

# Matrix-Based Modeling of Blue Crab Population Dynamics with Applications to the Chesapeake Bay

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**ABSTRACT:** Blue crab (*Callinectes sapidus*) plays an important ecological and economic role in estuaries from South America to New England. It supports a large commercial fishery in the United States with approximately one third of the landings taken from Chesapeake Bay. I developed a stage-based matrix model of the blue crab population to address three key questions: What is the ability of blue crab populations to support sustainable exploitation? What stages of the life cycle are most important in regulating the dynamics of the population? And specific to the Chesapeake Bay, what is the importance of a winter dredge fishery in determining long-term sustainability of the crab population? The model indicated that with the current pattern of exploitation blue crab populations are able to sustain a total instantaneous mortality rate ( $Z$ )  $\sim 0.7$ . If the natural mortality rate is estimated for a maximum life expectancy of 8 yr, this translates to moderate levels of exploitation ( $F < 0.32$ ). This value is less than the current estimate of exploitation in Chesapeake Bay (0.9–1.1) indicating that the level of exploitation in this system needs to be reduced to avoid overfishing. Transitions to and from small age-1 crabs were shown to be important in regulating the overall dynamics of the population. The egg production realized by large adults was also shown to be an important regulatory process. The model indicated that reductions in the winter dredge fishery would have a substantial role in ensuring the long-term sustainability of the population. Reductions in other sectors of the fishery are also required to ensure sustainability.

## Introduction

Blue crab (*Callinectes sapidus*) is an estuarine-dependent species that ranges from the Caribbean, throughout the Gulf of Mexico, and along the eastern seaboard of North America as far north as New England. Throughout this range, the blue crab is an important component of estuarine food webs (Hines et al. 1990). It is a dominant benthic predator and scavenger consuming a wide range of taxa including bivalves, crustaceans, and fish as well as other blue crabs (Hines et al. 1990; Mansour and Lipcius 1991, 1993; Hines and Ruiz 1995). In turn, the blue crab is food for several fish, particularly species in the families Sciaenidae and Moronidae. Concern has been expressed that predation by striped bass (*Morone saxatilis*) has been responsible for the recent decline in the abundance of blue crab in the Chesapeake Bay, with blue crab providing a link between the benthic and pelagic food webs (e.g., Baird and Ulanowicz 1989). If true, the status of blue crab stocks within an individual system, may yield important insights into ecosystem health and function.

In addition to its ecological role, the blue crab also supports important commercial and recreational fisheries. Statistics from the Food and Agri-

cultural Organization of the United Nations indicate that the worldwide catch of blue crab averaged 110,000 MT from 1989–1998, representing 26.5% of the total landings of swimming crabs (*Portunus* sp. and *Callinectes* sp.) worldwide (Food and Agricultural Organization 2000). Within the United States, commercial fisheries exist from Texas to New York. Between 1994 and 1997, the national average annual landings of blue crab were close to 102,000 MT with about 35% coming from the Chesapeake Bay (National Marine Fisheries Service 2000).

The fishery in many areas, and particularly in the Chesapeake Bay, is diverse (Briggs 1998; Rugolo et al. 1998; Evans 1998; Guillory and Perret 1998; Heath 1998; Henry and McKenna 1998; Stehlik et al. 1998). Although the majority of the landings are of hard-shell crabs from pot fisheries, other components do contribute significantly to the landings. There is a sizeable fishery that exploits smaller crabs for the soft and peeler market. Recent evidence suggests that this component is growing in importance in several areas (O'Reilly personal communication). There is also a sizeable winter dredge fishery in coastal waters of New York and in the Chesapeake Bay that exploits crabs overwintering in the sediments. In the Chesapeake Bay, this fishery is restricted to southern waters that coincide with the overwintering areas

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of mature, egg-bearing females. The dredge fishery may have a disproportional effect on the spawning biomass of blue crab in the Chesapeake Bay, and the stock in the Chesapeake Bay may be overexploited (Rugolo et al. 1998; Miller and Houde 1999).

A stage-based matrix projection model to examine patterns in the dynamics of blue crab populations is developed here with special reference to the Chesapeake Bay. Stage-based models are highly flexible, heuristic tools that have been used extensively in the ecological literature. They are discrete, time invariant, probabilistic models that resemble life-table analysis (Caswell 2000). Life tables use age as a state variable and generally have a yearly time step. Individuals remain in each age class for a single time step. Models of this structure are widely used in demographic studies of species for which age is a good predictor of an organism's behavior, performance, and fate. For many species age is not a good predictor of an individual's fate, and it is more appropriate to use size or life history stage as the state variable. Stage-based models still function with a discrete time step. The stage duration is often longer than the model time step and individual organisms may remain in a single stage for multiple time steps. Given the discrete nature of crab growth, a stage-based model is ideally suited to examine the dynamics of blue crab populations.

