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Modeling physical controls on northern shrimp (Pandalus borealis) dispersal, retention and settlement success in the Gulf of Maine

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Abstract
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Keywords
Biology, Oceanography, Physical Oceanography, Agriculture, Fisheries and Aquaculture

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MODELING PHYSICAL CONTROLS ON NORTHERN SHRIMP (*PANDALUS BOREALIS*) DISPERsal, RETENTION AND SETTLEMENT SUCCESS IN THE GULF OF MAINE

BY

MICHAEL J. BATES

BA, State University of New York, Potsdam College, 1990

THESIS

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May 10, 2007
Date
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ABSTRACT

MODELING PHYSICAL CONTROLS ON NORTHERN SHRIMP (*Pandalus borealis*) DISPERSAL, RETENTION AND SETTLEMENT SUCCESS IN THE GULF OF MAINE

By

Michael J. Bates

University of New Hampshire, May, 2007

Understanding the population dynamics of commercially harvested species is critical to fishery management. Coupled physical-biological models are powerful tools for exploring interactions among species and their environment. This study creates a coupled, individual-based model to explore interactions between northern shrimp in the Gulf of Maine and their physical environment to try to understand the variability in their population from year to year and to draw hypotheses regarding spawning grounds, larval dispersal and settlement success zones for further study.

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INTRODUCTION

The early life stages of many marine fish and benthic invertebrate species are planktonic and thus subject to dispersal by local currents. For species living on or near the bottom this means that the physical forcing and biological processes occurring in the water column during their pelagic larval stages influences the location of their final settlement. For at least some demersal fish species, the variability of year-class strength (i.e. recruitment to the adult phase) is usually determined in the larval stage (Myers and Cadigan, 1993). Based on this understanding I used coupled physical-biological modeling to investigate correlations between physical forcing variability and recruitment variability in the Gulf of Maine northern shrimp (*Pandalus borealis*) population and evaluate whether the prediction of year-class strength can be improved by understanding the physical forcing affecting the cohort in previous years.

Coupled physical-biological modeling offers opportunities to formulate and test hypotheses about the role of interactions between biological development and planktonic larval retention and transport success in population dynamics. Here I outline techniques for hypothesis building and evaluation using biological and physical modeling tools and northern shrimp in the western Gulf of Maine as an example of the role of retention and transport in recruitment processes. There are several recent studies that set the precedent for this approach. Cowen et al. (2006) used a high-resolution coupled biophysical model to investigate typical dispersal distances and the effect that the timing of the onset of larval movement in the water column has on those distances in a variety of reef fish
species that have planktonic larval phases in the Caribbean region. This study investigated the connectivity of larval release and settlement zones. It also found an important link between the onset of larval mobility in the water column and the ability of a local population to self-recruit and ultimately survive. Baumann et al. (2006) used a hydrodynamic model in combination with a Lagrangian tracking algorithm and coupled it to a biological model of sprat in the Baltic Sea. This coupled model was used to investigate variations in larval dispersal and correlations between the time-averaged bottom depth over which the larvae were transported (the drift index) and recruitment. The drift index was significantly correlated to recruitment success and explained, together with spawning stock biomass, 82% of recruitment variability between 1979 and 2003. Mullon et al. (2003) used a coupled biological-physical model to examine relationships between various biological parameters (such as buoyancy, growth and swimming behavior) and transport success in an anchovy species of the southern and western coasts of South Africa. A key finding of this study was the importance of transport success to recruitment variability.

In this study I test the hypothesis that variability in physical forcing in the Gulf of Maine has a first order effect on recruitment of the northern shrimp population in this habitat through its effect on larval settlement success. While this study shares common techniques with the earlier studies discussed, a key component that is missing here is extensive data on the locations of spawning and nursery areas of northern shrimp in the western Gulf of Maine. This study is therefore especially focused on generating hypotheses regarding the physical range of these spawning and nursery areas to help inform future field studies.
Quantifying transport, retention and settlement of northern shrimp (Pandalus borealis) larvae in the Gulf of Maine is essential to understanding the population dynamics of the species in this area. While biological factors are most important in the juvenile and adult stages of development, physical factors (advection and exposure to temperature fields) are thought to have marked importance in the early life stages. These factors will influence when and where the larvae settle and thus whether they settle in environments that are biologically favorable to their survival to reproductive age (Apollonio et al., 1986). Survival to reproductive age determines annual recruitment into the fishery.

Understanding transport and development rates is especially relevant for P. borealis in the Gulf of Maine, which has no reliable external supply of planktonic larval stages and is exposed to mean currents that tend to flush their planktonic early life stages out of the local habitat. The Gulf of Maine represents the southern-most habitat of northern shrimp (Apollonio et al., 1986), and P. borealis in this area are physically isolated from other regional populations. Areas farther south are too warm to support the species; hence population migration from these areas is not a factor in maintaining the Gulf population (Shumway et al., 1985). The supply of shelf water in the northern region comes from the Scotian Shelf, which does not supply a significant number of northern shrimp to the Gulf (Clark et al., 2000). These conditions create what is a called a “unit stock”; i.e. the population relies only on its own larval production for replenishment. Therefore, what happens to larvae that are released within the Gulf and specifically how they manage to stay in the Gulf, despite mean currents that would tend to flush them out to the south, is of primary importance in understanding the large variation in annual P.
borealis recruitment, and thus landing, rates. In this study an individual based model (IBM) is used to determine key physical and biological factors influencing the transport, retention and settlement success of P. borealis larvae in the western coastal Gulf of Maine.

Individual based modeling provides insight into bottom-up environmental influences on marine ecosystem dynamics. IBM’s allow us to understand how variability at the individual level and in the physical characteristics of the ecosystem affects the large-scale population dynamics of a species (Grimm, 1999). In this model an individual particle represents an individual plankton larval stage of northern shrimp. How each individual reacts to its physical environment within the modeling domain (the Gulf of Maine) is tracked and a composite settlement success index is derived for the larvae population of a given year, known as the year-class. This is accomplished by giving each individual in the modeling domain its own biological characteristics (e.g. release date, development rate, vertical migration behavior, settlement time, survival likelihood) that depend on the physical characteristics of the system (e.g. depth, temperature distribution, wind speed and direction, density distribution).

The IBM used in this work is a coupled physical-biological model. The individuals are particles with biological responses to physical conditions based on the best available data. The particles are advected according to the known physics of the region. The model consists of three key components: 1) output from a hydrodynamic model that provides monthly mean currents and hydrography (density data) for the region 2) a particle-tracking model that uses the hydrodynamic data, along with wind data, to calculate the path of each individual and 3) a biological model that calculates the
response of each individual to the concurrent physical parameters of the particle-tracking model and determines its settlement success. The hydrodynamic model output includes mean monthly velocity fields for the entire Gulf on a square 3 km grid (at 15 depths for each grid point) based on climatological density and Scotian Shelf input data as outlined in Pringle (2006). The particle-tracking model performs linear interpolations between monthly means and between the three-dimensional grid points and adds high temporal-resolution wind data from a single point in the Gulf to obtain Lagrangian velocity and temperature histories for each particle. Finally, the biological model endows each particle with specific biological characteristics, such as temperature-dependent development rate, release date, release depth, latitudinal release zone and vertical migration, that affect how long the individual remains in the water column. Mortality is considered as a range of success reduction factors in the discussion but is not specifically modeled.

In order to better understand the model it is helpful to review aspects of the life history of *Pandalus borealis* in the Gulf of Maine. Adults are benthic. Ovigerous (egg-bearing) females migrate inshore during autumn and winter (Apollonio et al., 1986). Larvae are released inshore from mid February to mid April (Richards, unpublished data) in a mobile planktonic form capable of vertical migration (Pedersen et al., 2003; Ouellet and Lefaivre, 1994). At this time they are normally fully developed stage I larvae (Shumway et al., 1985) and feed on plankton (Stickney and Perkins, 1981). Immediately after release, adult females move offshore (Clark et al., 2000). There are six larval stages (I – VI) before a final molt to the juvenile stage (Shumway et al., 1985). By the juvenile stage the shrimp have settled and become benthic. Prior to settling they reside in the
water column (pelagic) and susceptible to advective currents (planktonic). The depth at which they reside in this region is not known and is modeled at various depths to determine the sensitivity of success to this parameter. Water column surveys for larval shrimp in the Gulf of Maine began in 2005. In these field surveys negligible numbers of stage IV larvae are observed in the water column (Gordon et al., unpublished data) and it is assumed that at stage IV all larvae are benthic. The planktonic larval development, through the completion of stage III, and the location of settlement are modeled in this IBM study.

