INCORPORATING SPACE INTO MODELS OF THE CHESAPEAKE BAY BLUE CRAB POPULATION

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ABSTRACT

Few models of blue crab population dynamics have accounted for the spatial aspects of crab life history in their formulations. Here I develop a spatially-explicit model of the Chesapeake Bay blue crab population that reflects our understanding of the general life history. Best available estimates of growth, mortality and fecundity were used. Currently, we lack empirical data on which to base estimates of movement probabilities. Thus, movement probabilities were based on the relative area of each region. The model results show that the current pattern of exploitation in blue crab is likely not sustainable and needs to be reduced substantially. The model appears relatively insensitive to the estimated probability of survival during early life history. Moreover, variation in the proportion of crabs that recruit to the fishery at age-1 appear to have little impacts on projected rates of population growth. Model results also show that restriction of a winter dredge fishery in the lower Chesapeake Bay is not sufficient to ensure a sustainable pattern of exploitation. Until further empirical data are available to improve accuracy, the model serves as a useful tool for exploring consequences of different spatial distributions and patterns of exploitation.

The blue crab (*Callinectes sapidus*) is an important member of estuarine communities throughout its range. Often, the blue crab is a dominant estuarine benthic predator and scavenger (Eggleston et al., 1992; Mansour and Lipcius, 1993). It is an opportunistic predator with a highly variable diet that may include a wide range of taxa including bivalves, crustaceans and fish (Hines et al., 1990; Mansour and Lipcius, 1991). Thus, blue crab may be a keystone predator in the estuary, sensu Paine (1966), possibly playing a dominant role in structuring benthic communities throughout its range (Hines et al., 1990). In turn, crabs may fall victim to several fish species including sciaenids and moronids. Thus, blue crab may provide an important link between the benthic and pelagic food webs (Baird and Ulanowicz, 1989).

Besides its ecological importance, blue crab supports important commercial fisheries throughout its range. In the U.S., important coastal and estuarine fisheries for blue crab occur from the Gulf of Mexico, along the Atlantic coast of the United States, and as far north as New England. In 2001, 38% of the US blue crab catch came from Chesapeake Bay, with a dockside value of $60 million. However, analyses of both fishery-independent and fishery-dependent data from Chesapeake Bay have indicated deterioration in several important measures of population health (Lipcius and Stockhausen, 2002). In response, the Governors and Legislatures of Maryland and Virginia established the “Bi-State Blue Crab Advisory Committee” (BBCAC) in 1996 to give them independent advice on the status and future trends of the blue crab population and the fishery it sustains. In 1998, BBCAC endorsed the findings of its technical work group and reported that overall abundance for all age groups was down (Lipcius et al., this volume), fishing mortality was increasing and fishing effort was at near record levels (Rugolo et al., 1997; Miller and Houde, 1999), spawning stock biomass was below the long-term average (Lipcius and Stockhausen, 2002), the average size of crabs

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was decreasing (Abbe and Stagg, 1996), there was a decreasing percentage of legal size crabs (Abbe and Stagg, 1996), and that the reproductive potential of the population may be comprised due to the reduced size of males and lack of mature females (Jivoff, 1997; Jivoff et al., this volume).

These observations have intensified interest in the dynamics of blue crab populations throughout the species’ range. Different approaches have been used to understand and predict the dynamics of the blue crab population in Chesapeake Bay (Tang, 1985; Lipcius and Van Engel, 1990; Smith, 1997; Rugolo et al., 1997; Uphoff, 1997; Miller, 2001). All models of population dynamics examine the consequences of patterns in key vital rates such as growth, mortality and fecundity on the future abundance and structure of the population. Two assumptions have commonly been made to simplify model development. Growth has been assumed to be continuous, and vital rates have been assumed not to vary spatially or temporally. The first assumption allows the use of well-studied growth models such as the von Bertalanffy model. However, continuous growth models cannot adequately capture the discontinuous nature of the growth in crabs (Smith, 1997; Miller and Smith, this volume). Alternative formulations to the traditional approach are possible. Smith (1997) developed a molt-process model of crab growth. Miller (2001) developed a stage-based matrix model of the entire crab life history that accounted for discontinuous growth. Stage-based models are discrete, time invariant, probabilistic matrix models that have similarities with life tables (Caswell, 2000). In such models, growth of an individual crab is determined by the probability that it will survive and either remain the same size, or move into a different stage within a specified time.

The consequences of the assumption that vital rates vary in neither space nor time has yet to be addressed. Yet we know that key features of the life history and ecology of blue crabs vary in space and time. In Chesapeake Bay, the distribution of blue crabs differs according to age, size and sex (Chesapeake Bay Program, 1997). Following early zoeal development on the continental shelf, newly settled crabs are concentrated in the high salinity waters in the lower Bay in summer and early fall (Lipcius et al., 1990; Metcalf et al., 1995). Submerged aquatic vegetation (SAV) is believed to be an important habitat for newly-settled and young crabs (Orth and van Montfrans, 1997; Orth et al., 1996). Eggleston et al. (1998) have shown that structured habitat in general is important, not necessarily SAV per se. Later stage juveniles leave the structured habitat (Pile et al., 1996) and, together with adults, become more widely dispersed. Once mature, the distribution of the two sexes is markedly different. Mature males tend to dominate in lower salinity waters in tributaries and the upper Bay later in the season (Abbe and Stagg, 1996). Mature females aggregate in the lower Bay, near the Bay mouth, between late fall and early summer to release zoea (Lipcius and Stockhausen, 2002). Following the summer and fall growth seasons, both immature and mature crabs overwinter in the sediments. During this phase, individuals become torpid and neither feed nor grow. Moreover, there are distinct differences in movement within the Bay according to age, size and sex. A recent analysis of extensive tagging conducted by Drs. Truitt and Cronin at the Chesapeake Biological Laboratory (CBL) from 1925–1948 supports this contention (T. J. Miller, unpubl. data). For example, female crabs moved an average distance (±SD) of 32.25 ± 35.5 nm (nautical miles) between release and recapture, whereas males moved 9.91 ± 16.37 nm. Females moved more than males in every season. The difference was particularly large in summer (41.5 ± 43.5 nm vs. 8.05 ± 14.5 nm, female vs. male) and fall (47.58 ± 34.5 nm vs. 17.29 ± 23.3 nm). The greatest distance moved by any crab was 125 nm by an individual female. Crabs of both
sexes moved more in spring and fall, but the longest movements were observed in fall. Indeed the pattern of female movement in fall appears almost bimodal. This bimodality stems from differences between the release sites. Females released in more southerly locations moved significantly less than females released at more northerly locations, as would be expected based on spawning behavior.

