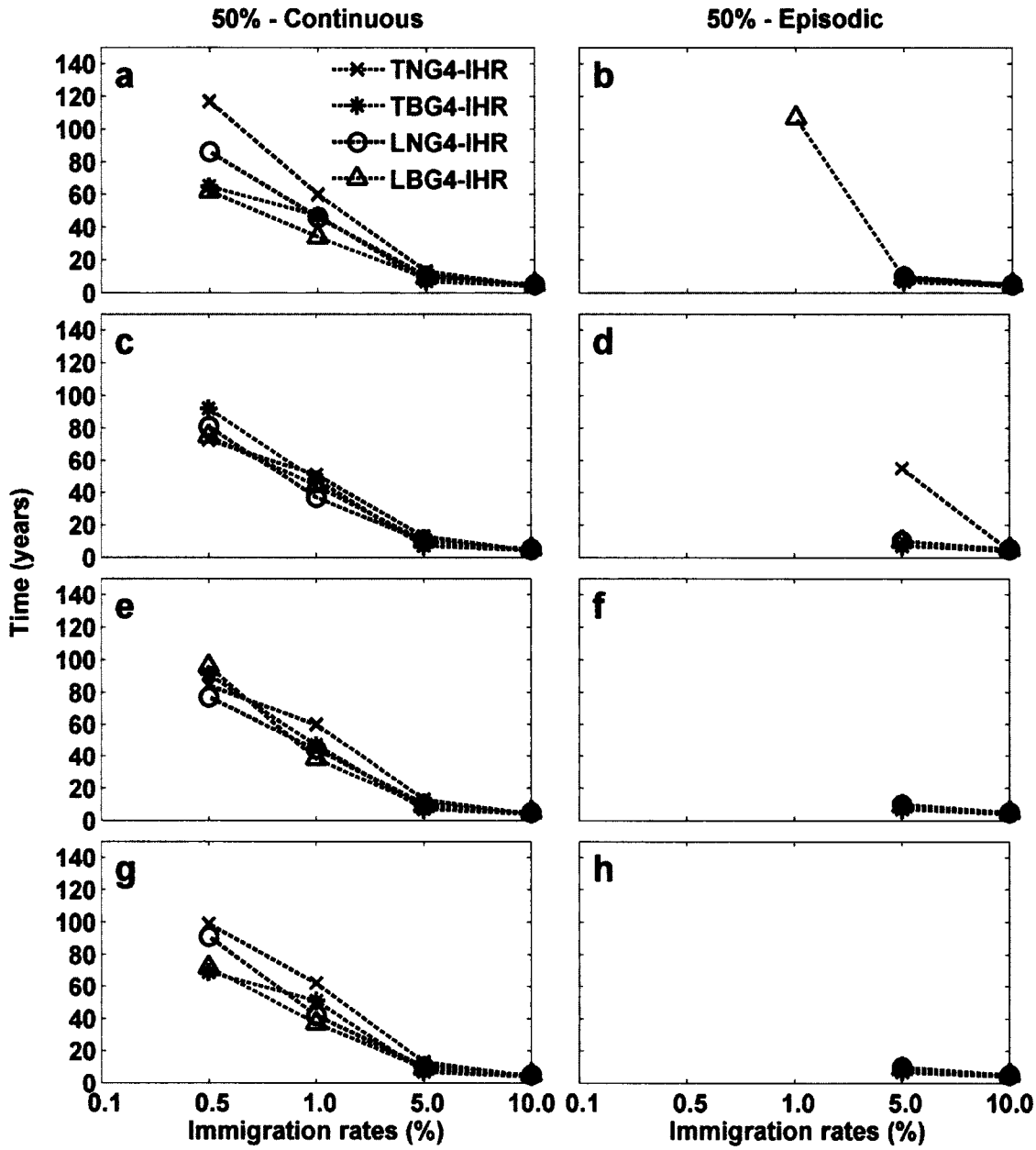

Figure 34. Elapsed times from the arrival of immigrants to the allele frequency reach 50% for continuous and episodic immigrations for multi-locus simulations (TNG4, TBG4, LNG4 and LBG4). Simulations correspond to high disease-resistant immigrants ("11" individuals) arriving in low disease-resistant populations ("00" animals).