During the periods of inshore migration and larval release of the ovigerous females, the shrimp fishery is open in the Gulf of Maine. The exact timing of activity varies within the six-month period between December and May depending upon annual recommendations of the Northern Shrimp Technical (formerly Scientific) Committee (NSTC) and the Atlantic States Marine Fishery Commission (ASMFC) (Clark et al., 2000). This type of regulation has been widely applied in the Gulf's shrimp fishery since 1980, after the last closing of the northern shrimp fishery in 1978-79. Since that time landings of *P. borealis* in the Gulf of Maine have fluctuated substantially but the population has not collapsed, as happened twice before 1980 (Figure 1). Although regulation has likely had positive effects on the industry, better understanding and prediction of recruitment variability of the species is needed as a part of an overall regulation strategy. Greater predictability in *P. borealis* population fluctuation would lead not only to greater marketability but also a greater capacity to manage the fishery in an ecologically sound manner. This includes the possibility of increasing the predictability
Figure 1: Commercial Landings of Northern Shrimp 1938 – 2005

Data from before 1958 are from Clark et al. 2000. From 1958 forward the data were obtained from the 2006 ASMFC Northern Shrimp Report. Prior to 1982 only annual (calendar year) data were compiled. After 1994 only seasonal data were compiled. Where both data were available it is plotted to show the close correlation between the two.
of species interacting with the northern shrimp in the food web. All of these outcomes are steps toward ecosystem-based management of species in the Gulf of Maine.

This study has two goals: 1) to develop the techniques for design and analysis of an IBM for the study of the early planktonic life history of marine organisms, using northern shrimp as an example and 2) to use this model to examine whether variability in environmental forcing has an order-one effect on \( P. borealis \) recruitment success, as Baumann et al. (2006) have found for sprat in the Baltic Sea. There is evidence that larval survival usually determines recruitment success in marine demersal fish species (e.g. Myers and Cadigan, 1993). Based on this understanding the juvenile mortality rate (from settlement to recruitment), which is not well studied for this species, is assumed constant in this study and thus not a factor in analyzing the relationship between settlement success and recruitment. By making this assumption wind driven settlement success is tested as a proxy for survival to adult recruitment and the effect of environmental forcing on settlement success will be examined using the model described.

This study examines the null hypothesis that wind-driven settlement success is a first-order determinant of recruitment success. The term "settlement success" refers to the number of larvae that survive divided by the number that are released. In order to survive a larva must end its pelagic life stage within the prescribed physical boundaries favorable for survival (the "retention zone") and overcome the mortality probability based on settlement depth within the retention zone. For purposes here, the retention zone comprises the inner Gulf of Maine (Figure 2) within the 100 m isobath. A retained individual will not necessarily attain settlement success, but it must be retained to have any chance of success. Similarly, a successfully settled individual will not necessarily
Figure 2: Gulf of Maine and Designated Areas for this Study

Study area and various zones and features referenced throughout this work. The Gulf of Maine (dashed/dotted line) includes the retention zone defined as all areas within the Gulf where depth < 100 m. The release zone encloses the area from Penobscot Bay to Cape Ann that has a depth between 30 and 100 m. Zones 1-4 represent release and potential settlement zones; zones 5 and 6 represent potential settlement zones only. Relevant features are: A – Cape Cod Bay, B – Stellwagen Bank, C – Massachusetts Bay, D – Cape Ann, E – Portsmouth Harbor, F – Casco Bay and G – Penobscot Bay.
survive through the juvenile stages but settlement success is assumed to be an essential prerequisite for recruitment into the adult population. The specific parameters defining settlement success, both physical and biological, will be outlined in the methods section.

It has been shown that conditions favorable to *P. borealis* survival in a particular year-class correspond to strong shrimp landings two years later. This correlation has been strongest with temperature conditions (Dow, 1964 as cited in Shumway et. al., 1985). This study investigates whether there is a relationship between settlement success and commercial landings two to five years later.

Physical forcing varies with fluctuations in meteorological forcing, in the form of wind stress, and hydrological forcing in the form of density gradients. Wind stress in this region has a decorrelation timescale of about three days and there is high temporal-resolution data for this parameter. Density gradient decorrelation timescales are less well constrained and monthly climatological averages were used to determine the hydrographic velocity fields in the model.

Biological development time to the benthic phase varies with changes in the temperature field, food availability and mortality rate. Food sources, and thus availability, are not well known for this population and therefore not modeled. Climatological temperature data is used and mortality rate variations, which are also not well constrained, are discussed but not explicitly included in the model.

In the following sections the methods for incorporating the physical and biological parameter data into the model are detailed and the results are presented and interpreted. Conclusions are made as to how the results of this study can lead to greater predictability of year-class recruitment for northern shrimp.
CHAPTER I

METHODS

Study Area

The Gulf of Maine is a semi-enclosed body of water off the northwest Atlantic Ocean bounded by the northeastern United States and southeastern Canada. Its boundaries with the Atlantic extend from Cape Sable Island off of Nova Scotia to the north, Cape Cod to the south and Georges and Brown’s Banks to the east. It includes the Bay of Fundy and has three distinct basins: George’s Basin just inside the Northeast Channel, the only access for deep water in the Gulf, Jordan Basin in the northern section and Wilkinson Basin in the southwestern section of the Gulf (Figure 3).

The surface currents in the Gulf tend to enter from the Scotian Shelf over the northern border of the Gulf and generally circulate in a cyclonic direction, exiting the Gulf either through the Northeast Channel or the Great South Channel. As the surface currents circulate they form the Maine Coastal Current, which is in turn divided into two principle currents, the Eastern Maine Coastal Current (EMCC) and the Western Maine Coastal Current (WMCC). The Coastal Current flows generally from the eastern boundary of Maine, at the mouth of the Bay of Fundy, southwest along the coast of New England to Cape Cod. The EMCC is considered the branch from the Eastern Maine Boundary to approximately Penobscot Bay where the Coastal Current, depending on season and conditions, divides more or less strongly into two branches: a branch that
Figure 3: Physical Features of the Study Area

W = Wilkinson Basin, J = Jordan Basin, G = George’s Basin, GB = George’s Bank. Inflow from the Scotian Shelf and Northeast Channel are shown as well as the cyclonic flow and the out flow through the Great South Channel and Northeast Channel.
tends to circulate anti-cyclonically around Jordan Basin and the WMCC, which continues down the New England coast (Geyer et al. 2004).

While this study concerns the population of *P. borealis* in the Gulf of Maine as a whole, the principle release area extends along most of the WMCC, specifically from Penobscot Bay to Cape Ann (Figure 2). The actual along shelf distribution of larvae, which is not well known, is assumed uniform in the model in order to compare the settlement success indexes for larvae that are released in various latitudinal bands (Figure 2). The northern and southern extents of the release area are based on Northeast Fisheries Science Center (NEFSC) bottom trawl survey data from 1977 to 1993 (Clark et al., 2000). The cross-shelf distribution of larval release in the model, between the 30 and 100 m isobaths, is based on the currently available field survey data (Gordon et al., unpublished data). During model runs with climatological wind forcing larvae generally remain in the WMCC or advect closer into Massachusetts Bay until settlement or flushing out of the Gulf, mainly through the Great South Channel.

**Hydrodynamic Model**

Larval paths were calculated using velocity fields calculated by an early generation of the Finite Volume Coastal Ocean Model (FVCOM). FVCOM is an unstructured-grid, primitive-equation hydrostatic numerical model that has been shown to perform well in various coastal applications (Chen et al., 2003). The velocity fields generated by the model were monthly mean velocities on an unstructured, triangular grid at various depths. To obtain the 12 monthly velocity fields used in the particle-tracking model, FVCOM was first initialized with monthly mean hydrographic fields derived from
all available hydrographic data for the Gulf of Maine and the Scotian Shelf from the Bedford Institute of Oceanography and National Ocean Data Center databases (Pringle, 2006). The model was then brought to a quasi-steady state of circulation for each given hydrographic field. The model was first run for 10 tidal cycles to minimize variations in currents associated with the stabilization time for inertial currents in this region, which is about 3 – 5 tidal cycles, and to ensure a well-established density driven velocity field with minimal variation. The Lagrangian velocity field for each given hydrographic field was then calculated by determining the mean tidal residual Lagrangian velocity over four tidal cycles at each point on the grid (Pringle, 2006).

The triangular, unstructured grid type is one of the features of the model that makes it favorable for modeling coastal systems. It allows the grid to have a greater horizontal resolution in shallower areas around islands and coastlines where variability is likely to be greater (Chen et al., 2003). The resolution in runs relevant to this research was about 8 km in the central Gulf of Maine, reducing to 1.4 – 4 km in coastal regions where the bathymetry has shorter length scales (Pringle, 2006). Once the velocity field for a particular month was determined for this unstructured grid, it was transferred to a rectangular grid for use in linear interpolation algorithms in the particle-tracking model. The rectangular grid consists of over 75,000 points. At each point the velocity was calculated at 15 evenly spaced depths from surface to bottom, regardless of depth. This means that in shallower water the horizontal transport gradient in the vertical direction is more highly resolved.

