# A SIMPLE MODEL OF THE BLUE CRAB, *CALLINECTES SAPIDUS*, SPAWNING MIGRATION IN CHESAPEAKE BAY

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## ABSTRACT

The blue crab, *Callinectes sapidus,* supports large commercial and recreational fisheries along the southern and eastern coasts of the United States. Females of the Chesapeake Bay stock, the most important commercially, spawn in summer near the mouth of Chesapeake Bay. Estimates of crab population density on the spawning grounds, based on 18 cruises during the 1986 and 1987 spawning seasons, were published in 1990. In an attempt to put those estimates into a conceptual framework, I have developed a simple model of the blue crab spawning migration in Chesapeake Bay. When fit to the data from 1986 and 1987, the model represented the within-year patterns of population density reasonably well. The model is based on a scaled normal probability function and requires estimation of only four parameters; these provide year-specific estimates of the female spawning stock size, the average residence time of a female on the spawning grounds, and two quantities related to migratory timing. For the two years examined, the estimates of spawning population size were strongly negatively correlated to the estimates of residence time, and each estimate had a high coefficient of variation. Thus, in the absence of external information about residence time, the model could not furnish precise estimates of the spawning-stock size. As a plausible working hypothesis, I assumed that the mean residence times in 1986 and 1987 were identical and between 4 and 21 days. Under this assumption, parameter estimates from the model suggest an approximate 60% decline in spawning-stock size from 1986 to 1987.

The Chesapeake Bay stock of blue crab, *Callinectes sapidus,* supports large commercial and recreational fisheries in Maryland and Virginia. Since the decline of the oyster stocks in Chesapeake Bay and its tributaries, the blue crab fishery is the most valuable in the area. Despite the blue crab's economic and biological importance, its population biology is relatively poorly known. For example, there are no published quantitative time series of spawning stock size, recruitment, or fishing effort, although several investigators have attempted to study stock and recruitment by using catch data or trawl samples from portions of the stock (Hurt et al., 1979; Applegate, 1983; Lipcius and Van Engel, 1990). The species synopsis by Millikin and Williams (1984) points out that the reproductive biology is relatively poorly known.

Despite the lack of quantitative detail on the population level, the spawning behavior of *C. sapidus* has been well documented. Fertilization is external; in this stock, it takes place in the upper reaches of Chesapeake Bay and in its tributaries. After receiving spermatophores from the male, the female extrudes fertilized eggs onto her abdominal apron and later migrates to the spawning grounds at the mouth of Chesapeake Bay (Pearson, 1948; Van Engel, 1958; McConaugha et al., 1983). Males do not take part in this spawning migration. Hatching consists of releasing zoea larvae from the eggs, which are still attached to the abdomen. Hatching takes place mainly during nighttime ebb tide. The larvae are then transported offshore (Provenzano et al., 1983) by surface currents and, after passing through several developmental stages, are recruited back into the bay in early autumn, probably by wind-driven currents (Johnson et al., 1984).

In the first work to estimate spawning-stock size by sampling the spawning grounds themselves, Jones et al. (1990, their Table 2) estimated the density of

this stock on its spawning grounds at the mouth of Chesapeake Bay throughout the spawning seasons of 1986 and 1987. Here, those estimates are incorporated into a migration model, which places the two years' estimates into a common framework. It also provides better comparisons of the relative spawning-stock sizes in those 2 years. Because the data are sparse, a very simple model is used.

## CONCEPTUAL MODEL

With detailed knowledge of blue crab behavior and its relationship to environmental factors, one could construct a complex simulation model of the migratory behavior associated with spawning in the blue crab. Such a model might include the effects of population size, water temperature, tidal and lunar cycles, and biological interactions, among possible factors. However, with our present knowledge of the stock's population biology, such a model would be vastly underdetermined, and would thus require many assumptions. The model described here takes a different approach: it attempts to broadly approximate the major observed features of the spawning migration by a few simple equations, rather than to identify and mimic the underlying mechanisms. Such a simple statistical approach has a long history in population biology; perhaps the best-known example is the logistic model of population growth, introduced by Verhulst (1845) and used or developed by Pearl and Reed (1920), Lotka (1924), Graham (1935), Schaefer (1954, 1957), Pella (1967), and Prager (1994), among others.