5.3.2 Immigrations of individuals from medium disease-resistant populations

Immigrations of medium disease-resistant individuals ("01" animals) increased the elapsed time for the introduced alleles to become common (Figure 35) or dominant (Figure 36) in the population. For the new allele to become common with low continuous immigrations (<1%), it required 2-3 times longer than for high disease-resistance immigrants. The only exception was for immigrations of 0.5% for TBG1 simulations (Figure 35c), where high and medium resistant immigrations had similar transference rates. The differences became smaller when the immigration was higher (>5%). Only immigrations larger than 5% effectively transferred the introduced allele during episodic immigrations (Figure 35). For the new allele to become dominant, the differences between high and medium disease-resistant simulations were larger, especially for higher number of immigrants (Figure 36). As the high disease-resistant immigrations, individuals conferring benefit and/or larvae immigrants had greater effects in the allele retention (Figure 36).

5.3.3 Effects of simulated larval dispersion on gene flow

In the previous Chapters, larval exchange rates were estimated among oyster populations in the Delaware Bay estuary using a coupled larval-hydrodynamics model. Here those exchange rates are used to get a better estimation of the number of larvae release from high and medium disease-resistant populations that potentially arrive in low disease-resistant populations. Delaware Bay oyster were separated into low (Hope Creek and Arnolds), medium (Ship John and Shell Rock) and high (Bennies and Egg Island) disease-resistant populations [*Powell et al.*, 2008]. Larvae were release every 5 days for the spawning season of 1984, 1985, 1986, 2000 and 2001. The mean and standard deviation for each year are shown in Figure 37. Low disease resistant populations in the upper Bay (especially Hope Creek) received few larvae from the

middle and lower Bay populations (Figure 37). There is a clear relationship between number of larvae and the distance from the settlement location. For instance, larvae released from Egg Island had less influence over the low disease-resistant populations than larvae released from Ship John (Figure 37). Exchanges rates also had some interannual variability, which was been previously discussed.