This process generated monthly velocity fields due to hydrographic forcing alone \( (V_{H}) \) that were used in the model. Similar steps were followed to generate the monthly
velocity fields due to hydrographic forcing combined with a 10 m/s alongshore wind 
\( (V_{H+A}) \) and hydrographic forcing combined a 10 m/s cross-shore wind \( (V_{H+C}) \) used in the 
model as a baseline to interpolate velocities due to other wind strengths. The alongshore 
component of wind stress in the hydrodynamic model was aligned with the Maine coast, 
55° from north being the positive alongshore direction. The positive cross-shore 
component was 145° from north (Johnson et al., 2006).

The winds used to force the model were based on National Center for 
Environmental Prediction (NCEP) reanalysis winds from a single point, roughly at the 
center of Georges Basin. This single point was used due to the high correlation of winds 
throughout the domain over the decorrelation timescales of winds for this region (Pringle, 
2006).

Finally, monthly velocity fields due to hydrographic forcing combined with 
Scotian Shelf input \( (V_{H+S}) \) were generated. These four velocity fields were used in the 
particle-tracking model to interpolate velocities at various wind stress and Scotian shelf 
inflow conditions.

**Particle-Tracking Model**

The particle-tracking model was derived using interpolations of the velocity data 
provided by FVCOM and the subsequent transformation of that data to the rectangular 
grid described above along with daily wind stress data from 1960 through 2001.

The four grids generated for each month \( (V_H, V_{H+A}, V_{H+C}, V_{H+S}) \) were assumed to 
be the velocity fields resulting from the various parameters in the middle of the given 
month. The four velocity fields at any point in time were determined by linear
interpolation between the two nearest monthly velocity fields resulting from each parameter. The velocity field due to hydrographic forcing alone ($V_h$) was then subtracted from each of the three other velocity fields to determine the velocity contributions of the along ($V_a$) and cross-shore ($V_c$) wind forcing and the Scotian shelf input ($V_s$) at the rectangular grid points:

$$V_a = V_{h+a} - V_h$$

$$V_c = V_{h+c} - V_h$$

$$V_s = V_{h+s} - V_h$$

The four velocity fields were then summed to determine the net velocity field ($V_n$). During this summation the velocity fields due to wind forcing were multiplied by a factor of the wind stress being modeled ($\tau_a$ or $\tau_c$) divided by the wind stress corresponding to the 10 m/s wind used in the hydrodynamic model output (0.144 N/m²) to determine the contribution of the wind at that point in the model:

$$V_n = V_h + (\tau_a/0.144)V_a + (\tau_c/0.144)V_c + V_s$$

Finally, with a 3D rectangular grid of the net velocity field, the velocity at any point in the domain was determined by performing a 3D linear interpolation between the three nearest points in the velocity field.

Using this Lagrangian particle-tracking model individual positions are determined at time steps equal to one tidal cycle in order to reduce the effect of variability in the
velocity fields on timescales shorter than tidal timescales. At each position the biological condition of each particle was assessed by the biological model to determine its development stage and thus its status as either pelagic or benthic.

**Biological Model**

**Vertical Position and Behavior**

Behavior of larval *P. borealis* was modeled as two components: an initial depth selection and a depth-adjustment behavior. The initial depth simulates the depth to which larval shrimp migrate upon release. The main factor that determines initial depth may be food availability and may correspond to the depth of the subsurface chlorophyll-a maximum (Ouellet and Lefaivre, 1994). The depth of the chlorophyll-a maximum is not well known for the study area, however, so this hypothesis was not tested. In this study the initial depth is varied within the photic zone, between 0 and 45 m in order to determine the sensitivity of survival to initial depth selection. The depth adjustment behavior is modeled such that larvae maintain their initial depth. The assumption is made that the initial depth is the optimal depth for development and that the larvae actively maintain this depth for that reason. While diel, or daily, migration is acknowledged as a factor that is documented in other populations of this species and may affect the results of the study, it is not included in the model due to a lack of solid data regarding such behavior in this population. Larvae intersecting the bottom before development to the appropriate larval stage are repositioned to 80% of the depth of intersection.
**Release Date**

The release date of the larvae was also varied in model runs. Unpublished analysis by A. Richardson (National Marine Fisheries Service, Woods Hole) of data collected over 20 years shows the mean year-day of 50% cumulative larval release of the female population to be 55 (February 24) and the mean year-day for 10% and 90% release to be 34 and 76 respectively. Linear interpolation of these data show the average year-day of 25% and 75% release to be 42 and 68 respectively, or about February 11 and March 9. Runs were done beginning on these three dates to determine the sensitivity of settlement success to the time of release.

**Development Rate and Pelagic Duration**

The development rate of the shrimp larvae was modeled as a function of their exposure to varying temperatures at each time step according to the formula found in Storm and Pedersen (2003) based on the following assumptions: 1) the zoea (larval) stages develop isochronally, meaning that development rate at a given temperature is constant and independent of larval stage and 2) stage duration is dependent only on temperature and follows the Belehradek function in the form:

\[ D = 872 \cdot (T + 10.5)^{-1.55} \]  

where \( D \) is the stage duration in days (d) at the given temperature (T) in °C. The three constants are derived from fitting the general equation to observations of temperature-dependent stage durations from three different studies (Storm and Pedersen, 2003). The
assumption of isochronal development is not agreed upon and a laboratory study of populations from two northern Norwegian fjords found growth rate to be stage dependent (Rasmussen and Tande, 1995). The daily stage increment of a modeled larva is given by the reciprocal of equation 1 \((1/D)\) in units of \(d^{-1}\). In the model, this quantity was then divided by the number of seconds per day \((s/d)\) to determine the stage increment per second \((1/s)\):

\[
1/d \cdot (1/(s/d)) = 1/s
\]

This quantity was then multiplied by the number of seconds in each tidal time step to determine the incremental stage change during a tidal time step corresponding to the temperature during that time step. All larvae start with a stage value of 1 and have their incremental stage change added to this value at the end of each time step. Any larva entering stage IV during a tidal time step is considered benthic at the end of the time step and is no longer advected. Its settlement depth is recorded for use in the settlement success index algorithm.

**Settlement Success Index**

The settlement success index is examined as a possible index of recruitment into the Gulf of Maine northern shrimp population. The index is defined as the number of larvae that succeed divided by the number of larvae released in the model run. Northern shrimp are known to mature inshore before migrating offshore. Apollonio et al. (1986) found that most shrimp less than one year old remain within 20 miles of the coast. For these reasons the assumption is made that the larvae need to settle in water shallower than

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100 m in order to recruit into the fishery. If they meet this requirement they are considered “retained”. The retention zone is the area where the juvenile stages are assumed to be able to survive to maturity. The success criteria within this retention zone are based on the depth at which the stage IV larvae settle. Larvae that settle at the 50 m isobath or shallower are assumed to have a 100% chance of survival. Larvae that settle at the 100 m isobath or deeper are assumed to have a 0% chance of survival. The chance of survival for larvae that settle between these two isobaths is determined using a linear interpolation between the 50 m value and the 100 m value for lack of better data. Sensitivity analyses on this settlement success function may be a useful extension of the work done here. These success criteria apply only within the Gulf of Maine, which for this model is bounded on the Atlantic Ocean side by a line running from Yarmouth, Nova Scotia to the northern tip of Cape Cod and includes Cape Cod Bay. The relevance of Cape Cod Bay in settlement success is analyzed in this study, but it meets the conditions for the retention zone and all runs in this study assume that it is a part of the retention zone. Individuals leaving the Gulf of Maine as described here are considered lost to the population and are not considered successful. The settlement index is calculated for each year-class as a whole and for individuals starting in each of four zones running north to south (Figure 2) to determine the effect of location at release on the survival index. Each zone spans 0.5° of latitude.