The present blue-crab migration model relies upon three main simplifying assumptions. Although not completely realistic, they could be relaxed, at the cost of added model complexity, if more data become available. The first assumption is that the number of crabs on the spawning grounds on 1 January of each year is negligible in comparison to the number present during the peak spawning season. The abundance estimates of Jones at al. (1990) and the natural history of the species support this assumption. Because of this assumption, each year's spawning migration can be (and will be) modeled as a separate event.

The second assumption is that all changes in the number of crabs on the spawning grounds can be grouped into just two categories, immigration and emigration. The term "immigration" includes all movements onto the spawning grounds; two important components of immigration are the seaward migration of crabs from the upper bay and the upward (vertical) movement of crabs that have over-wintered in the sediments. The term "emigration" includes the combined effects of fishing mortality, natural mortality, and all other active and passive forces that remove crabs from the grounds. Under this second assumption, changes in the number of crabs on the spawning grounds can be described by a simple differential equation,

$$\frac{dN_t}{dt} = i_t - e_t, \tag{1}$$

where $N_t$ is the number of crabs on the grounds at instant $t$, $i_t$ is the rate of immigration at instant $t$, and $e_t$ is the corresponding rate of emigration. It follows that the number of crabs on the spawning grounds on day $\tau$ can be modeled by integrating equation 1, which leads to

$$N_\tau = N_0 + \int_0^\tau i_t \, dt - \int_0^\tau e_t \, dt, \tag{2}$$

where $N_0$ is the number of crabs on the spawning grounds at $t = 0$, here defined as January 1. Under the assumption that $N_0$ is negligible, the first term of equation 2 can be omitted.

The model's third assumption is that the rates of immigration and emigration over time can be adequately represented by unimodal curves that are identical but offset in time. The amount of offset, designated $R$, is the mean residence time of a crab on the spawning grounds. Under this assumption, the rate of immigration (in number of crabs per unit time) is modeled by a dome-shaped curve with a single peak, and the rate of emigration by a curve of the same shape, but later in time. The cumulative immigration (or emigration) over time thus describes an S-shaped curve approaching an asymptote. The use of two identical curves reduces the number of parameters in the model; once the immigration curve is specified, only one additional parameter ($R$) is needed to specify the emigration curve.

## MATHEMATICAL MODEL

To write the migration model explicitly requires specifying a dome-shaped mathematical function with three parameters: location (placement of the peak in time), scale (height of the peak in number of crabs gained or lost per unit time), and width (some measure of the broadness of the curve relative to its height). In addition, the function must approach or become zero at both extremes of $t$, rather than become negative (as, e.g., a parabola does). A common function that possesses these properties
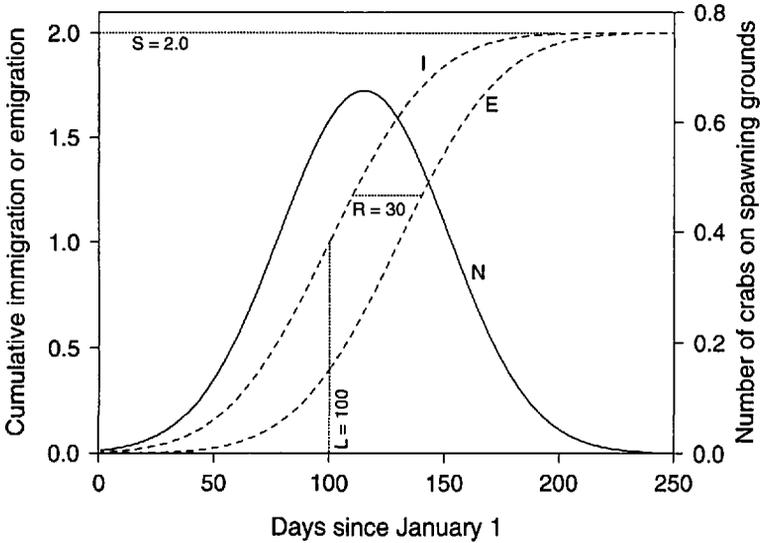
Figure 1.   Illustration of blue-crab migration model using identical scaled normal distribution functions to represent cumulative immigration and emigration. Parameter values (for illustration only) are $S = 2.0$, $L = 100$, $R = 30$, and $W = 50$. Dashed lines are cumulative immigration (I) and emigration (E) curves. Solid line is the resulting time trajectory of number of crabs on the spawning grounds, $N_\tau$. Dotted lines illustrate the relationship of $S$, $L$, and $R$ to the immigration and emigration curves.

is the normal probability density function $f(x)$ multiplied by a scale factor $S$. Because of its mathematical properties, that function will be used as the basis for the migration model. Other functions, e.g., the logistic, might also serve.