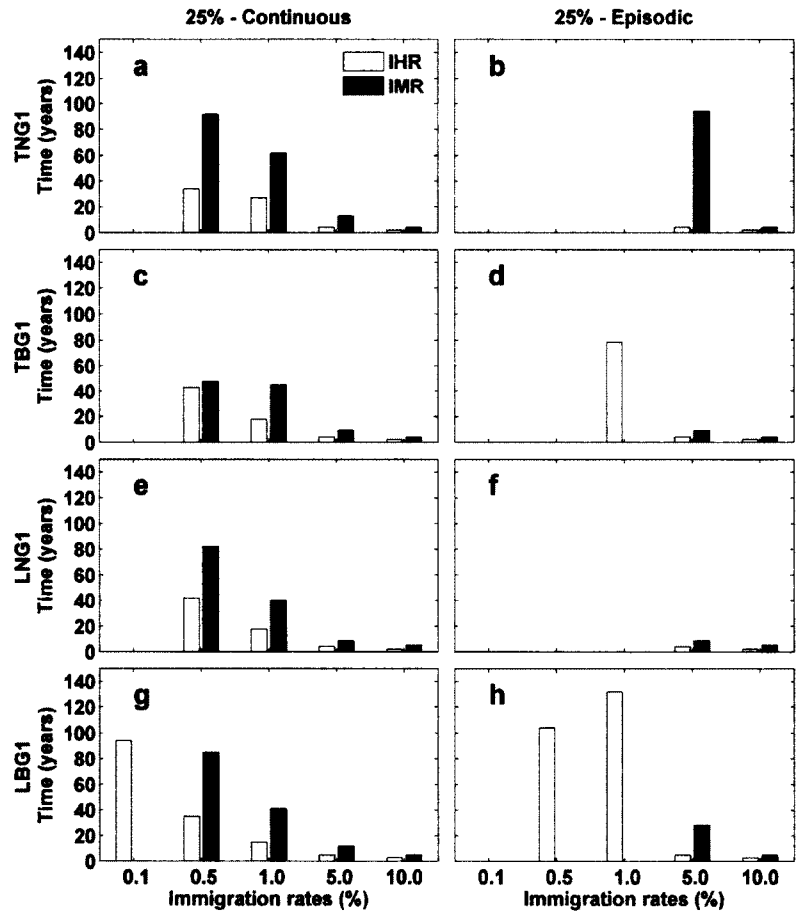

Figure 35. Elapsed times from the arrival of immigrants to the allele frequency reaching 25% for continuous and episodic immigrations for immigrants from high disease-resistant populations (IHR, "11" individuals) and medium disease-resistant populations (IMR, "01" individuals). Simulations correspond to single-locus configurations (TNG1, TBG1, LNG1 and LBG1).