Besides the spatial and temporal variability in crab biology, there is similar variability in the pattern of exploitation. There are two principal sectors in the blue crab fishery: the soft and peeler, and hardshell components. The soft and peeler segment harvests crabs for sale as soft-shell crabs for consumption or for the bait industry. Peeler crabs (those caught just prior to molting) are harvested throughout the spring and summer in both Maryland and Virginia. Harvests typically peak in late spring. There can be high mortality in the shedding phase of the fishery, suggesting that the reported landing may be only a fraction of the actual catch. Moreover, there have been considerable increases in the number of soft and peeler licences granted and in reported landings in the last five years (R. O’Reilly, Virginia Marine Resources Commission, pers. comm.). The hardshell fishery uses pots, trotlines and dredges. Each gear type is used in different areas and at different times. The winter dredge fishery occurs exclusively in Virginia in the vicinity of the Bay mouth. The total harvest in this fishery is small compared with the total hardshell harvest. Nevertheless, the dredge fishery exploits females immediately before the release of zoea. Thus, the potential impact to the population may be substantial. The pot fishery occurs throughout the mainstem of the Bay, but it commences several weeks earlier in the lower Bay than in the upper Bay. Only trotlines are permitted in Maryland’s tributaries to the Bay.

These spatial and temporal patterns in life history and exploitation can be expected to interact to produce complex temporal and spatial patterns in key vital rates such as growth and mortality. However, existing attempts to model the Chesapeake Bay blue crab population have not included this variability. Thus, existing model results may not accurately predict the crab population structure. Here, I extend the stage-based model developed previously (Miller, 2001) to include appropriate levels of both spatial and temporal variability.

**Model Development**

Full details of the basic stage-based model for blue crab are available in Miller (in press), and are only summarized here. I modeled the blue crab life history on a six-month time step and involving four stages within each time step to account for the seasonally variable patterns of growth and mortality (Fig. 1). The model developed here tracks the female component of the population. I represented the blue crab population by its abundance in each of four life history stages (Fig. 1). The time step was chosen to account for alternating periods of activity and growth during summer, followed by torpid periods during winter. Summer was defined as July–December, and winter January–June. Transitions between life history stages are modeled for each season separately. The transition matrix \( A_{summer} \) defines all dynamics affecting summer life history stages (dashed transitions in Fig. 1). Given the 4 life history stages, \( A_{summer} \) is a \( 4 \times 4 \) matrix. A similar \( 4 \times 4 \) matrix, \( A_{winter} \), was used to define the dynamics of winter life history stages (solid transitions in Fig. 1).

Each seasonal matrix defines the transitions initiated during that season. Accordingly, when the seasonal vector of population abundance is multiplied by the appropriate transition matrix, the population vector for the following season is predicted. To project the population forward by one year one simply multiplies
Figure 1. Life cycle diagram for blue crabs. The life cycle is represented by four stages that occur both in summer (left-hand column) and winter (right-hand column). Transitions from summer to winter are shown as dashed lines. Transitions from winter to summer are shown as solid lines.

the two $A$ matrices. For example, to project the population from one summer to the next, one multiplies a summer population vector by $A_{\text{winter}}A_{\text{summer}}$. The analysis of the combined projection matrix is straightforward (Caswell, 2000; Ebert, 1999). The dominant eigenvalue of the combined matrix is an estimate of the population growth rate $\lambda$. From $\lambda$, the instantaneous rate of growth of the population, $r$, can be calculated as $\ln(\lambda)$. Eigenvectors associated with the dominant eigenvalue represent the stable stage distribution (right eigenvector) and stage-specific reproductive values (left eigenvector) (Caswell, 2000). The proportional sensitivity or elasticity of the population growth rate to changes in individual transition probabilities can be calculated from the dominant eigenvalue and eigenvectors (Caswell, 2000; de Kroon et al., 2000).

To illustrate how spatial variability can be included in the stage-based model, I develop here a 2-region extension of the basic model (Miller, 2001) specific to Chesapeake Bay. The two regions are the upper Bay and the lower Bay (Fig. 2). The upper Bay encompasses the waters of the mainstem of Chesapeake Bay north of Cove Point at the mouth of the Patuxent River and includes the Black, Chester, Choptank, Elk, Little Choptank and Sassafras Rivers. The lower Bay encompasses all of the mainstem south of Cove Point and includes Tangier and Pocomoke Sounds plus the Honga, James, Patuxent, Potomac, Rappahannock and York Riv-
ers. The division was chosen so that the lower Bay region encompasses all potential settlement areas.

Seasonal transition matrices $A_{\text{winter}}$ and $A_{\text{summer}}$ were defined for each region (Fig. 3). These matrices include both probabilities of life history transitions and probabilities of immigration and emigration. The combined probabilities of each life history transition and movements between regions allow the estimated Bay-wide population in one season to be projected forward to the next season. To understand the model structure it is useful to follow the life history and potential movement of crabs beginning with the larval stage.

Larval stage crabs are found only in the lower Bay during summer, and become newly settled crabs that overwinter as juveniles in either region. Little is known of the movement of crabs within Chesapeake Bay, or any estuary. Accordingly, I estimated movement probabilities based on the relative areas of each region. The probability of a newly settled crab remaining in the lower Bay was equal to the proportion of the total Bay area represented by the lower Bay. I estimated the area of the lower Bay to be $6.065 \times 10^3$ km$^2$ and the area of the upper Bay to be $1.865 \times 10^3$ km$^2$. This translates to an estimate of the probability of a newly settled crab remaining in the lower Bay to overwinter of
Figure 3. Spatially explicit life cycle diagram for blue crabs. The life cycle is represented by four stages that occur in each of the two regions both in summer (left-hand column) and winter (right-hand column). Transitions within a single region are shown by faint solid lines and are identical to those in Figure 1. Summer time transitions that involve movement from one region to another are shown in heavy solid lines. Winter time transitions that involve movement from one region to another are shown in dashed lines. All fecundity terms, regardless of the region of origin are shown in dotted lines.
\[ T = \frac{6.065 \cdot 10^3}{6.065 \cdot 10^3 + 1.865 \cdot 10^3} = 0.765 \]

Similarly, I defined the probability of a newly settled crab moving to the upper Bay to overwinter as \( R = 1 - T = 0.235 \). However, not all megalopae survive, and thus movement probabilities must be multiplied by the survival probability.