The following questions are addressed with the stage-based model: What levels of gross fishing mortality are sustainable by blue crab populations? Which life stages or vital rates (e.g., survival and growth) have the biggest impacts on population rate growth? What is the importance to population resilience of winter dredge fisheries that remove predominantly pre-reproductive and mature females?

### Model Development

#### LIFE CYCLE DESCRIPTION

The blue crab life cycle involves several distinct stages within which seasonally variable patterns of growth and mortality occur. For juvenile and adult crabs there are periods of activity in the summer during which growth occurs, followed by torpid overwintering periods. The challenge in modeling blue crab population dynamics is to capture both aspects of the life history. The blue crab population is represented by its abundance in each of four life history stages. The model runs on a yearly time step, but includes seasonal submatrices, representing summer and winter, following an approach developed by Schmidt and Lawlor (1983). Four stages occur in each season (Fig. 1). The first

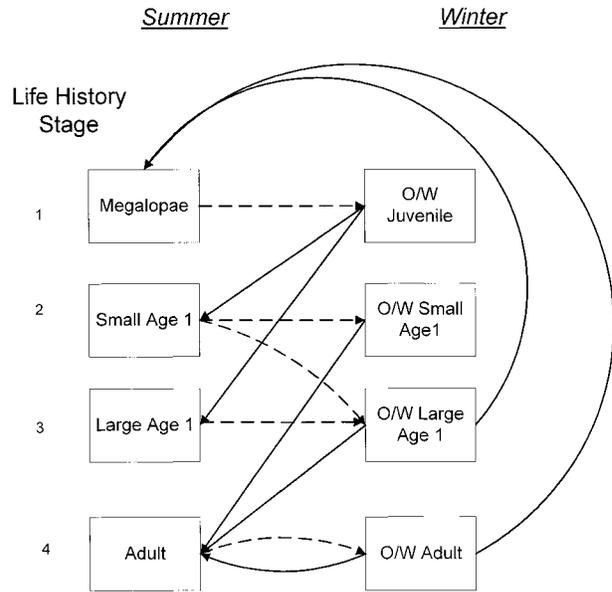


Fig. 1. Life cycle diagram for blue crabs. The life cycle is represented by four stages that occur both in summer (left hand column) and winter (right hand column). Transitions from summer to winter are shown as dashed lines. Transitions from winter to summer are shown as solid lines.

stage represents megalopae in the summer and overwintering (o/w) age-0 crabs in the winter. The second stage represents small age-1 crabs in the summer and small o/w age-1 crabs in the winter. The third stage represents large age-1 crabs in the summer and large o/w age-1 crabs in the winter. The final stage represents adult crabs in the summer and o/w adult crabs in the winter. Summer is defined as June–November, and winter as December–May. Transitions within each season are modeled in separate projection matrices. These seasonal transitions occur on a six-monthly time step.

The  $4 \times 4$  transition matrix  $A_{\text{summer}}$  defines all of the dynamics affecting summer life history stages (dashed transitions in Fig. 1; Table 1). In the summer months crabs exist as either megalopae/newly settled crabs, as small or large age-1 crabs, or as adult crabs (Fig. 1). Summer megalopae/newly settled (summer first-stage) crabs can only become o/w juvenile (winter first-stage) crabs. A proportion,  $f$ , of small age-1 crabs in summer (summer second-stage) overwinter as large age-1 (winter third-stage) crabs, whereas a proportion  $(1-f)$  overwinter as small age-1 (winter second-stage) crabs. Large age-1 crabs in the summer (summer third-stage) can only become o/w large age-1 (winter third-stage) crabs. Adults in the summer (summer fourth-stage) can only become o/w adult (win-

ter fourth-stage) crabs. The transition matrix for summer is defined as:

$$A_{\text{summer}} = \begin{pmatrix} as_{11} & 0 & 0 & 0 \\ 0 & as_{22} & as_{32} & 0 \\ 0 & 0 & as_{33} & 0 \\ 0 & 0 & 0 & as_{44} \end{pmatrix} \quad (1)$$

where the individual  $as_{ij}$  represent transition probabilities;  $as_{11}$  represents the probability that a megalopae/newly settled crab will survive the summer to become an overwintering juvenile crab,  $as_{22}$  represents the probability that a small age-1 crab will survive the summer and remain a small o/w age-1 crab, and  $as_{32}$  represents the probability that a small age-1 crab will survive the summer but grow to become large o/w age-1 crab. The definitions and estimates of all elements in  $A_{\text{summer}}$  are provided in Table 1.

A similar  $4 \times 4$  transition matrix,  $A_{\text{winter}}$ , can be defined to express all possible life history transitions in winter (solid transitions in Fig. 1; Table 1). Elements in  $A_{\text{winter}}$  reflect not only survival transitions, but also fecundities, as it is large o/w age-1 and o/w adult crabs that release zoea on the last day of the winter season in the model (Table 1).  $A_{\text{winter}}$  is defined as:

$$A_{\text{winter}} = \begin{pmatrix} 0 & 0 & aw_{13} & aw_{14} \\ aw_{21} & 0 & 0 & 0 \\ aw_{31} & 0 & 0 & 0 \\ 0 & aw_{42} & aw_{43} & aw_{44} \end{pmatrix} \quad (2)$$

To project forward from one year to the next, one must combine the two seasonal projection matrices. The matrix:

$$A = A_{\text{winter}} \times A_{\text{summer}} \quad (3)$$

will project estimated summer abundances forward one year. The matrix formed by  $A_{\text{summer}} \times A_{\text{winter}}$  would project a vector of winter abundances forward by one year.