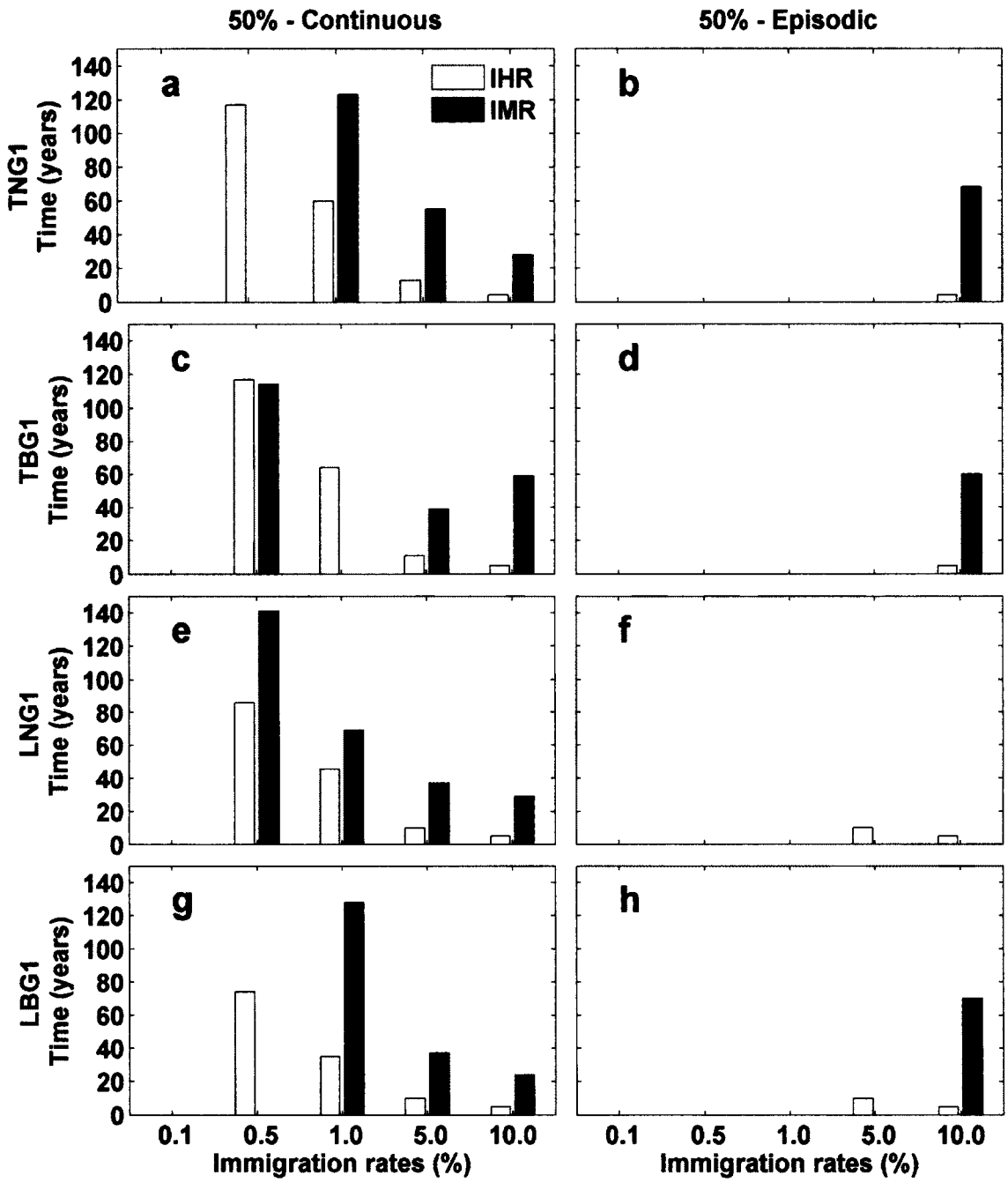

Figure 36. Elapsed times from the arrival of immigrants to the allele frequency reach 50% for continuous and episodic immigrations for immigrants from high disease-resistant populations (IHR, "11" individuals) and medium disease-resistant populations (IMR, "01" individuals). Simulations correspond to single-locus configurations (TNG1, TBG1, LNG1 and LBG1).