There have been no published studies on survival of zoea and megalopae, and few systematic studies on the mortality of newly settled crabs. To develop an estimate of early life history survival I assumed that early life history survival could be represented as the product of survival through component stages, following Quinlan and Crowder (1999) and Diamond et al. (1999). I calculated the survival of zoea and megalopae based on the stage duration (40 d—Pleth, 1992) and an instantaneous mortality rate estimated from Peterson and Wrobleski’s (1984) size-dependent relationship for mortality of aquatic organisms. Pleth (1992) estimated the dry weight of zoea as 3.25 \( \mu \)g. Substituting this value into Peterson and Wrobleski’s (1984) predictive relationship for mortality of \( M_0 \) (d\(^{-1}\)) = 5.26 \times 10^{-3} W^{-0.25} \) (g) yields an estimated daily instantaneous mortality rate during the zoeal and megalopodal stages of \( M_0 = 0.1238 \). The daily probability of survival during the 40 d zoeal and megalopodal periods is \( S_i = e^{-M_0} \). To calculate the survival of newly settled crabs (older than 40 days after release), I assumed that the daily instantaneous mortality rate, \( M_1 \), would decline linearly from 0.1238 d\(^{-1}\) to the background mortality 0.00102 d\(^{-1}\) (\( M = 0.375 \) yr\(^{-1}\)) over the next 142.5 d. On each day of subsequent development, I interpolated the daily mortality rate, \( M_1 \), and estimated the survival as \( S_i = e^{-M_1} \). Finally, the probability of survival for the entire zoea/newly settled crab period is defined as \( P = S_i = 1.196 \times 10^{-6} \).

Those individuals that survive the megalopodal stage overwinter as juveniles in both regions of the Bay. During the winter time step, overwintering juveniles are subject to mortality. On emergence the following summer, overwintering juveniles enter one of two life history stages (small age-1 and large age-1) based upon size. The model accounts for the possibility that emerging age-1 crabs in the lower Bay could migrate out of this region. The probability of migration was based on considerations of the relative area of each region, as with newly settled crabs. Accordingly, I used \( T \), the estimate of the relative area of the lower Bay to estimate the probability that a newly emerged age-1 crab would remain in the lower Bay. Newly emerged age-1 crabs in the lower Bay migrated to the upper Bay with a probability \( R = 1 - T \). Age-1 crabs in the upper Bay were not permitted to migrate to the lower Bay. This is in accordance with the generally accepted life history information (Van Heukelom, 1991).

In the model, the fates of age-1 crabs in the summer depended on size and location. Small age-1 crabs do not enter the fishery during the summer and thus are exposed only to natural mortality. In contrast, the larger size class does enter the fishery and thus are subjected to both natural and fishing mortality. The proportion, \( f \), of age-1 crabs that grew sufficiently large to recruit to the fishery and mature in their first summer was estimated from fishery-independent size-distribution information from Chesapeake Bay to be 0.15 (Rothschild et al., 1988). However, to explore the sensitivity of the model to this factor, \( f \) was allowed to vary \( 0 < f < 1 \). All age-1 crabs were exposed to natural mortality, \( M \), regardless of location. All large age-1 crabs were exposed to fishing mortality \( F \). Estimates of \( M \) and \( F \) did not vary spatially.

Small age-1 crabs in the lower Bay could overwinter as either small or large age-1 crabs in either the lower or upper Bay. The probability of each transition was determined by estimates of \( T \), the relative area of the lower Bay, and \( f \), the
proportion of the age-1 size frequency > legal carapace width. In contrast, large age-1 crabs in the lower Bay were restricted to the lower Bay. Small age-1 crabs in the upper Bay could overwinter as either small or large crabs. The probability of each fate varied with f. No upper Bay small age-1 crabs were permitted to migrate out of the upper Bay. Upper Bay large age-1 crabs overwintered as large age-1 crabs in the upper Bay, or as adults in the lower Bay. The probability of following either path was related to the relative area of the two regions.

Overwintering age-1 crabs all experienced natural mortality, M. Large age-1 crabs in the lower Bay region were also subject to exploitation in the winter dredge fishery, F_dredge. Thus, these crabs experienced a total mortality rate of M + F_dredge. Large age-1 crabs in the lower Bay were modeled as producing zoea at the end of the winter period. The fecundity of these younger crabs was determined by a size-dependent fecundity relationship from Prager et al. (1990). However, because zoeal release was assumed to occur at the end of the winter period, the effective fecundity was weighted by the probability that an individual age-1 crab would survive.

All age-1 crabs emerge from the overwinter period as adults. All adults were subjected to natural mortality, M and fishing mortality F. Adults surviving the summer overwinter as adults. Adults in the upper Bay could overwinter in the upper Bay, or in the lower Bay. The proportion that migrated was assumed to be equal to the relative area of the two regions. All overwintering adults experience natural mortality, M. Adults in the lower Bay also experience exploitation in the winter dredge fishery. Thus, their total mortality rate is M + F_dredge. Adults in the lower Bay, produce zoea at the end of the winter period. The number of zoea produced was determined by a size-dependent fecundity relationship from Prager et al. (1990). Similar to the age-1 reproduction, the fecundity of adults was further reduced by the probability of adult overwinter survival.

Parameter estimates used in the model are presented in Table 1. Several parameters used in the model (natural mortality rate, fishing mortality rate, fecundity, the survival of zoeal and megalopal stages, the fraction of age-1 crabs recruiting to the fishery and the dredge fishery mortality multiplier) are estimated externally to the model.

The natural mortality rate, M, was estimated based on a maximum life expectancy, α, of 8 years. This value is based upon returns of tagged crabs in the North Carolina Fishery (Fischler, 1965). As α is defined as the maximum expected age in an unfished population, Fischler’s documented maximum age was adjusted upwards. Based on this estimate, M was estimated as 3/α = 0.375. However, this provides an estimate of the annual rate, whereas the model requires an estimate for a six-month period. Accordingly, I used M/2 in model projections.