**Mortality Rate**

Table 1 shows mortality indexes for various instantaneous mortality rates after 45 days, approximately the amount of time the larvae spend in the water column in the
<table>
<thead>
<tr>
<th>Z</th>
<th>(\frac{N_{45}}{N_0})</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.02</td>
<td>(4.07 \times 10^{-1})</td>
</tr>
<tr>
<td>0.04</td>
<td>(1.65 \times 10^{-1})</td>
</tr>
<tr>
<td>0.06</td>
<td>(6.72 \times 10^{-2})</td>
</tr>
<tr>
<td>0.08</td>
<td>(2.73 \times 10^{-2})</td>
</tr>
<tr>
<td>0.10</td>
<td>(1.11 \times 10^{-2})</td>
</tr>
<tr>
<td>0.12</td>
<td>(4.52 \times 10^{-3})</td>
</tr>
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<td>0.14</td>
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<tr>
<td>0.16</td>
<td>(7.47 \times 10^{-4})</td>
</tr>
<tr>
<td>0.18</td>
<td>(3.04 \times 10^{-4})</td>
</tr>
<tr>
<td>0.20</td>
<td>(1.23 \times 10^{-4})</td>
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<tr>
<td>0.22</td>
<td>(5.02 \times 10^{-5})</td>
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<td>0.25</td>
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<tr>
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<td>(8.29 \times 10^{-6})</td>
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<tr>
<td>0.28</td>
<td>(3.37 \times 10^{-6})</td>
</tr>
<tr>
<td>0.30</td>
<td>(1.37 \times 10^{-6})</td>
</tr>
</tbody>
</table>

Table 1: Effect of Variation of Natural Mortality Rate on Larval Survival

The ratio of individuals surviving after 45 days \((N_{45})\) relative to the number of individuals at time zero \((N_0)\) for various instantaneous mortality rates \((Z)\) calculated from \(N_t = e^{-Zt}\) where \(t\) is the time in days.)
model runs ($N_t = e^{Zt}$ where $N$ is the number of individuals, $Z$ is the instantaneous daily mortality rate and $t$ is the time in days). Mortality rate data are difficult to obtain for this population. Estimates are wide ranging and it is often not possible to determine the units and methods used to obtain them. Mortality rate was not specifically modeled in this study; it is instead discussed as reduction factor applied to success indexes. Part of the reason for this is that values from the few studies that have been done vary widely. Also, there are no data on the mortality of the earliest developmental stages (I and II), which are of particular concern in this study.

**Modeling Method**

Because it is not clear at what depth shrimp larvae live in the Gulf of Maine, runs were initiated at varying release depths within the four release zones in order to examine the retention and settlement response of the individuals.

To understand the response to wind forcing in the study area at various depths 64 runs were done at each depth modeling eight different forcing regimes for each cross-shore (x-direction) and alongshore (y-direction) wind direction (Table 2). The forcing regimes were as follows: no wind, climatological winds, climatological winds +/- 1 standard deviation, climatological winds +/- 2 standard deviations, 10 m/s wind in the negative direction and 10 m/s wind in the positive direction. To perform runs based on climatological winds, first monthly averages were determined by analyzing daily wind data from 1960 through 2001 and finding the monthly mean for all 12 months for each year. These winds are from the National Center for Environmental Prediction's 40-year
Table 2: Model Runs Using Standardized Winds

The large, bold boxes represent the 64 cross and alongshore wind combinations run. Within each of these are the release day and depth combinations run. Each “x” represents a model run. Terms in parentheses are the format of the wind type as displayed in figures. Numbers below each wind type are the average wind speed for the wind type starting on day 55 in m/s.
reanalysis project (Kalnay et al., 1996). Monthly climatology was then determined by averaging the 42 values for each month. Each monthly mean was assumed to be the actual wind stress in the middle of the month and wind stress values were linearly interpolated between these values. The standard deviations for each month were determined from the same 42 annual values thus they represent the standard deviations of the inter-annual variation of the monthly mean winds. Runs done with standard deviation adjustments simply had the appropriate quantity added to or subtracted from monthly climatology before the linear interpolations were performed. These runs were done with larvae at five different initial depths, for a total of 320 model runs, to get an idea of how along shore and cross-shore wind forcing affects larval transport and survival for particles starting at 0, 15, 25, 35 and 45 m and within each of the four zones.

These 320 runs were first done beginning at each of the three release dates corresponding to the mean year-day determinations of 25, 50 and 75% larval release based on 20 years of data from 1980 through 2004 as described above. This was done to determine the overall effect of earlier and later start dates. Since the total range of start dates is less than one month it was not expected that the larvae would be exposed to substantially different temperature histories and thus the change in release date was not expected to change survival indexes significantly.

Once 320 runs had been done for each of the three release dates, another set of 320 runs (all 64 winds, all 5 depths) using each of two temperature fields beginning on release day 55 was done. The temperature fields in the original runs were climatological monthly means. The temperature fields for these runs were defined by increasing the climatological monthly temperature fields by one and two standard deviations. Standard
Temperature Exposure and Success Changes Over Varying Temperature Fields

<table>
<thead>
<tr>
<th>Temperature Field</th>
<th>Mean Temperature Exposure (°C)</th>
<th>Tides to Settle</th>
<th>Mean Settlement Success</th>
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<tr>
<td>Climatological Average</td>
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<td>86</td>
<td>0.559</td>
</tr>
<tr>
<td>Climatological Average + 1 Standard Deviation</td>
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<td>82</td>
<td>0.562</td>
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Temperature Exposure and Success Changes Over Varying Release Days

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<th>Tides to Settle</th>
<th>Mean Settlement Success</th>
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<td>86</td>
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<tr>
<td>Delta</td>
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40 Year Temperature Standard Deviations

<table>
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<tr>
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<td>20</td>
<td>0.8298</td>
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<tr>
<td>30</td>
<td>0.6142</td>
</tr>
<tr>
<td>40</td>
<td>0.6117</td>
</tr>
</tbody>
</table>

Table 3: Temperature Exposure and Success Variation

The top part of this table shows, in the first column, the mean temperature exposure of all individuals over all model runs completed (beginning on day 55) using various temperature fields. Column 2 shows the results of a simple calculation using equation 1 from the text, substituting the mean temperature exposure from column 2 for \( T \) to obtain stage duration in days at that temperature. This number was then multiplied by three, the number of stages an individual must complete before settling. Finally, the result was multiplied by the number of tides per day (1.92) to determine the average number of tides an individual in this temperature field would take to settle. The last column is the mean settlement success for runs done using the corresponding temperature field averaged over all individuals in all runs using the particular temperature field.

The middle part of this table contains the same information but is now averaged over all individuals in all runs beginning on a given release day with no alteration in the temperature fields.

The bottom part of the table shows the standard deviations used to modify the climatological average temperature field in runs summarized in the top part of the table.
deviation values were determined using all available data from the last 40 years at four depths (10 m, 20 m, 30 m and 40 m) from the Bedford Institute of Oceanography ocean climate database. Average values were calculated using all February and March data at each depth and only included those years that had at least two data points. The standard deviations of these data were linearly interpolated onto the rectangular 3D depth grid of the model to be added to the grid of climatological temperature data in the model (Table 3).

Finally, there is some question as to the favorability of Cape Cod Bay to the survival of *P. borealis* larvae. Its southern location, and therefore warmer temperatures, may be detrimental to their development and survival, but its shape and location may help retain individuals that would otherwise advect further south or east. The impact of this region on the total survival indexes of each model run was analyzed to draw some preliminary conclusion regarding the importance of this area in the survival of this species.
CHAPTER II

RESULTS

The range of settle times from all runs beginning on year-day 55 that used temperature-dependent development is 70 to 97 tides with an average settle time of 89 tides (Figure 4). In order to evaluate the extent to which population retention is attributable solely to advection, as opposed to favorable development times, the mean retention after each tide was calculated for model runs of 174 tides, representing a fixed pelagic durations of 90 days (Figure 5). This duration extends beyond the time that the larvae are found in the water column in recent surveys, which is about 150 tides (about the first week of May) from the mid-February release date (Gordon, unpublished data). The assumption is that survival may drop off rapidly after this date due to starvation or predation. The figure shows data averaged from all runs beginning on day 55. Since it is a requirement (but not a guarantee) for settlement success, “retention” is synonymous with “potential settlement success”. There is a relatively rapid loss of larvae from the retention zone within the first 20 tides with steady loss through approximately tide 120 to 130 and a leveling off at a retention index of about 0.57. Adding temperature-dependent larval stage development does not have, on average, a large impact on total retention. However there is a more pronounced effect when considering a narrower range of zones and depths (Figures 6 – 7).
Figure 4: Settlement Times for All Runs Beginning on Day 55

Histogram of settlement times for all 5000 particles in the 320 model runs (includes all 64 forcing regimes and 5 release depths) initiated on the middle release day (55) with climatological temperature fields. The mean settle time for all particles across all runs is 89 tides.
Figure 5: Mean Retention, Day 55

Mean retention, after each tide, for all model runs initiated on day 55 without temperature-dependent development times beginning on day 55. The vertical lines represent the range of settle times for runs using temperature-dependent development (70 – 97 tides). The top horizontal line shows the mean retention for the average settle time of 89 tides. The lower horizontal line is the mean retention at 150 tides, roughly the time that larvae are last seen in the water column in recent surveys. Averaged over all runs, temperature-dependent development has a small potential to affect settlement success of northern shrimp larvae.
Mean retention, after each tide, of all individuals originating in zone 2 at 15 and 25 m depths for model runs done beginning on day 55 without temperature-dependent development and not including any extreme wind forcing regimes (+/- 10 m/s in the cross or alongshore directions). The vertical lines represent the range of settle times for all runs beginning on day 55 (70 - 97 tides). The top horizontal line shows the mean retention for the average settle time of all runs beginning on day 55 (89 tides). The lower horizontal line is the mean retention at 150 tides, roughly the time that larvae are last seen in the water column in recent surveys. This plot is shown to examine the possible effect of the temperature-dependent development on settlement success given the possibility that shrimp larvae are released primarily in one region (Zone 2) at the most successful depths. Temperature-dependent development time has the potential to help maintain a high settlement success index for these individuals.
Mean retention, after each tide, of all individuals originating in zone 3 at 15 and 25 m depths for model runs done beginning on day 55 without temperature-dependent development and not including any extreme wind forcing regimes (+/- 10 m/s in the cross or alongshore directions) is plotted. The vertical lines represent the range of settle times for all runs beginning on day 55 (70 - 97 tides). The top horizontal line shows the mean retention for the average settle time of all runs beginning on day 55 (89 tides). The lower horizontal line is the mean retention at 150 tides, roughly the time that larvae are last seen in the water column in recent surveys. This plot is shown to examine the possible effect of the temperature-dependent development on settlement success given the possibility that shrimp larvae are released primarily in one region (Zone 3) at the most successful depths. Temperature-dependent development time has the potential to help maintain a high settlement success index for these individuals.