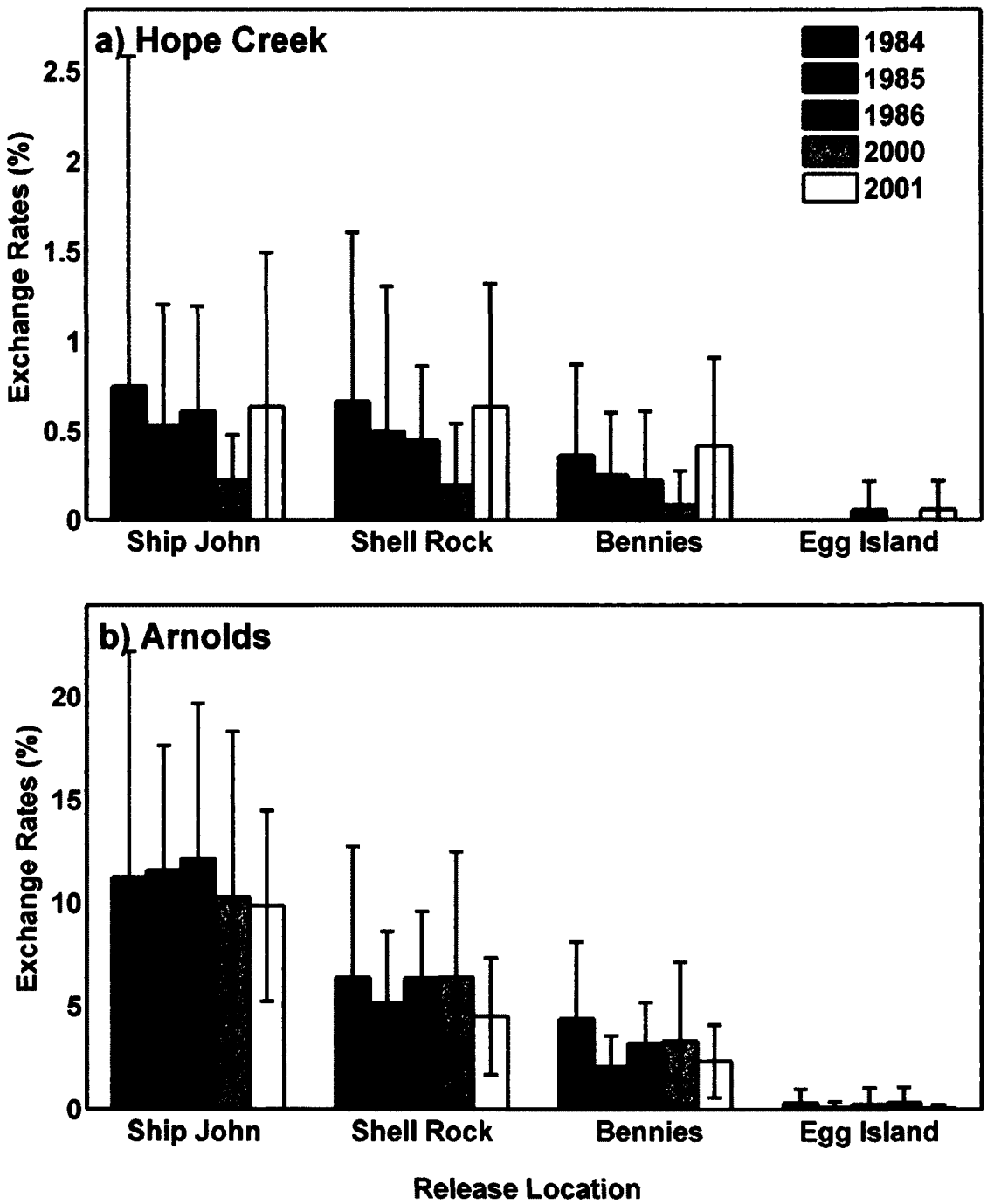

Figure 37. Exchange rates obtained from the larval dispersal simulations in Chapter 3 and 4. Each bar represents the mean for the 19 releases in each spawning season with its correspondent standard deviation. Each value is the percent of larvae released in the x-axis oyster bed that settled in Hope Creek (upper panel) and Arnolds (lower panel) populations.

The exchange rates in Figure 37 were calculated from the number of larvae released from a particular location, i.e., they represent a percent of the released larvae. For the genetic simulations presented here, the number of immigrants represents a percent of the modeled population size. Therefore, in order to connect the exchange rates with the results of the genetics simulations, we have to represent the number of immigrants from the exchange rates as a fraction of the population size instead of a percent of the release number of larvae. The number of immigrants (NI) is related to the number of released larvae (NRL) such as: NI = NRL x ER/100, where ER is the exchange rates. The number of immigrants in the genetic simulations (NIG) is related to the population size (PS) and the immigration rates (IR) and can be estimated by: NIG = PS x (IR/100). Then, we can express the immigrations rates (IR) in terms of the exchange rates by equating both of the previous equations such as, IR = ER x NRL/PS. The number of release larvae (NRL) is related to spawning abundances which are not available for the Delaware Bay oyster reefs. Nevertheless, there is information of biomass for the different populations [*Powell et al.*, 2008]. Assuming that the spawning number is proportional to the biomass, NRL can be estimated. Similarly, the populations size (PS) also was obtained from the biomass data available. As an example, the ratios NRL/PS between different high and low resistant populations were estimated for the year 2000 (Table 14). The population biomass have similar order of magnitude for all the reefs (rations between 0.6-1.2), except for Ship John in the middle of the Bay, which have large biomass producing the largest ratios (Table 14).

Table 14. Oyster biomass ratio for Delaware Bay populations for 2000.

Resistance		Low Resistance Populations	
		Hope Creek	Arnolds
Medium	Ship John	11.5	9.8
	Shell Rock	1.2	1.0
High	Bennies	1.3	1.1
	Egg Island	0.8	0.7

The large population size of Ship John caused the highest immigrations rates to be from larvae released in this area, even for small exchange rates (Table 15). For Hope Creek, immigration from medium disease-resistant population such as Ship John might surpass >5-10% (the highest immigration in our simulations), which would result in introduced alleles becoming common in <20 years and dominant in <60 years (see LNG1 and LBG1 in Figure 35). Immigrations from Shell Rock and even Bennies (e.g., 1984, 2001, Table 15) might cause immigrations as large as 1% in Hope creek. This suggests that continuous immigrations from these populations could transfer disease-resistant genes rapidly enough that they will become common in <40 years (for Shell Rock) and <20 years if coming from Bennies (Figure 35). Immigrants from Egg Island could also have an impact in the genetic structure of upper estuary populations, but over a much longer time scale. In general, the percent of larvae arriving in Hope Creek is less than 0.1-0.2%, according to the results in Figures 31 and 32, larvae can become common but only after than 100 years.