Time series of F’s were calculated from time series of total mortality rates calculated from the average size in the catch using Hoenig's (1987) method. Miller and Houde (1999) present details of the calculations. Using an estimate of M = 0.375, the average F in Chesapeake Bay for the period 1955–1997 was 0.88 (Miller and Houde, 1999). Over this period F varied from 0.62–1.26. Higher values of M, reflecting shorter life expectancies, lead to reductions in the estimated F. Accordingly, in modeled scenarios, F was allowed to vary between 0–1.5. Similar to the case with the natural mortality rate, F/2 was used in model runs to convert the annual estimates to six-month equivalents. A simple multiplier, a, was used to relate estimates of F, based largely on the impacts of the summer pot fishery, to that exerted by the winter dredge fishery. I allowed 0 < a < 1.5 to account for a range of possible levels of effort in the dredge fishery.

Prager et al. (1990) conducted an extensive study of fecundity patterns in Ches-
apeake Bay blue crab. They found that fecundity level varied seasonally. Fecundity was low early in the season, peaked in mid season and declined at the end of the season (Prager et al., 1990). They concluded that fecundity was an increasing linear function of female carapace width, given by Fecundity (millions) = $-2.248 + 0.377 \cdot CW$ (cm), $r^2 = 0.24$. I used $1.6 \times 10^6$ as an estimate of the number of female offspring produced by a mature female crab.

**Model Simulations**

I conducted four categories of simulations to explore the implications of the inclusion of space in population models of blue crabs. First I present base simulations in which I projected the blue crab population in Chesapeake Bay forward in time to quantify the intrinsic rate of population growth, the stable stage distribution, stage-specific reproductive values, and the elasticity of the projected population growth rate to changes in transition probabilities. Then I examined the response of the projected population growth rate to variation in the early life history survival probability. Next I explored the consequences of size at age. I did this by exploring the consequences of changing the fraction of the population that becomes large in the first year. These simulations represent how either environmental changes or parameter uncertainty may affect crab growth rates. Finally, I examined the impact of the winter dredge fishery on the projected rate of population increase by varying the dredge mortality rate multiplier.

A. **Base Simulations.**—Based upon the estimated parameters defined in Table 1, and with setting the fishing mortality rate $F = 0.9$, the natural mortality rate, $M = 0.375$, the proportionality constant for the winter dredge fishery, $a = 1$, and the proportion of fast-growing age-1 crabs to be 0.15, the two projection matrices are:

$$
A_{\text{summer}} = \begin{bmatrix}
0 & 0 & 0 & 0 & 2.8 \times 10^{-7} & 0 & 0 & 0 \\
0 & 0.166 & 0 & 0 & 0 & 0.166 & 0 & 0 \\
0 & 0.019 & 0 & 0 & 0 & 0.019 & 0 & 0 \\
0 & 0 & 0.124 & 0.124 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 9.1 \times 10^{-7} & 0 & 0 & 0 \\
0 & 0.539 & 0 & 0 & 0 & 0.539 & 0 & 0 \\
0 & 0.061 & 0 & 0 & 0 & 0.061 & 0 & 0 \\
0 & 0 & 0.404 & 0.404 & 0 & 0 & 0.529 & 0.529
\end{bmatrix}
\quad \text{and}
$$

$$
A_{\text{winter}} = \begin{bmatrix}
0.705 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.124 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.829 & 0.195 & 0.829 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1.3 \times 10^6 & 0 & 0 & 5.6 \times 10^5 & 8.5 \times 10^5 \\
0 & 0 & 0 & 0 & 0.539 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.061 & 0 & 0 & 0 \\
0 & 0.634 & 0.634 & 0 & 0 & 0.829 & 0.529 & 0.529
\end{bmatrix}
$$

To project the population forward from one summer to the next one creates a combined projection matrix $A = A_{\text{winter}} A_{\text{summer}}$, given by:
Table 1. Definitions for all parameters and transitions used in the model together with their estimates for the base simulation.