Figure 7: Mean Zone 3 Retention, Day 55

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Figure 8: Mean Settlement Success Indexes for Cross-Shore Winds, Day 55

Average total and zonal settlement success across all cross-shore wind forcing regimes modeled in this study. Zones represent release zones 1-4. Zones 5 and 6 are settlement zones only. Winds are in order of decreasing offshore component. Winds to the left of "None" have a wind velocity component in a southeasterly direction while winds to the right have a northwesterly component. The data for this plot are averaged over runs done with all alongshore wind types and release depths beginning on release day 55 (with climatological temperature fields) for each cross-shore wind type. The effect of the cross-shore wind variation on both total and zonal success is very small except when extreme winds are applied to the model.
Figure 9: Mean Total Settlement Success Indexes for Various Release Days

Release days 42, 55 and 68 correspond with the average cumulative release of 25, 50 and 75% of larvae. Releasing all the larvae in the model on any one of these days does not affect the mean total success index significantly. The mean total success at each depth is the average success for runs using all wind forcing combinations (with climatological temperature data) for larvae originating at that depth.
There were clear correlations between success and three parameters: zone of release, depth of release and the strength of the alongshore component of the wind. Variability in cross-shore winds (Figure 8) and timing of release (Figure 9) were not found to have an important effect on total larval success, though the release date did have an effect on the zonal success (Figures 10 – 12). The results discussed here are based on model runs beginning on year-day 55, when 50% of larvae on average are released, except where specifically stated otherwise. Due to Ekman transport, cross-shore wind variability tends to affect transport along the coast more than cross-shelf transport and it is cross-shelf transport that plays the larger role in retention and settlement success. The importance of cross-shelf transport in larval settlement success is addressed in this study.

**Zone of Release**

The more northerly the zone, the greater the average settlement success of the larvae over all winds modeled. Figures 10 – 12 show the average success indexes at the model depths for larvae originating in each zone for the three release dates. The average success of particles beginning in zone 1, the most northerly, is much greater than the survival of particles starting in any other zone. This was true for model runs beginning at all three release dates. It is also the case that the success index of individuals beginning in zone 4, the most southerly, is much less than the indexes for all other zones for runs beginning on all dates.

Figures 10 - 12 also show that zones 2 and 3 switch their positions with regard to success index as the date of release gets later. For model runs with the earliest release date, particles beginning in zone 2 have a greater success index than those beginning in
Figure 10: Mean Settlement Success Indexes for Release Day 42

Total and zonal settlement success for larvae released on year-day 42 in zones 1 through 4. Settlement success decreases from the most northerly zone to the most southerly zone except at the surface. The data for this plot is averaged over all runs done beginning on release day 42 with climatological temperature fields. Note that zones 5 and 6 are not designated release zones.
Figure 11: Mean Settlement Success Indexes for Release Day 55

Total and zonal settlement success for larvae released on year-day 55 in zones 1 through 4. Larvae originating in Zone 3 have a greater settlement success than those originating in Zone 2 at shallower depths while the Zone 2 larvae have greater settlement success at greater depths. The data for this plot is averaged over all runs done beginning on release day 55 with climatological temperature fields. Note that zones 5 and 6 are not designated release zones.
Figure 12: Mean Settlement Success Indexes for Release Day 68

Total and zonal settlement success for larvae released on year-day 68 in zones 1 through 4. Larvae originating in Zone 3 have a greater settlement success than those originating in Zone 2 at all depths. The data for this plot is averaged over all runs done beginning on release day 55 with climatological temperature fields. Note that zones 5 and 6 are not designated release zones.
zone 3. This reverses as the release date gets later in the year. Particles released in zone 3 have the greater success index at all depths for model runs beginning on latest release date.

**Depth of Release**

Figure 11 shows the correlation between depth of release and the success on release day 55, with the strongest total survival occurring among larvae that are released at 15 m. Zones 1 and 4 show some deviation from these trends though their settlement indexes at 15 m are still relatively high. Zone 1 shows a generally increasing settlement success index as depth increases while zone 4 shows a generally decreasing settlement success index with increasing depth.

**Alongshore Wind Type**

Variability in survival is affected more significantly by the strength of the alongshore component of winds than that of the cross-shore component (Compare figure 13 with figure 8). Figure 13 shows the total population settlement success for all alongshore wind strengths modeled in this study. Each data point is an average settlement success index compiled over all of the corresponding cross-shore wind strengths and release depths for a particular alongshore wind strength on release day 55. The alongshore wind strengths are presented in order of decreasing coastal upwelling effect (or increasing coastal downwelling effect) of the wind from left to right. Note that the average alongshore wind component in the study area is a slightly upwelling favorable wind (Table 2). The pattern of variability of total settlement success with
Figure 13: Mean Settlement Success Indexes for Alongshore Winds, Day 55

Average total and zonal settlement success across all alongshore wind forcing regimes modeled in this study. Zones represent releases zones 1-4. Zones 5 and 6 are settlement zones only. Winds are in order of decreasing upwelling component. Winds to the left of “None” have a wind velocity component in a northeasterly direction while winds to the right have a southwesterly component. The data for this plot are averaged over runs done with all cross-shore wind types and release depths beginning on release day 55 (with climatological temperature fields) for each cross-shore wind type. The effect of the alongshore wind variation on total and zonal success is significant when compared to the effect on success caused by the variation in the cross-shore component of the wind shown in Figure 8.
Figure 14: Total Settlement Success Indexes Over Modeled Alongshore Forcing

This plot shows clearly why constraining the depth distribution of larvae is critical to predicting settlement success. The greatest upwelling wind (blowing toward the NE along the Maine coast) is in the upper left corner, the greatest downwelling wind is in the lower right corner. The most stable depth is at approximately 20 m where cross-shelf advection due to surface winds switches directions. Data are averaged over all cross-shore wind regimes on release day 55 with no temperature field offset.
alongshore wind variability is given more detail in Figure 14 than in figure 13 by including the depth profile of the success index for each wind regime. This breakdown of results by the strength of the alongshore wind component reveals details of the depth trends described above. In general, the more extreme the wind, the more monotonic the survival index is with depth; with upwelling winds favoring settlement success at greater release depths and downwelling winds favoring settlement success at shallower release depths. The three alongshore winds with the greatest upwelling effect show increasing success indexes with increasing depth except for a slight decrease in success at the 45 m depth where the alongshore wind component is one standard deviation greater than the average. Similarly, the three alongshore winds with the greatest downwelling effect show decreasing success indexes with increasing depth except for a slight increase in success at the 45 m depth where the alongshore component is two standard deviations less than the average.