Table 15. Exchange rates expressed as a function of the receiving population. Data represent the means and standard deviation estimated from data in Figure 37

	Medium disease-resistant		High disease-resistant	
	SHJ	SHR	BEN	EGG
		1984		
HOP	8.6 ± 21.1	0.8 ± 1.1	0.5 ± 0.7	0.0 ± 0.0
ARN	110.2 ± 107.5	6.6 ± 6.5	4.8 ± 4.1	0.2 ± 0.5
		1985		
HOP	6.1 ± 7.8	0.6 ± 0.9	0.3 ± 0.5	0.0 ± 0.0
ARN	113.4 ± 59.3	5.9 ± 3.6	2.3 ± 1.7	0.1 ± 0.2
		1986		
HOP	7.0 ± 6.7	0.5 ± 0.5	0.3 ± 0.5	0.1 ± 0.1
ARN	119.1 ± 73.4	6.5 ± 3.3	3.6 ± 2.2	0.2 ± 0.5
		2000		
HOP	2.6 ± 2.9	0.2 ± 0.4	0.1 ± 0.3	0.0 ± 0.0
ARN	100.9 ± 78.4	6.6 ± 6.2	3.7 ± 4.2	0.2 ± 0.5
		2001		
HOP	7.4 ± 9.8	0.8 ± 0.8	0.5 ± 0.6	0.1 ± 0.1
ARN	96.6 ± 45.1	4.6 ± 2.9	2.6 ± 1.9	0.1 ± 0.1

5.4 DISCUSSION

This study shows the applicability of the DyPoGEn model to the study of transmission and accumulation rates of certain genes. We focused on 2 cases: neutral genes and genes representing a trait with a benefit for the population. Neutral genes have neither a positive or negative effect in the population; on the other hand, beneficial

genes confer disease resistance to the population. The model results were used to address the time scales involved in the transmission of genes among populations of eastern oysters as well as the number of immigrants (larvae and adults) required to produce a change in the genetic structure. Our simulations represent a first approach to understand the implications of population variability in genetic shifts, providing insight into the adaptation of marine populations to climate change.

There was high variability in the elapsed time from the arrival of new immigrants to the introduced gene becoming common or dominant, but some general trends can be observed. For instance, when immigrants were introduced as larvae, the allele became established in a shorter period of time during both continuous and episodic immigrations. Thus, the simulations suggested that larval immigrants more effectively established the new allele (neutral or beneficial) in the population than adult transplanted from other populations. This difference between larvae and adults immigrants arises from the age-dependent mortality imposed in the simulated oyster population. Adult immigrants (individuals >2 years old) have fewer opportunities of reproduce; therefore, the chances for exchange of alleles is reduced compared to larval immigrants.

Continuous immigration was more effective in the transmission of the new allele. Nevertheless, large (>5% of the receiving populations) continuous and episodic immigration increase the retention of the new allele at similar rates. When a benefit is introduced with the new allele, the transference of the new trait in the population occurs in a shorter period of time. However, the differences between neutral and beneficial alleles were more significant at low immigration rates only.

5.4.1 Implications for natural development of disease-resistant genes

Oysters are sessile organisms so that once the larva settles it becomes permanently attached to the substrate and becomes part of the adult population. This implies that

the exchange of individuals among different populations and, therefore, the exchange of genetic material, occurs only during the larval stages. In the previous Chapters of this dissertation it was shown that environmental variability plays an important role in eastern oyster larval success and dispersal, which directly affects the exchange rates. Delaware Bay larvae drift mostly down-estuary; with upper estuary populations (Hope Creek, Arnolds) receiving very few of new settlers compared to middle and lower estuary reefs. The exchange of larvae toward upper estuary beds, especially Hope Creek, was very low suggesting a weak influence of the middle-lower populations upon this oyster bed. The results of the genetics simulations show that it could be possible to have a flow of disease-resistant genes from high (middle-lower bay) to low (upper bay) disease-resistant populations, but given the size of the populations and the exchange rates it is unlikely that this gene flow could establish the disease-resistant trait in periods shorter than 30 years (compare LNG1 and LBG1 in Figures 35 and 36 with Table 15). An exception could be larvae going from Bennies to Arnolds where the resistant trait can become common in less than 10 years. A more rapid transference of the resistant trait can be achieved by larvae moving from medium to low disease-resistant populations, especially from Ship John toward Arnolds (~5-10 years). This outcome is mainly due to the much higher biomass of the Ship John bed with respect to the Arnolds biomass combined with exchange rates of about 10%. Ship John could also export the resistant genes to Hope creek in less than 10 years.