<table>
<thead>
<tr>
<th>Transition</th>
<th>Definition</th>
<th>Parameter</th>
<th>Estimate (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fundamental parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natural mortality rate per six months</td>
<td>M</td>
<td>0.375/2</td>
<td></td>
</tr>
<tr>
<td>Current fishing mortality rate per six months</td>
<td>F</td>
<td>0.9/2 (0–1.5)</td>
<td></td>
</tr>
<tr>
<td>Fraction of small crabs age 1 growing to large size class</td>
<td>f</td>
<td>0.15 (0–2)</td>
<td></td>
</tr>
<tr>
<td>Fecundity</td>
<td>B</td>
<td>$1.6 \times 10^6$</td>
<td></td>
</tr>
<tr>
<td>Dredge fishing mortality</td>
<td>F_dredge</td>
<td>$a \cdot F (a – U (0 – 1))$</td>
<td></td>
</tr>
<tr>
<td>Probability of survival rate for megalopae and newly settled crabs</td>
<td>elhsurv</td>
<td>$1.196 \times 10^{-5}$</td>
<td></td>
</tr>
<tr>
<td>Relative area of upper Bay</td>
<td>R</td>
<td>0.235</td>
<td></td>
</tr>
<tr>
<td>Relative area of lower Bay</td>
<td>T</td>
<td>0.765</td>
<td></td>
</tr>
<tr>
<td><strong>Derived parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Summer to winter transitions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>as_{15}</td>
<td>Probability of newly settled crab moving to the upper Bay</td>
<td>R \cdot elhsurv</td>
<td>0.166</td>
</tr>
<tr>
<td>as_{22}</td>
<td>Probability of an upper Bay small age-1 remaining small age-1 in upper Bay</td>
<td>R(1 – f)e^{-M}</td>
<td>0.019</td>
</tr>
<tr>
<td>as_{32}</td>
<td>Probability of an upper Bay small age-1 becoming large age-1 in upper Bay</td>
<td>Rf e^{-M-F}</td>
<td>0.539</td>
</tr>
<tr>
<td>as_{82}</td>
<td>Probability of an upper Bay small age-1 becoming small age-1 in lower Bay</td>
<td>T(1 – f)e^{-M}</td>
<td>0.061</td>
</tr>
<tr>
<td>as_{92}</td>
<td>Probability of an upper Bay small age-1 becoming large age-1 in lower Bay</td>
<td>Tf e^{-M-F}</td>
<td>0.124</td>
</tr>
<tr>
<td>as_{83}</td>
<td>Probability of an upper Bay large age-1 becoming adult in upper Bay</td>
<td>Re^{-M+F}</td>
<td>0.404</td>
</tr>
<tr>
<td>as_{84}</td>
<td>Probability of an upper Bay large age-1 becoming adult in lower Bay</td>
<td>Te^{-M+F}</td>
<td></td>
</tr>
<tr>
<td>as_{55}</td>
<td>Probability of newly settled crab remaining in the lower Bay</td>
<td>T \cdot elhsurv</td>
<td>$2.275 \times 10^{-7}$</td>
</tr>
<tr>
<td>as_{96}</td>
<td>Probability of a lower Bay small age-1 becoming an upper Bay small age-1</td>
<td>R(1 – f)e^{-M}</td>
<td>0.019</td>
</tr>
<tr>
<td>as_{96}</td>
<td>Probability of a lower Bay small age-1 becoming an upper Bay large age-1</td>
<td>Rf e^{-M+F}</td>
<td>0.539</td>
</tr>
<tr>
<td>as_{66}</td>
<td>Probability of a lower Bay small age-1 remaining a lower Bay small age-1</td>
<td>T(1 – f)e^{-M}</td>
<td>0.061</td>
</tr>
<tr>
<td>as_{97}</td>
<td>Probability of a lower Bay large age-1 becoming a lower Bay large age-1</td>
<td>T f e^{-M-F}</td>
<td>0.529</td>
</tr>
<tr>
<td>as_{88}</td>
<td>Probability of a lower Bay adult remaining an adult</td>
<td>e^{-M-F}</td>
<td>0.529</td>
</tr>
<tr>
<td><strong>Winter to summer transitions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>aw_{21}</td>
<td>Probability of an upper Bay juvenile becoming an upper Bay small age-1</td>
<td>(1 – f)e^{-M}</td>
<td>0.705</td>
</tr>
<tr>
<td>aw_{31}</td>
<td>Probability of an upper Bay juvenile becoming an upper Bay large age-1</td>
<td>fe^{-M}</td>
<td>0.124</td>
</tr>
<tr>
<td>aw_{41}</td>
<td>Probability of upper Bay small age-1 becoming an upper Bay adult</td>
<td>e^{-M}</td>
<td>0.829</td>
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<tr>
<td>aw_{51}</td>
<td>Probability of upper Bay large age-1 becoming an upper Bay adult</td>
<td>Re^{-M}</td>
<td>0.195</td>
</tr>
<tr>
<td>aw_{81}</td>
<td>Probability of upper Bay large age-1 becoming a lower Bay adult</td>
<td>Te^{-M}</td>
<td>0.634</td>
</tr>
</tbody>
</table>
Table 1. Continued.

<table>
<thead>
<tr>
<th>Transition</th>
<th>Definition</th>
<th>Parameter</th>
<th>Estimate (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>aw_{41}</td>
<td>Probability of upper Bay adult remaining an upper Bay adult</td>
<td>e^{-M}</td>
<td>0.829</td>
</tr>
<tr>
<td>aw_{42}</td>
<td>Number of offspring produced by surviving upper Bay adults</td>
<td>Fec \cdot e^{-M}</td>
<td>1.326 \times 10^6</td>
</tr>
<tr>
<td>aw_{25}</td>
<td>Probability of lower Bay juvenile becoming upper Bay small age-1</td>
<td>R(1 - f)e^{-M}</td>
<td>0.166</td>
</tr>
<tr>
<td>aw_{35}</td>
<td>Probability of lower Bay juvenile becoming upper Bay large age-1</td>
<td>Rfe^{-M}</td>
<td>0.029</td>
</tr>
<tr>
<td>aw_{65}</td>
<td>Probability of lower Bay juvenile becoming lower Bay small age-1</td>
<td>T(1 - f)e^{-M}</td>
<td>0.539</td>
</tr>
<tr>
<td>aw_{75}</td>
<td>Probability of lower Bay juvenile becoming lower Bay large age-1</td>
<td>Tfe^{-M}</td>
<td>0.061</td>
</tr>
<tr>
<td>aw_{86}</td>
<td>Probability of lower Bay small age-1 becoming a lower bay adult</td>
<td>e^{-M}</td>
<td>0.829</td>
</tr>
<tr>
<td>aw_{87}</td>
<td>Probability of lower Bay large age-1 becoming a lower bay adult</td>
<td>e^{-M+F}</td>
<td>0.529</td>
</tr>
<tr>
<td>aw_{57}</td>
<td>Number of offspring produced by a surviving lower Bay large age-1</td>
<td>0.66 \cdot Fec e^{-M+F}</td>
<td>5.582 \times 10^6</td>
</tr>
<tr>
<td>aw_{88}</td>
<td>Probability of remaining a lower Bay adult</td>
<td>e^{-M+F}</td>
<td>0.529</td>
</tr>
<tr>
<td>aw_{88}</td>
<td>Number of offspring produced by a surviving lower Bay adult</td>
<td>Fec e^{-M+F}</td>
<td>8.458 \times 10^6</td>
</tr>
</tbody>
</table>

\[ A = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 3.5 \times 10^{-7} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 6.1 \times 10^{-8} & 0 & 0 & 0 \\
0 & 0.141 & 0.103 & 0.103 & 0 & 0.141 & 0 & 0 \\
0 & 3.4 \times 10^4 & 5.1 \times 10^5 & 5.1 \times 10^4 & 0 & 3.4 \times 10^4 & 4.5 \times 10^5 & 4.5 \times 10^5 \\
0 & 0 & 0 & 0 & 4.9 \times 10^{-7} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 5.5 \times 10^{-8} & 0 & 0 & 0 \\
0 & 0.596 & 0.214 & 0.214 & 0 & 0.596 & 0.279 & 0.279
\end{bmatrix} \]

Within the combined projection matrix, the upper left quadrant provides the aggregate transitions involving stages in the upper Bay only. Similarly the lower right quadrant provides the aggregate transition involving stages in the lower Bay only. The two other quadrants provide aggregate transitions involving movement between the regions. The fifth column of the matrix provides the transitions related to the production of offspring, whereas the fifth row provides transitions that follow the fates of the offspring.