#### MODEL DESCRIPTION

The fundamental equation to project the population forward in time is:

$$N_t = A^t \times n_0 \quad (4)$$

where  $N_t$  is a vector of the number of individuals in each stage at time  $t$ , and  $A$  is the full transition matrix for blue crabs given by Eq. 3. Note that for large values of  $t$ ,  $AN_t = \lambda N_t = N_{t+1}$ , where  $\lambda$  equals the finite rate of population increase and  $\ln \lambda = r$ , the intrinsic rate of increase. Three important demographic features:  $\lambda$ , the stable stage distribution, and the reproductive value of each stage, can be calculated from an eigenanalysis of  $A$  (Ebert

1999; Caswell 2000). For any  $n \times n$  matrix one may define up to  $n$  scalar values  $\lambda_{1..n}$  and  $n$  associated right and left vectors such that:

$$Aw = \lambda w \quad (5)$$

$$vA^T = \lambda v \quad (6)$$

where the  $\lambda$  are the eigenvalues and the  $w$  and  $v$  are the right and left eigenvectors. The blue crab transition matrix has four possible eigenvalues and eigenvectors. Because the blue crab projection matrix is nonnegative, irreducible, and primitive, there is a single, dominant eigenvalue  $\lambda_1$  that is real, positive, and strictly greater than all other possible  $\lambda$ . The right and left eigenvectors associated with  $\lambda_1$  will be strictly positive. It can be shown that the dominant  $\lambda$ ,  $w$ , and  $v$  represent the population growth rate, stable stage, and reproductive value distributions, respectively (Caswell 2000).

#### PARAMETER ESTIMATION

The model requires 6 parameters to be defined, from which all transition probabilities can be calculated (Table 1). The parameters required are: the natural mortality rate, the 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.

The natural mortality rate,  $M$ , was estimated based on a maximum life expectancy,  $\alpha$ , of 8 yr. This value is based upon returns of tagged crabs in North Carolina (Fischler 1965) and by recent age and growth studies that have documented the presence of 4-yr-old crabs in the current Chesapeake Bay population. Based on this estimate of  $\alpha$ ,  $M$  was estimated as  $3/\alpha = 0.375$  (Anthony 1982; Vetter 1988).  $M$  provides an estimate of the annual rate, whereas the model requires an estimate for a 6-mo period.  $M/2$  was used in the seasonal projection matrices.

The time series of the rate of fishing mortality,  $F$ , was calculated from the time series of total mortality rates calculated from the average size in the catch using Hoenig's (1987) method. Using an estimate of  $M = 0.375$ , the average  $F$  in Chesapeake Bay for the period 1955–1997 was 0.88 (Rugolo et al. 1998; Miller and Houde 1999). In the base projections,  $F$  was set equal to 0.9. Over this same period  $F$  varied from 0.62–1.26. Higher values of  $M$ , reflecting shorter life expectancies, lead to reductions in the estimated  $F$ . As with the natural mortality rate,  $F/2$  was used in model runs to convert the annual estimates to their 6-mo equivalents. The relative magnitude of exploitation during the summer and winter periods is difficult to quantify. A simple multiplier,  $a$ , was used to relate estimates of  $F$ , based largely on the impacts of the summer pot

TABLE 1. The definition and estimates of all transitions defined for the blue crab life history. The transition probabilities are estimated for the base projection. In other projections, the values of fundamental parameters were varied, thereby changing the estimated transition probabilities.

Transition	Definition	Parameter	Estimate
Fundamental parameters			
	Natural mortality rate	M	01875 (=0.375/2)
	Fishing mortality rate	F	0.45 (=0.9/2)
	Fraction of small crabs age-1 growing to large size class	f	0.15
	Fecundity	B	$1.6 \times 10^6$
	Dredge fishing mortality multiplier	a	1
as <sub>11</sub>	Probability of survival rate for megalopae and newly settled crabs	$\mu$	$1.19 \times 10^6$
Derived parameters			
as <sub>22</sub>	Probability of not growing to larger size (1 - f) and surviving source of natural mortality	$(1 - f)e^{-M}$	0.705
as <sub>32</sub>	Probability of growing to larger size (f) and surviving source of natural mortality	$fe^{-M+F}$	0.079
as <sub>33</sub>	Probability of surviving both natural mortality and exploitation	$e^{-(M+F)}$	0.529
as <sub>44</sub>	Probability of surviving both natural mortality and exploitation	$e^{-(M+F)}$	0.529
aw <sub>13</sub>	Number of offspring produced by large age-1, given crab survives	$0.66 \times Be^{-(M+aF)}$	$5.582 \times 10^5$
aw <sub>14</sub>	Number of offspring produced, given crab survives	$Be^{-(M+F)}$	$8.45 \times 10^5$
aw <sub>21</sub>	Probability of not growing to larger size (1 - f) and surviving source of natural mortality	$(1 - f)e^{-M}$	0.705
aw <sub>31</sub>	Probability of growing to larger size (f) and surviving source of natural mortality	$fe^{-M}$	0.124
aw <sub>42</sub>	Probability of a small crab surviving winter	$e^{-M}$	0.829
aw <sub>43</sub>	Probability of a large crab surviving winter	$e^{-(M+aF)}$	0.529
aw <sub>44</sub>	Probability of an adult crab surviving winter	$e^{-(M+aF)}$	0.529