A rapid genetic shift associated to development of resistance to MSX disease in the Delaware populations occurred in a period of time of 3-5 years [*Hofmann et al.*, 2009; *Ford and Bushek*, 2012]. Our simulations show that beneficial alleles can become common in 5-10 years, but for only a few of the studied populations. Thus, our results barely support the idea of a rapid transference of disease-resistant genes from high/medium to low resistant populations. However, given the time scales (~10 years) required for the resistant allele to become common under immigrations

>5-10%, it would be possible for the populations to maintain low levels of disease prevalence as occurs for MSX in the Bay. The "regime shift" in the genetic structure of oyster after the 1984-1986 MSX epizootic has been related to a repopulation of the bay by disease-resistant individuals [*Hofmann et al.*, 2009; *Ford and Bushek*, 2012]. The weak connections found in this study suggest that exchange of individuals driven by larval dispersal might not be very important in producing a genetic shift in adult populations. Results from a metapopulation genetic model showed that population mortality is more important than larval dispersion in the transference of neutral allele among the populations of the bay [*Munroe et al.*, 2012]. However, as shown for our simulations beneficial alleles could establish the new allele faster than neutral alleles. Although Delaware Bay oyster populations have developed resistance to Dermo disease, the timescales are longer than for MSX. *Powell et al.* [2011a] found that the development of Dermo resistance occurs in 50 years and is strongly related to mortality rates.

5.4.2 Model Limitations

The numerical approach has the main advantage of detect genetics shifts over large temporal scales, which otherwise would require very long data sets. The lack of information about the number of genes related to disease-resistance and location within the genetic structure created some limitations that arise from the idealized configuration used in these simulations. This configuration considers only 4 genes in each of the oysters 10 chromosome pairs. Only two cases were tested: single- or multi-locus. From the results it is clear that the time for a disease-resistant gene to become common and/or dominant increases for the multi-locus simulations. This difference occurred because of the transference of the allele is divided among more loci, i.e., if more genes where related to disease resistance the time for the new allele to become established in the population will be longer than the times estimated in

these simulations. In order to improve the estimates, a better genetic map with the number and locations of the genes related to disease resistance is required. This map is currently being developed in a complimentary study [*Hofmann et al.*, 2009]. Preliminary results suggest that several genes might be involved in disease resistance, but this might be independent of MSX or Dermo diseases [*Hofmann et al.*, 2009].

The benefit of disease-resistant genes was simulated by decreasing mortality of homozygous individuals with resistant genotype ("11" animals). Disease can also affect other oyster physiological functions such as reproduction, by inhibiting gametogenesis, decreasing gonad size or retarding rate of gamete development during fall [*Thompson et al.*, 1996]. The effects on reproduction impact mostly the oyster spawning size and time, which was not considered in this research. Nonetheless, long-term fluctuations of oyster recruitment in Delaware Bay, that can be used as a proxy for spawning variability, appears to have no association with MSX and Dermo diseases [see Figure 9 in *Powell et al.*, 2008].

The coupling between the genetic and larval model was based on the interaction between two populations (source and settlement). Yet, the exchange of individuals occurs among several of the subpopulations in the Delaware Bay estuary, in which each subpopulation might have different degree of resistance to diseases. *Munroe et al.* [2012] use this same genetic model converted to a metapopulation model to allow differential exchange of neutral alleles among all the subpopulations within Delaware Bay estuary and to include others processes affecting the dynamic of the populations, such as reproduction and mortality. Their study suggests that population mortality might be more important than larval dispersal.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Larval development and success controls the dispersal of oyster larvae, and therefore, the exchange of individuals within the Delaware estuary oyster populations. The temperature and salinity conditions experienced during transport modify larval growth rate, and hence affects dispersal and connectivity between populations. The salinity gradient in Delaware Bay underlies a down-estuary trend in larval success. Larvae produced in the upper estuary have less than a 40% chance of settling compared to an 80% chance for larvae produced in the lower Bay. Interannual variations in river discharge can modify the overall success rates, especially when the low salinity conditions are extended in space and time. Thus larval success in the Delaware estuary might be primarily defined by salinity variability for much of the spawning season.