An eigen analysis of the combined project matrix \( A_{\text{winter}} A_{\text{summer}} \) that projects from one summer to the next indicated that the population could be expected to decline, characterized by \( \lambda = 0.808 \) (equivalent \( r = -0.214 \)). This decline of approximately 20% per year is equivalent to a population half life of 3.2 years. For comparison, Lipcius and Stockhausen (2002) indicate that the abundance of the blue crab spawning stock declined by 81% in between 1988–1991 and 1992–2000. The population was projected to reach a stable stage distribution dominated by zoea/newly settled crabs. Standardizing the stable-stage distribution to the most abundant stage is conventional. However, the overwhelming numerical dominance of the zoeal/newly settled crab stage means that patterns in the abundances of the other stages are difficult to detect if this convention is followed. Accordingly, I
Table 2. Stable stage distribution and distribution of reproductive value when the population is growing at a rate equivalent to the dominant eigenvalue \( \lambda \) for the base simulation. The stable stage distribution and reproductive values are expressed relative to the proportion of adults expected in the lower Bay.

<table>
<thead>
<tr>
<th>Region</th>
<th>Stage</th>
<th>Stable stage distribution</th>
<th>Reproductive value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Bay</td>
<td>Megalopae/newly settled</td>
<td>0</td>
<td>3.19 \times 10^{-7}</td>
</tr>
<tr>
<td></td>
<td>Small age-1</td>
<td>0.325</td>
<td>0.988</td>
</tr>
<tr>
<td></td>
<td>Large age-1</td>
<td>0.057</td>
<td>1.153</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>0.165</td>
<td>1.153</td>
</tr>
<tr>
<td>Lower Bay</td>
<td>Megalopae/newly settled</td>
<td>7.543 \times 10^6</td>
<td>1.182 \times 10^{-6}</td>
</tr>
<tr>
<td></td>
<td>Small age-1</td>
<td>0.458</td>
<td>0.988</td>
</tr>
<tr>
<td></td>
<td>Large age-1</td>
<td>0.052</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

have standardized the stable stage distribution to the abundance of adult females in the lower Bay (Table 2). Sixteen percent of adult females occur in the upper Bay. Also, it is clear from the stable stage distribution that in the base scenario, the population is skewed away from the large age-1 crabs. The stable stage distribution indicates that large age-1 crabs baywide occur at 10.9% of the abundance of adult females in the lower Bay. In contrast, the baywide abundance of small age-1 crabs is 78% of that of the adult females in the lower Bay. Reproductive values of the different stages in the different regions also varied (Table 2). As with the estimation of the stable stage distribution \( \lambda \) standardized the reproductive values to the reproductive value of adults in the lower Bay. The calculations show that there are only small differences among the reproductive values of the age-1 and adult crabs. Large age-1 and adult crabs in the upper Bay, not being subjected to the dredge fishery, have the highest reproductive values. Reproductive value of these stages is 15% greater than the reproductive value of the equivalent stages in the lower Bay.

Two forms of sensitivity analyses were conducted. The most encompassing was an analytical elasticity analysis (Caswell, 2000; Ebert, 1999; De Kroon et al., 2000). The eigen-analysis permits estimation of the sensitivity of the projected population growth rate to changes in each transition probability. These are expressed as proportional sensitivities, or elasticities, to account for the difference between contributions of survival and fecundity (Caswell, 2000). The projected population growth rate changed most in response to changes in the reproductive contribution of lower Bay adults (Fig. 4A). It should be noted that the reproductive contribution involves both the overwinter survival of mature females and their subsequent release of zoea. Thus, one should not interpret the high sensitivity as reflecting simply changes in absolute fecundity. Equal proportional changes in either overwinter survival or fecundity would have the same impact. The next largest elasticity was for the survival during early life history associated with the transitions from larvae to small age-1 crabs in the lower Bay (Fig. 4B). The third highest elasticity was for transitions associated with growth from small age-1 to adults in the lower Bay (Fig. 4C). Overall, transitions associated with the lower Bay dominate the elasticities of projected population growth rates. Elasticities involving upper Bay stages are more minor (Fig. 4).

Additionally, I examined the sensitivity of the projected rate of population growth to systematic perturbation of several key parameters: fecundity, natural mortality and fishing mortality. I estimated the projected rate of population in-
Figure 4. Calculated elasticities of the projected population growth rate in the base simulation to changes in life history transitions associated with A) reproductive output, B) survival during early life history and C) contribution to adult abundances. The elasticities were calculated from the eigenvectors of an aggregate transition matrix that projected the population from one summer period to the next.

crease for each factor at 50, 75, 100, 125 and 150% of the base values. As expected, at all levels of fecundity the population growth rate contours were linear on the M, F surface (Fig. 5). This resulted from the definition of total mortality $Z = F + M$. At the lowest fecundity level (50% base), all combinations of F and M resulted in negative population growth (Fig. 5A). As fecundity increased, an increasing proportion of combinations of F and M resulted in positive population growth (Fig. 5). At the highest fecundity level used (150% base), all combinations of F and M less than 75% of the base estimates resulted in positive population growth (Fig. 5E).

B. Survival During Early Life History.—In many highly fecund organisms early life history survival is an important determinant of subsequent population dynamics. For example, small changes in the rate of mortality during fish early life history has been shown to have a dramatic impact on year class formation and rates of population growth in many fishes (Houde, 1987). To examine the
Percentage change from annual rate of natural mortality, $M$

Figure 5. Contours of projected rates of population growth ($r$) as a function of variation in the natural mortality rate $M$, and the fishing mortality rate $F$, for various levels of fecundity, expressed as percentage of the base simulations. The levels of fecundity shown are A) 50%, B) 75%, C) 100%, D) 125% and E) 150%. Shown on each panel are color mapped contours of $r$, and a single line contour of $r = 0$ (no population growth). The star in panel C) indicates parameter values for the base simulation. The scale indicates the percentage change in project population growth rates.

extent to which similar responses are found in blue crab, and to account for uncertainty in the estimate of early life history survival, I varied the survival during this stage (zoea-newly settled crabs in the lower Bay in the summer) and quantified the response in the projected rate of population increase.