Cape Cod Bay

Figure 15 shows the average impact of Cape Cod Bay on the total survival for model runs with each alongshore wind type. Within each forcing regime the results are shown for particles beginning at each of the five modeled release depths (integrated over all release zones) as well as the average impact over all depths. The wind types are again arranged in order of decreasing upwelling component. A stronger impact can be seen in the forcing regimes with no upwelling component and a moderate downwelling component though the overall average impact is never greater than 10%.
Figure 15: Impact of Cape Cod Bay on Total Settlement Success

Mean percentage of total survival attributable to particles settling in Cape Cod Bay for particles starting at depths shown in the table legend. The data are averaged over all modeled cross-shore winds (with climatological temperature fields) for each alongshore wind type and integrated across all release zones. All runs began on release day 55. The average impact (unshaded bar) is the mean percentage of total survival attributable to Cape Cod Bay settlement integrated over all depths.
Effects of Daily Variation in Wind Fields

Having established a baseline understanding of how the physical variables affect the settlement success of this northern shrimp population in the model, model runs were then performed using known daily wind data. Since the alongshore wind variability, which has been identified as one of the more significant factors affecting settlement success, and cross-shore wind variability are well constrained in this study, the effect of daily variation in winds on settlement success according to release depth and zone, the next two most significant sources of variability in this study, was investigated. Fifteen runs were performed using each of 20 years’ wind data, 1982 through 2001 for a total of 300 runs. One run was done at each of the five modeled release depths starting on each of the three release days modeled. Figure 16 shows the mean total and zonal settlement success results across the fifteen runs done for each year. These results are used later to examine the original hypothesis of this study that settlement success driven by wind variability is a first-order determinant of recruitment success.
Data is averaged over model runs initiated at all release dates and depths with daily wind data for each year modeled and climatological temperature fields. If the main area of larval release were in a different zone each year, success variability could be much greater than if it were in the same zone each year as plotted. This spatial release behavior is not well known.
CHAPTER III

DISCUSSION

The survival of individual *P. borealis* larvae is based on the balance between the time it takes an individual to develop to the benthic stage and the time it takes to flush it from the Gulf. The mean total retention (Figure 5) is not heavily affected by decreases in pelagic life stage duration (Figure 4). Since all larvae settle by approximately tide 150, it is interesting to note that faster development times brought about by temperature-dependent development do not seem to increase total mean retention significantly. However, when retention is examined for individuals beginning in specific zones and depth ranges (Figures 6 and 7) a different trend can be seen. If larvae begin their pelagic life stage in these zones and depth ranges, temperature-dependent development may lead to 12 to 17% greater retention.

The balance between flushing time and development time can be greatly affected by the environmental factors controlling these conditions. Flushing time for an individual is influenced by variable alongshore wind forcing, exposure to varying bathymetry based on the depth of larval release and the zone of release, which affects its distance (along the coastal current) from the Gulf of Maine boundary at which point an individual is considered to be lost from the population. Development time for an individual is affected by exposure to varying temperature fields and food availability. Feeding habits and food availability for northern shrimp is not well documented and was therefore not modeled in this study.
Variability in natural mortality rates has the potential to have first-order impact on the balance between modeled factors (flushing time vs. development time) in the Gulf. While the natural mortality rate is very poorly understood for this species in this region, some basic calculations have been done to determine maximum and likely mortality rates due to factors other than transport loss. The estimated fecundity, or number of eggs produced per ovigerous female, is 2000 for an average sized female (Shumway et al., 1985). Assuming a female has from one to three productive years then one in 2000, 4000 or 6000 eggs must achieve settlement success (and survive to reproductive maturity) in order for the population to maintain equilibrium. While it appears that most shrimp die after one reproductive cycle, some may live through another one or two cycles (Clark et al., 2000). If 1 in 4000 eggs settles successfully after 45 days, that is an $N_{45}/N_0$ ratio of $2.5 \times 10^{-4}$ in table 1 which corresponds to an instantaneous mortality rate, during the pelagic phase, of approximately 0.18 d$^{-1}$. This would indicate that the maximum average mortality rate that the pelagic larval stages can withstand is between 0.17 and 0.19 d$^{-1}$, using one, two and three productive years for calculations and assuming a settlement success of 1. At a nominal settlement success of 0.6 (approximately that seen in the standardized model runs) and assuming one productive year (the most common scenario), the maximum sustained mortality rate is 0.16 d$^{-1}$. These mortality rates fall within the range found in a study looking at mortality rates in all phases of a variety of fish with pelagic larvae. The study found a mean larval mortality of 0.12 d$^{-1}$ among the five species studied (Houde, 1988).

The impacts of varying factors in the model that affect flushing time (alongshore wind forcing regime, larval release depth and larval release zone) and the one factor
modeled that affects development time (exposure to varying temperature fields) are discussed below in order of decreasing effect on settlement success.

The alongshore wind forcing had the greatest impact on settlement success and is the most well quantified variable in the model. Sources of error in the model estimation of settlement success include latitudinal zone of release and vertical distribution of the larval stages. These two factors have a large effect on settlement success throughout all model runs. The effect of depth on settlement success can be as large as the effect of the alongshore wind regime. The effect of release zone on settlement success, while not as large as that of depth, is still significant.

**Alongshore Wind Forcing Regime**

At the depth extremes of the model runs (0 m and 45 m) mean survival indexes vary from near 0 to 1 depending on the alongshore wind regime (Figure 14). The cause for the noticeable trend from high survival success when release depths are near the surface to low success as release depths approach 45 m in the strongest upwelling wind regime (and the gradual flip of that trend as the regime shifts to downwelling) lies largely in the explanation of the physics of coastal upwelling and downwelling. Figure 17 shows a simplified drawing of a coastal ocean (in the northern hemisphere) and the effect of an upwelling and downwelling wind on advective velocities along with the resulting coastal upwelling or downwelling for which the winds are named (Austin and Lentz, 2002).
In these figures, “into page” represents a northeasterly direction. A wind blowing in this direction will force a mean transport of water to the right, or offshore in this model, due to the Coriolis effect and Ekman transport. This causes a coastal set-down of surface water that is compensated for by coastal upwelling. This coastal upwelling is fed by onshore advection. An upwelling wind leads to shallower individuals being driven offshore while deeper individuals are drawn onshore. Due to this vertical velocity structure there is a depth at which there is minimum motion among all alongshore wind intensities, about 20 m in our model. This depth may be favorable for planktonic larvae trying to attain the highest average retention and settlement success in all wind forcing regimes.
With this understanding of how upwelling and downwelling winds affect coastal transport it is reasonable that, at shallower depths, stronger upwelling favorable winds led to lower mean total settlement success as surface water was driven offshore while, at greater depths, the mean total settlement success increased with stronger upwelling favorable winds as the deep water was drawn inshore to replace the surface layers. It also makes sense that the shallow and deep trends were reversed for downwelling winds as advective velocities reversed (Figure 14).

The relationship between alongshore winds and release depth (along with the relationship between alongshore winds and release zone) is further illustrated in the spaghetti plots showing the Lagrangian path lines of particles in the model (Figures 18, 19 and 20). These figures represent the advective motion for subsets of particles released in zones 2, 3 and 4, respectively, for two downwelling alongshore wind regimes. Each column of plots in the figures presents a constant downwelling wind and go from a weaker to a stronger wind, left to right. Each row of plots in the figures presents a constant release depth and goes from a 15 m release depth in the top row to a 25 m release depth in the bottom row. Looking only at the top row, or 15 m release depth plots of each these figures it can be seen that the stronger downwelling winds hold a greater proportion of individuals closer to the coast for release zones 2 and 3. This does not hold in the case of larvae released in zone 4 and is discussed below. Similarly, the stronger downwelling winds push the individuals in all three zones further from the coast at the 25 m release depth in the bottom row of plots in these figures.
Figure 18: Representative Travel Paths for Individuals Starting in Zone 2

Travel paths for a subset of particles released in Zone 2 of the study area in various wind and release depth combinations. Plots in the left column are forced with alongshore winds that are one standard deviation less than the climatological average while winds in the plots in the right column are two standard deviations less. All are forced with climatological average cross-shore winds. Plots in the top row have a release depth of 15 m and plots in the bottom row are released at 25 m.
Figure 19: Representative Travel Paths for Individuals Starting in Zone 3

Travel paths for a subset of particles released in Zone 3 of the study area in various wind and release depth combinations. Plots in the left column are forced with a alongshore winds that are one standard deviation less than the climatological average while winds in the plots in the right column are two standard deviations less. All are forced with climatological average cross-shore winds. Plots in the top row have a release depth of 15 m and plots in the bottom row are released at 25 m.
Figure 20: Representative Travel Paths for Individuals Starting in Zone 4

Travel paths for a subset of particles released in Zone 4 of the study area in various wind and release depth combinations. Plots in the left column are forced with alongshore winds that are one standard deviation less than the climatological average while winds in the plots in the right column are two standard deviations less. All are forced with climatological average cross-shore winds. Plots in the top row have a release depth of 15 m and plots in the bottom row are released at 25 m.
**Depth**

The data from this model show that the inflection point between onshore and offshore advective velocity due to alongshore wind variability (as shown in figure 17) is at approximately 20 m below the surface. This is illustrated well in the trend line of the mean total survival success with depth as the alongshore wind field goes from upwelling to downwelling (Figure 14) as discussed in the previous section. At the 25 m depth, mean total settlement success varied from about 25 to 75% with most values being between 50 and 60%. At the 15 m depth settlement success varied quite similarly but was generally toward the opposite extreme as the 25 m value except where alongshore winds were very weak (middle two plots).