fishery, to that exerted by the winter dredge fishery. The multiplier was varied from 0-1 to examine a range of possible winter dredge fishing mortality rates.

The proportion, f, of age-1 crabs that grew sufficiently large to recruit to the fishery and mature in their first summer was estimated to be 0.15. This was estimated from fishery-independent size-distribution information from the Chesapeake Bay (Rothschild et al. 1988).

Prager et al. (1990) conducted an extensive study of fecundity patterns in Chesapeake Bay blue crab. They found that 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 the number of zoea produced was an increasing linear function of female carapace width, given by Fecundity (millions) =  $-2.248 + 0.377 \times CW$  (cm),  $r^2 = 0.24$ ,  $n = 135$ , where CW is the carapace width of the mature crab. I assumed a 50:50 sex ratio and therefore used an estimate of  $1.6 \times 10^6$  as an estimate of the number of female offspring produced by an average (14.5 cm CW) mature female crab.

There have been no published studies on survival of zoea and megalopae, and few systematic studies on the mortality of newly settled crabs. Following the approach of Quinlan and Crowder (1999) and Diamond et al. (1999), early life history survival,  $\mu$ , was estimated as the product of daily survival through the entire stage. I estimated the

daily survival of zoea and megalopae based on the stage duration (40 d; Pletl 1992) and an instantaneous mortality rate was estimated from Peterson and Wroblewski's (1984) size-dependent relationship for mortality of aquatic organisms. Pletl (1992) estimated the dry weight of zoea as 3.25  $\mu$ g. Substituting this value into Peterson and Wroblewski's (1984) predictive relationship for mortality of  $M$  ( $d^{-1}$ ) =  $5.26 \times 10^{-3} W^{-0.25}$  (g) yields an estimated daily instantaneous mortality rate of  $0.1238 d^{-1}$ , giving the daily probability of survival for the first 40 d (larval period up to first settlement) as 0.883 ( $S_i = e^{-0.1238}$ ). To calculate the daily probability of survival of newly settled crabs, I assumed that the mortality rate would decline linearly from  $0.1238 d^{-1}$  to the  $0.00102 d^{-1}$  background mortality ( $M = 0.375 yr^{-1}$ ) over the next 142.5 d. On each day of subsequent development, the daily mortality rate,  $Z_i$ , was interpolated and the survival was estimated as  $S_i = e^{-Z_i \times 1}$ . The probability that an individual survives the entire zoea/newly settled crab period is  $\mu = \prod S_i = 1.196 \times 10^{-6}$ .

#### MODEL SENSITIVITY

Both sensitivity and elasticity analyses of the aggregate matrix were performed (Ebert 1999; Caswell 2000). Sensitivity is the change in  $\lambda$  that results from a change in the probability governing a transition from stage i to any other stage (including remaining in i). Since transition probabilities

TABLE 2. The stable stage and reproductive value distributions calculated from matrices that project the crab population from summer–summer or from winter–winter. The stable stage distributions are expressed as a proportion and the reproductive values are calculated relative to the value of the first stage.

Stage	Summer–summer Projections		Winter–winter Projections	
	Stable Stage	Reproductive Value	Stable Stage	Reproductive Value
1	0.99	1	0.41	1
2	$1.21 \times 10^{-6}$	$7.45 \times 10^5$	0.27	1.26
3	$1.98 \times 10^{-7}$	$8.35 \times 10^5$	0.036	1.69
4	$1.54 \times 10^{-6}$	$9.54 \times 10^5$	0.28	2.15

vary only between 0 and 1 but fecundity is not so constrained, it is also helpful to report the elasticity of  $\lambda$  to the transition. This is defined as the proportional change in  $\lambda$  for proportional changes in any transition element. Elasticities are calculated as:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\delta\lambda}{\delta a_{ij}} \quad (7)$$

Since elasticities are additive, the sum of elasticities for each stage defines the proportional contribution of  $a_{ij}$  to overall population growth,  $\lambda$ . Elasticities depend on a stable stage distribution and should be compared qualitatively.