Early life history survival was allowed to vary from $0.1$–$2 \times$ its value in base simulations. The projected rate of population growth remained negative over this entire range (Fig. 6). The relationship between early life history survival and the population rate of increase was nonlinear. There appear to be diminishing returns to increasing early life survival to blue crab populations. Changes in early life history survival had less effect at higher estimated survival levels, than at lower survival levels.

C. VARIATION IN FISHING MORTALITY AND GROWTH.—Individual growth can be
highly variable, both through inter-annual and inter-individual variation. Moreover, in many exploited species, increased exploitation leads to a decrease in the age at maturity. The impacts of variation in both aspects of crab life history would be expressed in the proportion of age-1 crabs entering the large size fraction. I varied both the rate of fishing mortality, \( F \), and the proportion of age-1 crabs that recruit to the fishery in their first year, \( f \). Variation in \( f \) can result from environment variability causing differences in growth potential, or changes in management regulation that protects or exposes different proportions of the population to fishing. In simulations, I varied \( F \) from 0–1.5, and \( f \) from 0–0.5.

The population growth contours on the \( F \), \( F \) surface are shown in Figure 7. Over a wide range of \( f \) and \( F \) values, the population growth rate contours were almost parallel to the \( f \) axis. This indicated that population growth was almost independent of the proportion of crabs that recruit to the fishery in their first year. However, there was more curvature to the population growth rate contours when populations were increasing or decreasing (Fig. 7). This implies that when a population was not at equilibrium there was a trade off between the fishing mortality rate and the proportion of age-1 crabs recruiting to the fishery.

D. Winter Dredge Fishery.—There has been considerable recent concern over the impact of the winter dredge fishery on the sustainability of the blue crab population in the Chesapeake Bay. In a report to the Virginia State Legislature, Burreson et al.\(^2\) found that although the winter dredge fishery was a source of substantial mortality for blue crabs in the Chesapeake Bay, the impact of the dredge fishery was not unduly high. The results of an analysis of a single regional model of blue crabs in the Chesapeake Bay indicated that reductions in the winter

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dredge fishery could stabilize the Chesapeake Bay blue crab population, but that this limited action would not be as effective as reductions in fishing mortality overall (Miller, 2001). However, these analyses do not account fully for the known spatial pattern in blue crab life history. Accordingly I reexamined this question using the spatially-explicit model to address concerns over exploitation in the winter dredge fishery.

I simulated reductions in the winter dredge fishery by systematically reducing the fishing mortality rate that overwintering adult and large-1 crabs were exposed to in the lower Bay. All parameters, other than the fishing mortality rate in the winter in the lower Bay, were as defined for the base simulations. The winter dredge fishing mortality rate varied from 0–150% of the summer fishing mortality rate. Analysis of model results indicates that complete cessation of the winter dredge fishing is just sufficient to cause the population to begin to increase in abundance (Fig. 8).

**DISCUSSION**

The spatially explicit model developed here indicates that under current exploitation patterns, the blue crab population in Chesapeake Bay is likely to decline in abundance. This is the same conclusion as developed from a nonspatial stage-based model (Miller, 2001) and from more traditional stock assessment models (Lipcius and Stockhausen, 2002). However, it should be noted that Rugolo et al. (1997), based on a stock assessment involving earlier data, concluded that the exploitation of blue crab was sustainable. The results presented here show that the annual rate of fishing mortality should be reduced to a rate equivalent to $F = 0.3$. One should be cautious in interpreting this figure, as the model developed
Figure 8. Relationship between percentage change in the estimated fishing mortality rate in the dredge fishery and the projected intrinsic rate of population growth. All other parameters except a, the dredge fishery mortality multiplier, were as defined in the base simulation. Zero population growth rate line (dotted) is shown for reference.

herein tracks the female component of the population. Yet the estimates of fishing mortality are calculated on the whole catch, which can be strongly skewed toward males.

The eigenvectors of the combined projection matrix provide information on characteristics of the projected population. Not surprisingly, when the population reaches the stable stage distribution it is dominated by the larval/newly settled forms. However, somewhat surprisingly, adult females in the lower Bay were the next most abundant stage. In fact when examined within a spatial framework, the model suggests that there will be almost five females in the lower Bay for every female in the upper Bay even though the area of the lower Bay is only 3.2 times that of the upper Bay. The abundance of age-1 crabs was about 77% of the abundance of mature females in the lower Bay, and the majority of these were small age-1 crabs. Despite large differences in the stable stage distribution, except for larval/newly settled forms, there were only relatively minor differences in reproductive values among different crabs. For age-1 and older crabs in both regions, reproductive values varied from 1 to 1.15. The high mortality associated with the larval/newly settled stages is readily apparent in their low reproductive values (1.07 × 10⁻⁶).

Survival rates during blue crab early life history both in the offshore zone and for newly settled crabs are poorly known and likely highly variable. The value used in the model was estimated from Peterson and Wroblewski's (1984) general size-dependent model, and thus is of unknown accuracy. However, while the projected rate of population increase did respond to changes in the estimate of early life survival used in the model, the nature of the response suggests that the model may be resilient to errors of less than an order of magnitude in early life history survival. Moreover, the nature of the relationship between the estimate of early life history survival and the projected rate of population growth indicates that reductions in the survival probability will have a more substantial impact on projected rates of population growth than will increases in the survival rate. The
approach used to model early life history survival assumed a linear decline in instantaneous risk of mortality. Thus it is likely that the estimate used in the model underestimates survival rather than overestimating it. Thus, I suggest that the errors introduced by estimating early life history mortality may be relatively small. However, improvements in our understanding of the magnitude of early life history mortality would be beneficial. Recent attempts to follow patches of zoea over time while resampling from them do offer the potential to estimate natural rates of mortality for these stages (C. E. Epifanio, University of Delaware, pers. comm.). Moreover, studies on the potential predation on newly settled crabs in different habitats are also underway (J. von Montfrans, Virginia Institute of Marine Sciences, pers. comm.). These studies will provide critical data to estimate the mortality of these life stages.