Intraseasonal variability in larval success and transport was influenced by a combination of the spring-neap tides affecting the larval pathways and episodic increases in river discharge, the same that cause the interannual variability. Larvae released during neap tides in the upper-middle estuary regions are transported up-estuary to low salinity waters. Low salinity decreases larval growth which influences the success of larvae to reach a competent size to settle. Although the larval transport occurs within 5 days from the spawning, the high retention in the upper estuary maintains the larvae in these areas affecting the overall success. In contrast, spring tides drive barotropic outflows, which in turn move larvae down-estuary toward high salinity waters, increasing the chances of success. River discharge affects the larval dispersal by decreasing the percent of larvae arriving at upper estuary populations when large river discharge occurs. This is caused by a combination of decreased larval success and down-estuary transport by large river discharge. Because spring-neap tidal cycles

are common in all the years and increases in river discharge are episodic in only some years, interannual variability in success is most likely due to salinity modifications by river discharge. Only a few of these events might cause large interannual variability in larval success. The well mixed conditions in the estuary, especially in the shallow areas might be responsible of the weak effect of larval behavior in the dispersion of larvae, thus physical transport could be more important than biological behavior in the Delaware estuary.

The simulated transport patterns showed that oyster larvae tend to drift down-estuary during the spawning season. The net result is that mixing of oyster larvae throughout Delaware is extensive. This result is consistent with studies that show that most of the oysters in the main region of Delaware Bay are genetically homogeneous [*He et al.*, 2012]. However, within local regions larval dispersal can deviate from this general pattern. Dispersal of oyster larvae from some of the reefs in the middle and lower regions of Delaware Bay is limited and some show high rates of self recruitment. Mixing of larvae spawned in the upper reaches of the Bay is limited, in part because of the lower overall survival in the low salinity regions. Up-estuary transport by neap tides could be important in sustaining upper bay populations by increasing the export of larvae from middle to upper estuary populations. However the low exchange rates suggest that this mechanism by itself can not completely explain the survival of upper estuary populations, such as Hope Creek. Oysters in the upper Bay have been shown to be genetically different from those in the middle and lower Bay [*He et al.*, 2012], which also suggests little exchange with other populations in the Bay. The simulated dispersal patterns suggest that the upper Bay exports rather than receives larvae. This has implications for the establishment of genetic characteristics, such as disease resistance, and for the maintenance of oyster populations that are susceptible to diseases [*Hofmann et al.*, 2009]. The genetics simulations show larval dispersal might be important in the movement of disease-resistant genes from high

(middle-lower bay) to low (upper bay) disease-resistant populations. The transfer of the resistant trait will occur in periods shorter than 30 days even with the small exchange rates between middle-lower and upper bay populations. However, rapid genetic shift such as the decrease of MSX prevalence in the Delaware Bay in 3-5 years are unlikely to be driven only by dispersion of larvae. Thus, other biological processes such as adult mortality, population abundance or the size of the spawning cohort could play a more important role.

This research confirms that both physical and biological processes influence the dispersion pattern of larvae, and thereby, the pattern of recruitment and genetic dispersal over Delaware Bay. The circulation of Delaware Bay is critical to the patterns of larval dispersal. Changes in atmospheric forcing and freshwater inflow can alter the Bay circulation. This in turn can modify the source and destination regions for oyster larvae, with the implication that the distribution and retention of particular genetic characteristics is not guaranteed. Changing environmental conditions will result in modified transport and settlement patterns of oyster larvae in Delaware Bay. Addressing the consequences of such modifications should be a component of management strategies and polices that are developed for Delaware Bay oyster populations.

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