#### SIMULATIONS OF THE EFFECT OF PARAMETER VARIATION ON $\lambda$

In addition to the analytical approach described above, the effect of systematic variation in estimates of lower level parameters on the predicted rate of population growth was quantified. To quantify the impact of reductions in fishing effort on the projected rate of population growth, the fishing mortality rate  $F$ , was reduced from  $F = 1$  to  $F = 0$ . In these simulations,  $M = 0.375$ . The total mortality rate,  $Z (= M + F)$ , in these projections varied from 1.375 to 0.375. To examine the impact of changes in the proportion of young crabs that recruit to the fishery,  $f$  was allowed to vary from 0 to 1 in the model. To examine the impact of reducing fishing mortality in the winter dredge fisheries, the parameter  $a$ , the multiplier of  $F$  that defined the fishing mortality rate in the dredge fishery was varied (Table 1). For each parameter that was varied, the changes in  $r (= \ln \lambda)$  and changes in the predicted distributions of abundance and reproductive values by stage was quantified.

### Results

#### BASE PROJECTION

An initial projection of the model, using the values of all parameters based on current conditions thought to be operating in the Chesapeake Bay

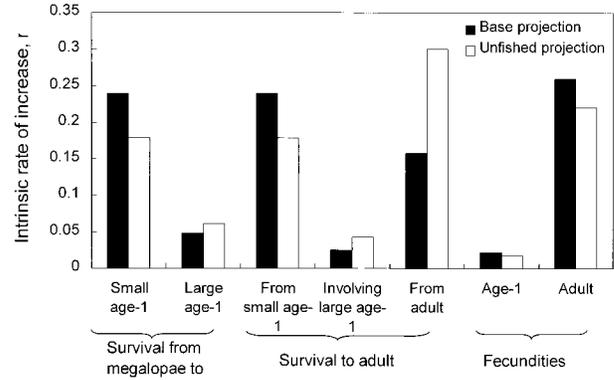


Fig. 2. Elasticities of the aggregate projection matrix  $A$ , parameterized to represent current conditions and an unfished population in Chesapeake Bay (Table 1). The first five pairs of bars are for transitions into the stages indicated by the braces from the stages indicated for the specific columns. The two right most pairs of bars represent elasticities involving stage-specific fecundity.

(Table 1), predicted that the crab population is declining by approximately 25% per yr ( $\lambda = 0.748$ , equivalent to an instantaneous rate,  $r = -0.167$ ). The stable stage structure of the population differed for summer–summer and winter–winter projections (Table 2). The dominance of megalopae/newly settled crabs in the stable stage structure for the summer–summer projection reflected the high fecundity of blue crabs. The winter–winter projection stable stage structure may more accurately represent the expected stage distribution of crabs in the estuary. The distribution of reproductive values also differed between the two projection matrices (Table 2). The reproductive values calculated from the summer–summer projections reflected the high mortality experienced at the megalopal stage. The reproductive values calculated from the winter–winter projection reflect more subtle differences in the reproductive value of crabs once they have entered the estuary.

#### MODEL SENSITIVITY

The elasticity matrices for both methods of projection (summer–summer and winter–winter) were equal, so the projection method does not affect conclusions regarding the contribution of variation in individual transitions to overall population declines. Elasticities for transitions associated with the survival and fecundity of adult crabs were the highest. High elasticities were associated also with transitions to and from the small age-1 stage (Fig. 2). Given the additive nature of elasticities, the distribution of elasticities indicated that the population will respond most to changes in vital rates affecting transitions to and from small age-1 crabs. Such transitions would be affected by variation in surviv-

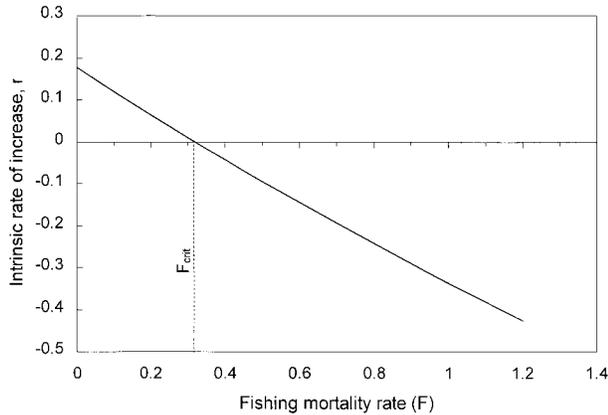


Fig. 3. Relationship between the intrinsic rate of increase of blue crab populations predicted by the stage-based model as a function of the fishing mortality rate experienced. Projections were made using parameter estimates representative of the current conditions in Chesapeake Bay (Table 1).

al during early life history, together with variation in  $M$ , and  $f$  (Table 1). Elasticities for stages involving large age-1 crabs were low. The pattern was broadly similar for an unfished population ( $F = 0$ ), with high sensitivities for small age-1 crabs and reproductively active adults (Fig. 2). The elasticities for fecundity and survival of adults in the unfished projection increased relative to all other transitions.