The model indicates that the proportion of overwintering juveniles that grow sufficiently rapidly to enter the fishery in the following summer is not a particularly sensitive feature of the population dynamics of blue crabs. This suggests that management action to change the size limit of legal size crabs may not be effective without complementary action to reduce the overall fishing mortality rate. However, if the blue crab population in Chesapeake Bay is currently some distance away from a sustainable pattern of exploitation, size restrictions may have more effect.

I used the model to explore the impact of the winter dredge fishery that operates in the lower Bay only. The implications of the model results are that restrictions on the winter dredge fishery in isolation are not sufficient to cause a sustainable pattern of exploitation. This finding is similar to that from a single regional model (Miller, 2001), and to the findings of a blue ribbon panel established by the Virginia State Legislature. Initially, these findings appear counterintuitive. The majority of females taken in the dredge fishery have likely been inseminated and would produce zoea at the end of the overwintering period (July). Given this reproductive potential, why does closing the winter dredge fishery not have a more substantial effect? The answer to this question lies both in the relative consistency of reproductive values among all age-1 and older crabs, regardless of their location, and in the reproductive reservoir of mature females that migrate into the lower Bay during the spring to spawn. These later females are protected from exploitation in the winter dredge fishery because of the spatial pattern in their distribution and the spatial distribution of exploitation.

Although the model is explicitly spatial in nature, many of the parameters that would be required to explore the importance of spatial processes in the population dynamics of blue crabs are lacking. This represents a hurdle to further model development. For example, the movement of newly-settled crabs and adult crabs were modeled based on relative areas, owing to the lack of empirical data. It is unknown if newly settled crabs distribute themselves in a fundamentally different way. A deviation from the area-based model may have profound impacts on the sustainability of the projected population. Similarly, data on exploitation rates is often collected at a coarse spatial scale. For example, within the Chesapeake Bay estimates for the landings by state and water code are available, but finer resolution is impossible. Not only are spatially explicit harvest data lacking, but our understanding of temporal patterns in also limited. While it is possible to examine the importance of the assumptions used in the model to predicted rates of population growth with both elasticity and perturbation analyzes, determining the accuracy of the model is clearly not possible until the required data are available. I suggest that research on the movement of crabs within their estuarine and coastal habitats is a critical need if spatially-explicit processes are to be explored further.
The elasticity analysis indicates that the population growth rate projected in the base model simulation is most sensitive to changes involving life history transitions in the lower Bay. This results from the fact that both reproduction and settlement, the two stages with the highest associated elasticities in the model, both occur in the lower Bay. However, life history transitions involving upper Bay stages also make substantial contributions to the overall pattern in model elasticities. It is likely that the pattern observed in elasticities reflects, in part, the assumption regarding the distribution of crabs. If empirical estimates of movement were to become available and were they to differ from those used in the model, the pattern of elasticities may change.

Despite concerns over the paucity of data, the role of spatial processes in the ecology of blue crabs is receiving increasing attention. It has been recognized for several years that spatial processes at different scales influence recruitment processes (Johnson, 1995; Garvine et al., 1997). Spatial patterns are also apparent later in the life history because of salinity-based differences in the distribution of male and female crabs within the estuary (Chesapeake Bay Program, 1997). Recently, Lipcius and colleagues have proposed adopting spatially-explicit management for the Chesapeake Bay blue crab population (Lipcius et al., 2001; Seitz et al., 2001). The proposal involves expanding spawning sanctuaries in the lower Bay (Seitz et al., 2001), and establishing migration corridors that connect other areas of the Bay to the spawning sanctuaries (Lipcius et al., 2001). The spawning sanctuary/corridor network directly reflects knowledge of the spatial distribution of blue crabs within the Chesapeake Bay. However, our knowledge of the potential impact of these protected areas is limited.

The modeling framework presented here could be used to explore the utility of the sanctuary/corridor network. A potential approach would be to further divide the lower Bay region into a sanctuary and non-sanctuary region, and adjust the movement pathways within the life cycle diagram. The probability of movement between the different regions could be adjusted to reflect the relative size of the sanctuary and non-sanctuary areas. All females within the sanctuary would not experience fishing mortality, while those in the non-sanctuary area would. The effects of the relative size of the sanctuary could be varied and its impact on the population rate of growth examined. It would also be possible to account for the possible additional fishing mortality due to displaced effort by increasing the fishing mortality rate in the model.

There are two deficiencies in the general framework I develop here. The model does not include density dependence in any life history stage. Yet we know density dependence occurs in blue crab populations (Lipcius and Van Engel, 1990; Pile et al., 1996). It is possible to include density dependence, but in doing so the elegant analytical approaches used here are inapplicable. The analyses reported here reflect projections forward in time of the consequences of current population status, and will be accurate when the population is close to equilibrium. They will be inaccurate if the population shows wide fluctuations in abundance. Another deficiency of the current model framework is its focus on female crabs. For many populations, this aspect of stage-based models is not too restrictive. In many species there are enough males to fertilize all the females, and thus the female component drives the dynamics (Caswell, 2000). Moreover, for other species males and females share similar life histories. Thus, stage-based models of fishes (Pertierra et al., 1997; Cortes, 1999; Diamond et al., 1999; Quinlan and Crowder, 1999; Brewster-Geisz and Miller, 2000), sea turtles (Crouse et al., 1987; Heppell et al., 1996), and whales (Brault, 1999; Brault and Caswell, 1994) can follow only females, yet remain accurate. In sharp contrast, male and female blue crabs
differ in both life history and the pattern in their exploitation. Moreover, the differences are often spatial in nature. For example, harvests in the summer pot fishery are biased toward males in the upper Bay, whereas they are more even in the lower Bay. Two-sex life tables have been developed for insects (Chi, 1988; Chi and Getz, 1988) and human populations (Keyfitz, 1968). However, the framework for two sex stage-based models is less well advanced. Development of such a framework will be crucial to improvements in the application of stage-based models to blue crabs.

In summary, the spatially explicit stage-based model offers promise for understanding important patterns in the ecology and exploitation of blue crabs. We already appreciate spatial patterns in the ecology of blue crabs, but lack a framework within which the consequences of such patterns can be examined. Similarly, we know that there are spatial patterns in the exploitation of blue crabs, and researchers have proposed spatially-explicit solutions to management problems. However, once again, we lack a framework within which alternative management actions can be explored, and compared. Spatially-explicit stage-based modeling offers such a framework and may provide substantial insight into the ecology and exploitation of this important resource.

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