In writing the model, it is more convenient to use the (cumulative) normal distribution function, which models cumulative migration over time, rather than the probability density function, which models the intensity of migration. The unit-normal cumulative distribution function $F(x)$ evaluated at $t$ is

$$F(t) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{t} \exp\left(-\frac{t^2}{2}\right) dt. \tag{3}$$

To simplify notation, the model equations will use the symbol $F$, rather than incorporate Equation 3 explicitly. Let $I_\tau$ represent the cumulative number of crabs that immigrate onto the spawning grounds from the start of the year through day $\tau$. The model of cumulative immigration can be written

$$I_\tau \equiv \int_{-\infty}^{\tau} i_t\, dt = SF\left(\frac{\tau - L}{W/\sqrt{2}}\right), \tag{4}$$

where $S$ is the scale parameter, i.e., the number of female crabs that migrate during a season, presumed to define the spawning-stock size; $F$ is the unit-normal distribution function; $L$ is the location in time of the peak immigration, and is also the time at which half the total immigration has occurred; and $W$ describes the width (gradualness) of the migration in days: $W \equiv \sqrt{2}$ times the standard deviation of the immigration curve. Thus between $t = L - W$ and $t = L + W$, about 84% of the migration takes place.

Similarly, cumulative emigration through day $\tau$ is given by:

$$E_\tau = SF\left(\frac{\tau - L - R}{W/\sqrt{2}}\right), \tag{5}$$

where $R$ is the average residence time of a crab on the spawning grounds. The number of crabs present on the spawning grounds on day $\tau$ is the difference between the cumulative immigration and cumulative emigration through that day:

$$N_\tau = SF\left(\frac{\tau - L}{W/\sqrt{2}}\right) - SF\left(\frac{\tau - L - R}{W/\sqrt{2}}\right). \tag{6}$$

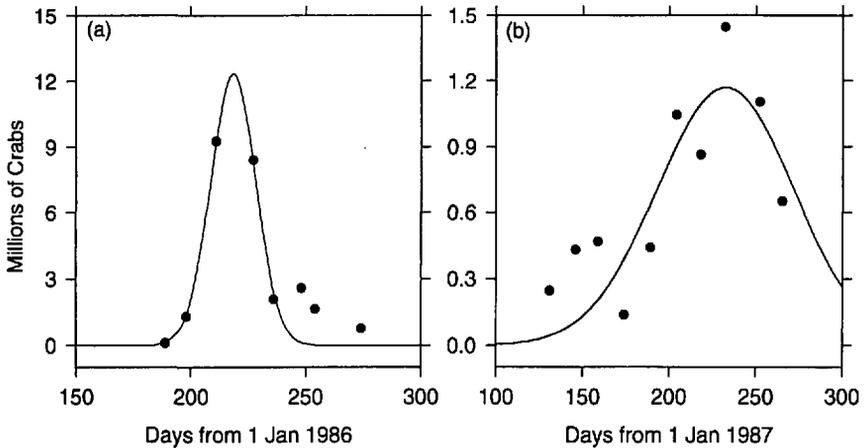Figure 1 illustrates the migration model with hypothetical parameter values.

Figure 2. Predicted (●) and observed (———) abundance of female blue crabs on the Chesapeake Bay spawning grounds (a) in 1986 and (b) in 1987. "Observed" abundances are the estimates of Jones et al. (1990), and are measured with error. Predicted abundances are the result of fitting the migration model separately for each year and assuming Normal independent errors of constant variance.

In the model, time in days is assumed to run from $-\infty$ to $+\infty$, whereas in a year, time runs from 0 to approximately 365. This approach is taken for ease of integration, and is allowed by the assumption that the number of crabs at the start of the year is close to 0 (which should hold where $W$ is sufficiently small and $L$ is far enough from the beginning of the year). Thus the integral from $-\infty$ to 0, and likewise the integral from 365 to $+\infty$, should be small enough to be ignored. This assumption can be examined easily when the model is fit to data.

## MODEL FITTING AND RESULTS

To fit a model to data, an error structure must be assumed. In this case, the simplest assumption was made; namely, that the errors associated with the estimates of abundance were independent, normal, additive, and of constant variance. The model was then fit to the population density estimates by nonlinear least squares, treating each year's data separately. The model appeared to fit the data reasonably well (Fig. 2), considering the small number of observations and the broad simplifications made. From Figure 2, it is apparent that the number of crabs at $t < 100$ was very small in both years, so that the assumption of few or no crabs on the grounds on 1 January was met. Although the parameter estimates were reasonable, their estimated standard errors were large, resulting in wide confidence intervals (Table 1). This precluded between-year comparisons of parameters, the one of most interest being the spawning-stock size, $S$.