#### SIMULATIONS OF THE EFFECT OF PARAMETER VARIATION ON $\lambda$

Systematic variation of the parameters in the model helped determine the relative importance of each to the rate of decline and the structure of the population. When fishing mortality rates varied over the range  $F = 0-1$ , projected values of  $r$ , the intrinsic rate of natural increase ( $= \ln \lambda$ ) varied from 0.17 to  $-0.427$  (Fig. 3). The relationship between  $F$  and  $r$  was almost linear over the range of fishing mortality rates explored. The sustainable limit to fishing ( $r = 0$ ) can be inferred from these results to be  $F_{crit} = 0.32$ . When combined with the estimate of  $M$  ( $= 0.375$ ) used in the model, these runs indicate that the crab population can withstand total mortalities of up to  $Z = M + F = 0.7$  without declining. Levels of total mortality greater than this, whether as a result of high  $F$  (exploitation) or  $M$  (natural mortality), are likely to cause declines in the abundance of crabs in the long term.

The response of the population to variation in four other parameters was quantified. The intrinsic rate of increase predicted by the model exhibited a similar pattern of variation in response to changes in  $M$  as it did to changes in  $F$  (Fig. 4). When  $M$

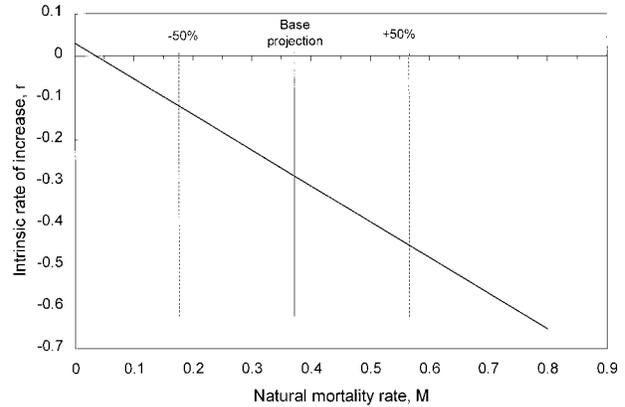


Fig. 4. Relationship between the intrinsic rate of increase predicted by the stage-based model and the estimate of the annual rate of natural mortality,  $M$ , used in projections. All other parameters were chosen to represent current conditions in Chesapeake Bay. Shown on the figure are the estimates of  $M$  used in the initial projection  $\pm 50\%$ .

$< 0.05$ , the population grew. This coincides with a total mortality of 0.95 ( $F + M$ ). This increase in the level of mortality sustainable by the population above  $F + M = 0.7$  reflected the fact that changes in  $M$  affected all life history stages, whereas  $F$  only affected stages that had recruited to the fishery. Changes in  $M$  by  $\pm 50\%$  brought about 2.4-fold changes in  $r$  (Fig. 4). Changes in the estimate of fecundity used in the model substantially altered the intrinsic rate of increase predicted by the model. Projected  $r$  varied nonlinearly from  $-0.611$  to  $0.053$  when individual fecundities varied from  $0.1-5 \times 10^6$  female offspring per female (Fig. 5). Changes in fecundity of  $\pm 50\%$  produced a 65% change in projected intrinsic rates of increase for

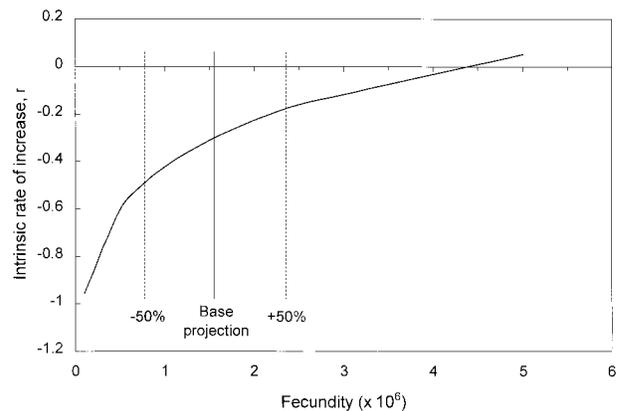


Fig. 5. Relationship between the intrinsic rate of increase predicted by the stage-based model and the fecundity of females (female offspring per female),  $B$ , used in projections. All other parameters were chosen to represent current conditions in Chesapeake Bay. Shown on the figure are the estimates of  $B$  used in the initial projection  $\pm 50\%$ .