The consequences of vertical depth distribution are also shown in the spaghetti plots (Figures 18 – 20). Each column represents a constant alongshore wind as depth goes from 15 m to 25 m. For all wind forcing fields and all larval release zones, individuals starting at a depth of 25 m stay further away from the coast and have a greater likelihood of being driven out of the Gulf of Maine. In particular, the plots show that by swinging wider around Cape Ann larvae at a 25 m depth are more likely to be caught by the bathymetry associated with Stellwagen Bank and swept outside the Gulf.

**Zone**

Variability among zones was greater at all depths below the surface than at the surface (Figure 21). This was due to the varying exposure to bathymetric features (especially Stellwagen Bank as mentioned above) and distance along the coast from the mouth of the Gulf. To illustrate consider figures 18 – 20 one plot at a time.
Figure 21: Zonal Settlement Success Indexes Over Modeled Alongshore Forcing

Data are from same runs as figure 14. The greatest upwelling wind (blowing toward the NE along the Maine coast) is in the upper left corner, the greatest downwelling wind is in the lower right corner. Total settlement success (bold) lines are re-plotted from figure 11 for comparison purposes.
The upper left plot in each of these figures represents a downwelling alongshore wind regime that was modeled by subtracting one standard deviation from the climatological mean alongshore wind and a release depth of 15 m. The mean total settlement successes at the various release depths for this wind regime are shown in the lower left plot of figure 14. Figure 21 shows the same plots with the zonal settlement successes added to them. It can be seen that while the total settlement success was relatively high at 15 m, the settlement success indexes in zones 2 and 3 were very high while the settlement success in zone 4 was low (Figure 21). The paths of individuals released in zone 2 (Figure 18) remain close to shore and most settle within zone 2. Individuals released in zone 3 (Figure 19) remain close to the coast and most settle either before reaching Cape Ann or because they get caught behind Cape Ann. A small contingent makes it around the Cape, but most of those settle before leaving the Gulf. Finally, individuals released in zone 4 (Figure 20) do not have the chance to settle before rounding Cape Ann and their relatively close proximity to the mouth of the Gulf allows them to be swept out before they have the chance to develop to the benthic stage.

To summarize, individuals released in zone 2 had the advantage of distance to be able to develop to the benthic stage before being affected by bathymetry or flushing. Individuals released in zone 3 had some combination of the advantages of bathymetry and distance to allow their high settlement success. Individuals released in zone 4 suffered mainly from the disadvantage of distance though about half of them settle successfully.

Now considering the lower left plots in each of these figures, which represent the same wind at a 25 m release depth, see similar factors are at work as we examine each
zone. In this case all individuals remain farther off the coast due to the greater depth and zone 2 individuals (Figure 18) still have the advantage of distance to keep their settlement success high. Individuals released in zone 3 (Figure 19) now find that bathymetry is a disadvantage as they are no longer caught behind Cape Ann and instead are swung wide around it where many individuals catch Stellwagen Bank and get flushed from the Gulf. A portion of them find the advantage of distance because they come in close around Cape Ann and stay inside Stellwagen Bank but their overall settlement success suffers due to the bathymetry change between 15 and 25 m. Zone 4 individuals (Figure 20) now have the double disadvantage of distance and bathymetry due to their depth. Individuals originating in this zone that stay inside Stellwagen bank now have less distance to travel before being flushed because they are farther off the coast. Zone 4 settlement success drops dramatically between 15 m and 25 m (Figure 21).

In the upper right plots of these three figures are the paths for a stronger downwelling wind (climatological average minus two standard deviations) at the 15 m release depth. The settlement successes for this and the next set of plots discussed are found in the lower middle plots of figures 14 and 21. In this scenario all paths are closer to the coast due to the stronger downwelling wind. Zone 2 individuals (Figure 18) once again have high success due to their distance from the mouth of the Gulf and the fact that their closer proximity to the coast puts more of them within the definite success zone inside the 50 m isobath when compared to the weaker downwelling wind at the same release depth. Zone 3 individuals (Figure 19) see even less flushing as more of them are caught behind Cape Ann compared to the weaker downwelling wind plot at the same release depth. Zone 4 individuals (Figure 20) seem to have greater settlement success
among individuals that stay inside Stellwagen Bank because they gather in a more
defined stream that is not as susceptible to flushing but a group of them is exposed to the
Stellwagen Bank bathymetry that sweeps them out of the Gulf decreasing their overall
settlement success compared to the weaker downwelling wind at the same release depth.

Lastly, the lower right plots in these figures represent the stronger downwelling
wind at the 25 m release depth and settlement success in all three zones drops
dramatically due to bathymetry exposure. Zone 2 individuals (Figure 18) still have the
advantage of distance and their settlement success does not drop as dramatically as the
other zones when compared to the weaker downwelling wind at the same release depth.
Zone 3 individuals (Figure 19) now have such a disadvantage due to the Stellwagen Bank
bathymetry that few individuals are able to take advantage of the distance needed to
tavel if they can stay inside the bank. Zone 4 individuals (Figure 20) are almost
exclusively flushed out of the Gulf on the outside of Stellwagen Bank as they swing far
outside of Cape Ann.

The main factor preventing the mean total settlement success from hitting 0% at
any depth was the consistently high settlement success in the northern-most zone at all
depths and wind forcing regimes (Figure 21). In all model runs the particles in this zone
tended to circulate near their starting points and have almost complete settlement success.
This is likely due to the fact that they are within Penobscot Bay; a small protected area
close to shore where the physical model used is not expected to be highly reliable.
**Temperature**

Developmental duration of the larval phase calculated in the model runs was not strongly affected by either change in the release day or increases in temperature fields by up to two standard deviations. While temperature is cited as a key factor in the development and survival of *P. borealis* larvae (Brillon et al. 2005; Storm and Pedersen 2003; Appolonio et al., 1986), the temperature range encountered by the larvae in the model, even with two standard deviations added to the climatological averages, was small enough to change mean development times by less than 10 tides, or approximately 5 days. Encountering water temperatures two standard deviations greater than the climatological mean increased total settlement success indexes by only 0.006 points, on average, from 0.559 to 0.565 (Table 3). This amount is much smaller than the effect that even a small mortality rate change would have over the same time period. The maximum increase in the settlement success index for any single run was 0.095 points. This suggests that changes in temperature exposure during the time of year the larvae are developing are not a significant source of variability for this population of the species. This does not, however, rule out the effect of these temperature changes on the later, juvenile phases of development.

**Release Day**

In general, the southern-most zone (Zone 4) experienced the lowest settlement success indexes while the northern-most (Zone 1) had the highest. The respective indexes changed little throughout development periods defined by the early, middle and late release dates (Figures 10 – 12).
The model results suggest that the currents, not the temperature field, are the primary determinant of success in these zones throughout the potential development periods. While temperatures that individuals are exposed to as the release date gets later, that increase is small due to the short time intervals between the release dates. Mean temperature fields do not increase enough from the early to the late release date to speed the development of zone 4 larvae to the point where they become benthic before being flushed from the Gulf. Similarly, the interannual variation in temperature from the mean does not go low enough to decrease development of Zone 1 larvae to the point where they remain pelagic until they are flushed from the Gulf or inner shelf regions. Secondly, the fact that the settlement success in these two zones remains fairly constant regardless of release date indicates that the physics does not change significantly in these zones over this time period.

The overall effect (taking into account all 4 release zones) of the exposure to different temperature fields due to a change in release date is not as clear for two reasons. First, the change in average temperature exposure between particles released on day 42 and those released on day 68 (0.22 °C) was less than one quarter that affected by increasing mean temperature exposures by two standard deviations (0.90 °C), which did not cause a significant change in the number of tides to settle or overall mean settlement success (Table 3). This suggests that variable temperature field exposure affected by differences in release date is not the source of significant changes in larval settlement success. On the other hand, although the average increase in settlement success from release day 42 to release day 68 was only 0.014 points, from 0.542 to 0.556 (Table 3), the settlement success in some runs increased or decreased of over 0.5 points. With better
latitudinal and depth distribution data for the larvae it may be found that the particular forcing regime combined with the release date has a significant impact on larval settlement success. Clarifying the relationship between release day and settlement success could be a useful area of study once more precise three-dimensional larval distribution zones are identified for *P. borealis*.

**Effects of Daily Variation in Wind Fields**

The results from the 20 years of model runs using daily wind data were compared to 20 years of catch data to examine the null hypothesis that settlement success is of order-one importance in determining recruitment success. Clark et al. (2000) indicate that peaks in the autumn survey abundance of northern shrimp that occurred in 1986, 1990 and 1994-95 reflect recruitment of the strong 1982, 1987 and 1992 year-classes. The autumn survey peaks also correspond with peaks in commercial catch in 1987, 1990 and 1995-97. This suggests a three to five year lag time from settlement success to commercial catch strength. Therefore statistical analysis was done between model run data from 1982 – 2001 and three different commercial catch ranges; 1985 – 2004, 1986 – 2005 and 1987 – 2006.