The large standard errors on the parameter estimates were accompanied by correlations of greater than 0.99 between all pairs of parameters. Such a variance-covariance structure indicates that one cannot estimate all the parameters of the model uniquely from the data at hand. It is necessary to provide additional (external) information to do so. In general, such external information might consist of more data or additional assumptions (Deriso et al., 1985).

For exploratory purposes, the assumption was adopted that mean residence time on the spawning grounds could be specified a priori. The model was then fit to the 1986 and 1987 data for a number of values of $R$, in each case estimating $S$, $L$, and $W$ separately by year, but assuming a known, constant value of $R$. Since no estimates of residence time were available in the literature, a range of 4 to 21

Table 1. Initial parameter estimates for a simple spawning-migration model of blue crab, *Callinectes sapidus*, in Chesapeake Bay. Each year's data were fit independently by nonlinear least squares. Model parameters have the following interpretations: *S*, female spawning stock size (million crabs); *L*, mean date of immigration onto the spawning grounds (days since Jan. 1); *R*, mean residence time (days) on the spawning grounds; *W*, measure of dispersion of immigration around *L* (days). Approximate confidence intervals are computed as ± 2 standard errors. These estimates illustrate the indeterminacy in the data; constrained estimates (Fig. 3) were more useful.

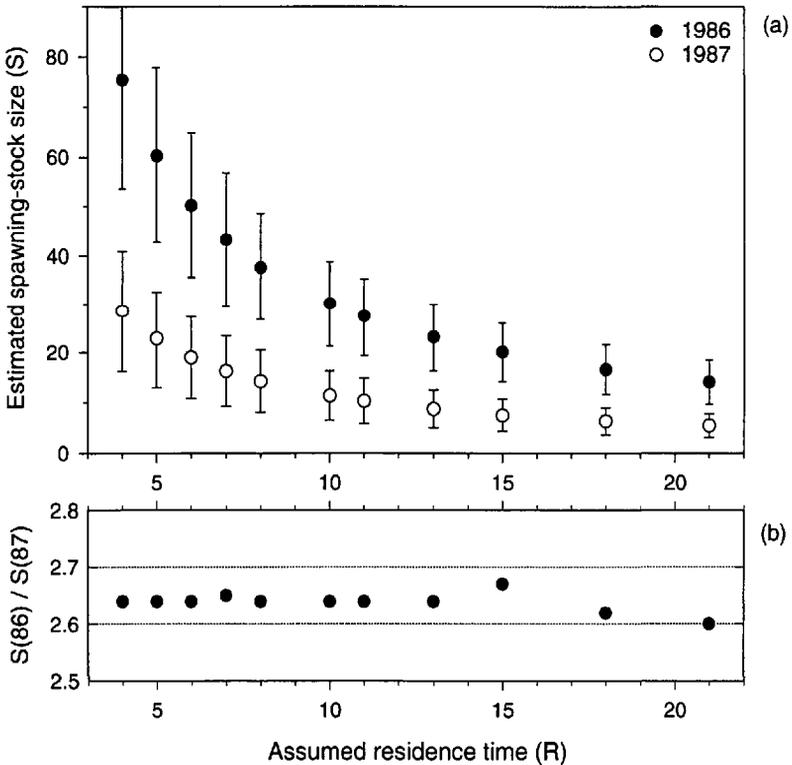| Parameter | Estimate | Lower 95% confidence bound | Upper 95% confidence bound |
|---|---|---|---|
| Estimates for 1986: | | | |
| *S* | 45.0 | −66.0 | 156.0 |
| *L* | 215.0 | 206.0 | 224.0 |
| *R* | 6.7 | −12.0 | 25.0 |
| *W* | 13.5 | 11.8 | 15.2 |
| Estimates for 1987: | | | |
| *S* | 7.9 | −2,470 | 2,486 |
| *L* | 225.0 | −2,281 | 2,731 |
| *R* | 14.6 | −4,556 | 4,587 |
| *W* | 55.2 | −246 | 357 |



Figure 3. Estimates from a model of blue crab spawning migration in Chesapeake Bay in 1986 and 1987. Estimates were made under the assumption of a known residence time on the spawning grounds. (a) Estimates of female spawning-stock size by year, with approximate 95% confidence intervals, as a function of assumed residence time. (b) Ratio of spawning stock size in 1986 to that in 1987, as a function of assumed residence time, assuming identical residence time in both years.