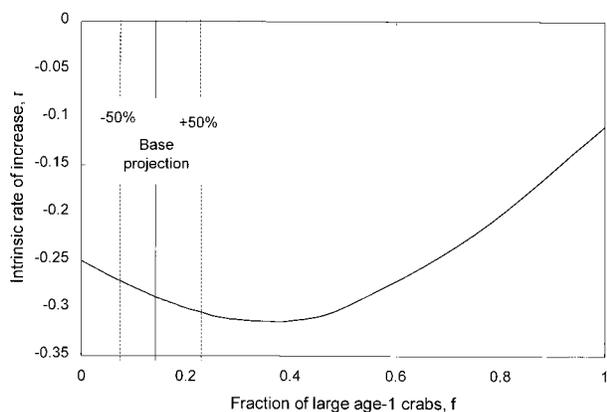


Fig. 6. Relationship between the intrinsic rate of increase predicted by the stage-based model and the estimate of proportion of age-1 crabs that recruit to the fishery and mature,  $f$ , used in projections. All other parameters were chosen to represent current conditions in Chesapeake Bay. Shown on the figure are the estimates of  $f$  used in the initial projection  $\pm 50\%$ .

the population. Projected intrinsic rates of increase were positive for fecundities greater than  $4.4 \times 10^6$  female offspring per female. The value assigned to the probability of survival through the zoeal and megalopal stages also affected the intrinsic rate of increase projected by the model. The relationship was identical to that for fecundity. Estimated zoeal survival rates must be increased by 1.5-fold to cause the population growth rate to become positive. Estimates of the proportion of individuals,  $f$ , that recruit to the fishery and mature as age-1 crabs also substantially affected estimates of the intrinsic rate of natural increase (Fig. 6). As  $f$  varied from 0 to 1,  $r$  varied nonlinearly from  $-0.25$  to  $-0.109$ , with a minimum of  $-0.314$  at  $f = 0.35$ . Although variation over the entire range of  $f$  values produced substantial changes in the estimate of  $r$  projected, variation of  $f$  by  $\pm 50\%$  produced only modest ( $\sim 11\%$ ) changes in the projected estimates of population growth.

#### IMPACT OF WINTER DREDGE FISHERY

For levels of fishing mortality ( $F = 0.9$ ), and natural mortality ( $M = 0.375$ ) currently thought to characterize the Chesapeake Bay stock, the projected intrinsic rate of increase of the population varied as the level of effort in the winter dredge fishery varied (Fig. 7), although the impact was relatively small. Even complete closure of the winter dredge fishery was not sufficient to bring the population into a region of positive population growth. As  $F$  varied from 1 to 0 reflecting a decline in and ultimately closure of the winter dredge fishery, the projected values of  $r$  increased by 75% from  $-0.29$  to  $-0.07$  but remained negative.

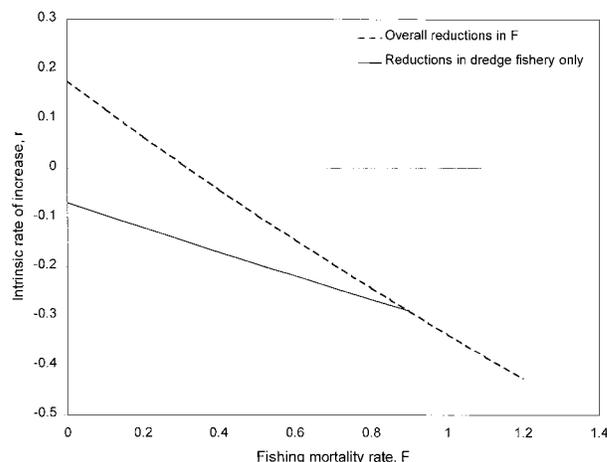


Fig. 7. Effects of reductions in overall fishing mortality and fishing mortality in the winter dredge fishery on the intrinsic rate of increase projected by the model. Parameter estimates used in projections were chosen to represent current conditions in Chesapeake Bay (Table 1).

#### Discussion

In common with many estuarine-dependent species, the blue crab has a complex and highly seasonal life cycle. Matrix-based population modeling is able to capture the principal aspects of this life history in a simple and elegant fashion, and has already been used to help understand the population dynamics of endangered sea turtles (Crouse et al. 1987; Crowder et al. 1994; Heppel et al. 1996), cetaceans (Brault and Caswell 1994; Brault 1999), sharks (Cortes 1999; Brewster-Geisz and Miller 2000), and several fishes (Perterra et al. 1997; Quinlan and Crowder 1999). The structure of the model developed here is sufficiently flexible to be able to address several areas of the ecology and exploitation of blue crab that are currently of concern to ecologists and managers.

Analysis of the blue crab model indicates that blue crab populations are likely to be able to support moderate levels of exploitation. The model suggests that levels of total mortality equivalent to an instantaneous mortality rate  $\sim 0.7$ – $1.0$  are sustainable. Whether or not fisheries are sustainable depends on the balance between natural mortality and fishing mortality in the population. The model indicates that levels of exploitation currently believed to be operating in the Chesapeake Bay (Miller and Houde 1999) are not sustainable. The model predicts that if natural mortality rate  $\sim 0.4$  exploitation rates should be reduced so that they do not exceed 0.3. The model also indicates that over the range of fishing mortality rates likely to be in effect, the relationship between the rate of population growth and the rate of fishing mortality is nearly linear. This means that increases in sustain-

ability will accrue in direct proportion to the reduction in fishing mortality achieved. Attempts to reduce fishing mortality have focused on limited entry, licensing, and effort limitation in many commercial fisheries, although establishment of marine protected areas or conservation corridors may be just as effective. Management actions that may lower the natural mortality rate, such as efforts to conserve areas of seagrass that are believed to be important nursery areas for young crabs (Wilson et al. 1987, 1990; Orth and van Montfrans 1990; Fitz and Weigert 1991; Orth et al. 1996) would also increase the sustainability of the blue crab population.