Figure 22 shows the annual landings of northern shrimp from 1985 – 2006, a subset of data from figure 1. Figure 16 shows the mean total and zonal survival indexes for model runs using wind data from 1982 – 2001. Using linear regression analysis there is not a significant correlation between any of the mean settlement success indexes, total or zonal (Figure 16), and the catch data three to five years later. Analysis was also done using the two-year lag time mentioned earlier but with no more significant results.
Figure 22: Commercial Shrimp Catch Data 1985 – 2006

Northern shrimp catch data provided by the 2006 ASMFC Northern Shrimp Report. These data are a subset of the data in figure 1.
Figure 23: Model Settlement Success Indexes at 15 m, 1982 – 2001

These data are from runs starting on release day 55 at a release depth of 15m with daily wind data for each year modeled and climatological temperature fields.
Figure 24: Model Settlement Success Indexes at 25 m, 1982 – 2001

These data are from runs starting release day of 55 at a release depth of 25m with daily wind data for each year modeled and climatological temperature fields.
Success Settlement Success For Release Day 55, 35m Start Depth

Figure 25: Model Settlement Success Indexes at 35 m, 1982 – 2001

These data are from runs starting on release day of 55 at a release depth of 35m with daily wind data for each year modeled and climatological temperature fields.
The total and zonal success index responses from each release depth were then separated out. Any consistent behavior by the species with respect to release depth or zone should be reflected as a correlation between the settlement success index and the wide variability in catch rates if the catch variability is the result of the parameters under study. Figures 23 - 25 show the survival indexes from the three most successful release depths at day 55. Again, there is no significant correlation between these success indexes and corresponding catch data three to five years later.

Many factors can play a role in the survival of northern shrimp in the three to five year gap between their settlement and their being part of the commercial fishery. Also, once they are recruited to the fishery, they may or may not be caught depending on effort variability and regulation restrictions. With this understanding correlations were sought between model success indexes and recruitment data two years later based on the dominant timescale of the pre-adult life stages for *Pandalus borealis* (Shumway et al. 1985).

Recruitment estimate data were found in the Atlantic States Marine Fisheries Commission’s (ASMFC) 2006 Gulf of Maine Northern Shrimp Assessment Report. This data, with a two-year lag from the yearly-wind model run data, is plotted in figure 26. When statistical analyses were done to compare this data to the mean annual settlement success indexes (Figure 16) using a two year lag times between settlement success and new recruit numbers, there were no significant correlations found. The data sets were then detrended before comparison to eliminate any upward trend in recruitment due to increased regulatory effectiveness. Again there was no significant correlation.

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Figure 26: Recruitment Estimates 1984 – 2003

CHAPTER IV

CONCLUSIONS

The results of the model runs done in this study provide insight into the factors controlling the population dynamics of *Pandalus borealis* in the Gulf of Maine. Importantly, they also highlight data and knowledge gaps for improvement of population prediction models.

From the standardized model runs examining the effect of variability in physical forcing on population dynamics, it was shown that temperature variability has little effect on larval development time and therefore on retention and settlement success. This was due to the low variability in the temperature fields both interannually and among the climatological mean temperatures experienced throughout the spawning season (Table 3). Temperature data for this region is very sparse both spatially and temporally but initial results indicate that more data would not likely have a significant effect on model runs. This is an interesting result because temperature-dependent development times have been shown to be important to species retention in general (Byers and Pringle, 2006).

Also, in these standardized wind regime runs done earlier in the study, it was seen that three factors, release zone, release depth and alongshore wind intensity, can have complex and combined effects on retention and settlement success, as illustrated in figures 17 - 19. Alongshore wind intensity is well documented but release zones and depths are not. There is a strong need for data to constrain these two variables more tightly within this model. The difference in success indexes between zonal and depth
extremes can be over a factor of two. Studies of three-dimensional larval distribution would provide the biggest benefit to the predictive abilities of this model and allow evaluation of multiple interacting factors causing the observed population variability in the Gulf of Maine.

While nearly all settlement success indexes in the standardized model runs could be considered high, it must be remembered that natural mortality rates were not modeled. At a nominal transport success of 0.6, and assuming an average fecundity of 2000 eggs per female over two reproductive years, the population could sustain an instantaneous daily mortality due to other factors (predation, starvation, etc.) of about 0.16 d\(^{-1}\). This is compared with an average number of 0.12 d\(^{-1}\) for pelagic fish larvae from a study done reviewing literature on five species with pelagic larvae [Houde, 1988]. Better mortality rate data would greatly increase the usefulness of this model. The model itself could be effectively used to help differentiate sources of loss (e.g. natural mortality, transport loss, advection combined with bathymetry) from the Gulf of Maine population if it were enhanced with lateral and vertical larval distribution data.

Catch and recruitment data show no correlation to total or zonal settlement success indexes derived by model runs using 20 years of actual wind data whether the comparison is done with those success indexes averaged over all depths or with individual values taken at the three most successful release depths (15, 25 and 35 m). Although this points strongly toward the rejection of the original hypothesis, that interannual wind variability has a first order effect on recruitment and abundance, these yearly model runs still produce significant results.
To begin, as with the standardized runs, individuals released in zones 2 and 3 show strong settlement success at all depths modeled (Figures 23 – 25). It is reasonable to hypothesize that shrimp release their larvae in these areas to increase their likelihood of settlement success. It would also be worth investigating the interaction of release zones 2 and 3 with the date of release date since these two zones switch their relative success strength throughout the season (Figures 7, 8, and 9). Time of release during the season may be related to the zone of release. These results make zones 2 and 3 good candidates for future field surveys looking at the larval release areas in the Gulf of Maine northern shrimp population and point to the general need for more detailed three-dimensional larval release zone surveys.

This leads to another important finding of this study. It is also possible that winds combined with other, biological, parameters studied may have a significant effect on survival. While the modeled yearly variability of larvae settlement success was generally small for particles starting at given depths and zones (Figures 23 – 25) when compared to the variability of commercial catch and recruitment (Figure 22), it is possible that unknown factors cause the depth and latitude of release to vary appreciably from year to year.

For example, if the zone of high larval release concentration varies from year to year, it is possible that settlement success may vary more dramatically than if the release zone were to remain constant (Figure 22). It is also possible that the effect of such zonal variability could be of the same order as wind variability alone (compare figures 10 and 22) so that the two factors combined may have a first order effect on recruitment. Long-
term release zone time-series studies on this population would be a valuable addition to this model.

Variability in release depth in the yearly runs also shows potential for causing significant variability in settlement success (Figures 23 - 25). The 15 and 25 m release depths have the most consistent settlement success indexes overall and within zones, (Figure 20). It would be useful to verify these findings with field surveys and further indicates the need for three-dimensional release zone surveys.

Finally, one other hypothesis that can be drawn from the results of this study is that part of the retention strategy of this northern shrimp population is its migration behavior. If the adult females spawn largely in zones 2 and 3 and are transported generally downstream along the WMCC, migration may be there only means of returning to the spawning grounds favorable for their retention.

Other possibilities for the wide fluctuation in shrimp catch are high variability in food supply, predation or some other source of mortality (such as viral or bacterial infections) in both the larval and juvenile phases. These factors were not modeled for the larval in this study because they are not well understood. Food supply will not just cause starvation but can lead to reduced survival due to slower development causing a higher susceptibility to flushing and predation (Shumway et al. 1985). Changes in any of these factors would affect the total mortality rate and even fairly small changes in mortality rate can have large effect on the survival index (Table 1). Though the exact diet of \textit{P. borealis} larvae is not well known, variation in its food supply is likely to be directly related to the timing of the spring bloom (Stickney and Perkins, 1981). It would be worthwhile seeking correlations between spring bloom timing for various years and the
corresponding recruitment for those year-classes. Greater delineation of mortality factors, specifically an inclusion of transport loss figures within natural mortality studies would be helpful for future research into the fluctuations of this population. Juvenile mortality rate were assumed constant in this study based on earlier research on pelagic larvae of demersal and pelagic species (Myers and Cadigan, 1993; Houde, 1988) but this may not be the case. In general, a more thorough understanding of the interannual variability in the overall mortality rate of this population would be a first step to understanding predation, food supply and other mortality factors related to recruitment data. Time-series studies in this area would be very useful.

In summary, much more mortality and three-dimensional distribution of larval release data is needed to increase the effectiveness of this model. This research indicates that there is no first-order cause-effect relationship between the settlement success indexes driven by annual variability in physical forcing and either commercial catch three to five years later or year-class recruitment two years later. Other, biological, factors may combine with the local physics to affect settlement success; the main factors being release zone, release depth and mortality. This model is able to test these hypotheses as more data become available. Finally, temperature variability during the pelagic larval phase does not seem to play a major role in recruitment variation in this species.
LIST OF REFERENCES


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