Table 2. Parameter estimates for a migration model of blue crab, *Callinectes sapidus*, in Chesapeake Bay. Parameters are $R$, mean residence time in days; $S$, female spawning-stock size; $L$, location in time of peak migration to spawning grounds (days since 1 January), $W$, relative width of migration pulse. Estimates are conditioned on $R$, and exhibit less than 2% variation in sum of squared errors over this range of $R$.

| | Estimates for 1986 | | | Estimates for 1987 | | |
|---|---|---|---|---|---|---|
| $R$ | $S$ | $L$ | $W$ | $S$ | $L$ | $W$ |
| 4 | 75.35 | 216.4 | 13.80 | 28.53 | 230.1 | 54.71 |
| 5 | 60.29 | 215.9 | 13.75 | 22.82 | 229.6 | 54.70 |
| 6 | 50.23 | 215.4 | 13.68 | 19.02 | 229.1 | 54.69 |
| 7 | 43.22 | 214.9 | 13.91 | 16.31 | 228.6 | 54.69 |
| 8 | 37.69 | 214.4 | 13.54 | 14.29 | 228.1 | 54.86 |
| 10 | 30.12 | 213.4 | 13.27 | 11.41 | 227.1 | 54.58 |
| 11 | 27.38 | 212.9 | 13.13 | 10.37 | 226.6 | 54.50 |
| 13 | 23.15 | 211.9 | 12.81 | 8.76 | 225.6 | 54.30 |
| 15 | 20.03 | 210.9 | 12.42 | 7.51 | 224.7 | 53.06 |
| 18 | 16.62 | 209.4 | 11.67 | 6.34 | 223.1 | 54.26 |
| 21 | 14.13 | 207.8 | 10.70 | 5.44 | 221.6 | 54.07 |

days was used, which is believed likely to encompass the true value (J. R. McConaugha, Dept. of Oceanography, Old Dominion Univ., Norfolk, VA, pers. comm.). Knowledge of the residence time can reduce the confidence intervals around the estimates of $S$ considerably (Fig. 3).

Within the range of residence times used, the goodness of fit, measured by the sum of squared errors, varied less than 2%. The lack of variation implies that the alternative solutions are equally valid from a statistical point of view. As the assumed residence time increased, corresponding estimates of spawning-stock size ($S$) decreased (Table 2, Fig. 3a); this was expected because the data describe a fixed number of crab-days on the spawning grounds (Jones et al. 1990).

By assuming a particular residence time for each year, one could make estimates of the ratio $S_{1986}/S_{1987}$, the relative strength of the spawning stock in the 2 years. A simpler assumption is that the residence time is unknown, but in the range explored and constant from year to year. Under that assumption, the ratio $S_{1986}/S_{1987}$ for all values of $R$ remained between 2.6 and 2.7 (Fig. 3b), suggesting that the 1987 spawning stock was only about 37% as large as in 1986. The approximate 95% confidence intervals on $S$ for the two years do not overlap for any constant value of $R$ in this range. (These parametric intervals must be considered approximate because of the possibility of specification error.) The lack of overlap between years suggests that, under the assumption of a constant residence time, the estimated reduction in spawning-stock size was unlikely to be due to chance.

## COMMENTS

The migration model fits the data reasonably well, considering the substantial standard errors of the data (Jones et al. 1990) and the small sample sizes. Because of the small data set and the broad assumptions needed for modeling, the conclusion drawn (a large population decrease from 1986 to 1987) cannot be assigned a precise statistical probability. Nonetheless, the estimated decrease in spawning-stock size, about 60%, seems worthy of further study.

The migration model was intended to be heuristic, and it serves that role well. Use of the model has clarified the relationships between known and unknown quantities and in particular has emphasized the value of further research on residence time, as emphasized by Jones et al. (1990). Annual estimates of spawning-

stock size could be made by sampling the spawning grounds, but it would be essential to estimate residence times, as well, to determine whether the assumption of a constant residence time is realistic. From such studies, more definite knowledge about the spawning-stock dynamics of this stock of *C. sapidus* could be obtained.

The simple model presented here might be of use in other data-poor situations in which modeling migration is of interest. The model could easily be incorporated into a more complex simulation model of blue crab when sufficient data become available to develop such a model.

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