The model indicates that reductions in the winter dredge fishery would increase the potential that exploitation would be sustainable. A decrease in the winter dredge fishery is less beneficial to the sustainability of the population than an equivalent proportional decrease in the summer fishing mortality rate. The goal of a sustainable pattern of exploitation cannot be achieved by reductions in the winter dredge fishery alone.

The proportion of age-1 crabs recruiting to the fishery strongly influenced the population growth rate. As the proportion that recruit to the fishery decreases from the level in the base projection, population growth rates increase, as the smaller age-1 crabs are not vulnerable to the fishery. While initial increases above the base projection level in the proportion of large age-1 crabs cause the population growth to decline, beyond a certain point, population growth rates begin to increase. The increase in population growth rates is caused by the lower survival of large age-1 crabs being offset by their reproductive contribution to the population.

An eigenanalysis of the projection matrices identified the importance of the reproductive stages. Adult crabs and large age-1 crabs were identified as having the highest reproductive values. This indicates that action to protect preferentially these stages should have a large impact on the sustainability of the overall population. The relative value of the reproductive value of stages in winter are higher than the equivalent stages in the summer months because, for the summer projections, individual females have to survive both summer and winter mortality (from both natural and fishery mortality) before reproducing, whereas for the winter projections, individual females only have to survive the winter before reproducing. Management to protect the migration or overwintering period of these crabs should be particularly encouraged. The use of relative reproduction values, such as demonstrated above, may offer a way of prorating reductions in all components of a fishery to

yield equivalent impacts on overall levels of population growth.

Several of the parameters that were required to develop the model are poorly known. The survival of individual animals from their release as zoea to settlement is poorly understood. I was forced to use arguments based on the expected duration of early life history stages. This deficiency reflects the lack of detailed knowledge of processes controlling the fate of not only zoea following release, but also of individuals after metamorphosis from the megalopal stage to the estuarine-resident stages. Although this approach is unsatisfactory, I have shown through the sensitivity analyses that errors on the order of 100% in the estimated value of most parameters alter the prediction only by degree and do not drastically change the pattern. For some parameters even errors of orders of magnitude do not appreciably affect the results reported. Any research that leads to improvement in the understanding of the growth and survival of young crabs, in particular, is likely to be extremely beneficial.

While matrix-based structured population models are attractive, they do have several drawbacks. The model presented here lacks any density-dependence. We know that blue crab populations do indeed exhibit density-dependence, both in their overall population dynamics as indicated by their stock recruitment relationship (Lipcius and Van Engel 1990) and as also indicated by density-dependent interactions in foraging (Pile et al. 1996). Introduction of density-dependent effects into matrix-based structured population models make the simple projections and sensitivity analyses conducted here impossible as the transition probabilities become functions of abundance itself. One of the major benefits of these models is lost.

A second drawback is that the model is deterministic. Uncertainty of and plasticity in vital rates such as growth and fecundity are ignored. Tuljapurkar (1997) and Nations and Boyce (1997) have discussed the potential biases that may result from basing harvest strategies on results from deterministic models, particularly when juvenile survival is closely tied to environmental conditions. In addition to potential biases in the results, a deterministic model produces only a point estimate of population growth rate. Cortes (1999) outlines an approach to overcome this aspect stage-based models. The impacts of stochasticity in survival, growth, and fecundity on the predicted crab population growth rates remain unknown.

A third drawback to the model presented here is specific to blue crabs, rather than being a weakness of matrix-based approaches. Blue crab life histories have an inherent spatial component. In the

Chesapeake Bay, zoea are released near the mouth of the Bay. Newly-settled crabs are concentrated in higher salinity water in the lower half of the Bay, often associated with submerged aquatic vegetation. Older and larger crabs disperse throughout the Chesapeake Bay system prior to mating. Following mating, females tend to migrate down the Bay to release zoea, whereas males remain in mid-Bay waters, or even move further into tributaries or up the main stem. On top of this biologically-driven spatial variability, there is spatial variability in exploitation. As already mentioned, the winter dredge fishery is restricted to the southern waters of the Bay. The pot fishery predominates throughout the mainstem; pots are banned in Maryland tributaries, only trot lines are permitted. Even though the model presented here assumes a well-mixed, spatially uniform population, the location of an individual in the Bay has a significant impact on its probability of surviving or successfully reproducing. Until efforts are made to include the observed spatial variability, the possibility that the results presented here do not accurately reflect the dynamics of blue crab in Chesapeake Bay specifically, or estuaries in general, cannot be precluded.

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