A mortality model for a population in which harvested individuals do not necessarily die: The stone crab

Victor R. Restrepo

University of Miami, Rosenstiel School of Marine and Atmospheric Science
Cooperative Institute for Marine and Atmospheric Studies
4600 Rickenbacker Causeway, Miami, Florida 33149

Stone crabs *Menippe mercenaria* support a valuable commercial fishery in the Gulf of Mexico, with most of the catch occurring near southwest Florida. Florida landings increased from about 400,000 lbs per fishing season (15 October–15 May) in the early 1960s to an average 2.7 million lbs since 1988. The 1990 landings were valued at over $15 million.

The stone crab fishery is unique in that only the crabs' claws can be harvested, provided that the claws are of legal size (70 mm in propodus length); declawed crabs must be returned to the ocean. Stone crabs can regenerate their massive claws which contain much of the crabs' edible meat (a large claw can weigh 250 g). In a sense, stone crabs are a "reusable resource" because claw regeneration by previously declawed crabs accounts for 1–10% of the annual landings (Savage et al. 1975, Ehrhardt and Restrepo 1989).

The main difficulty associated with estimating mortality rates in this unique fishery is that existing models are not applicable to the crabs' population dynamics. Traditional fisheries models are usually based on the equation (see Beverton and Holt 1957),

$$\frac{dN}{dt} = -(F+M)\,N_t,$$

where N is the population size, t is time, and F and M are the instantaneous fishing and natural mortality rates. An implication of this model is that all harvested animals die. Up to 50% of harvested stone crabs may survive, depending on fishing practices such as the amount of time animals are exposed to air and on the extent of the injury caused by declawing (Davis et al. 1979). Therefore, the above model is not appropriate for this fishery or others like it. In this paper I develop a mortality model that accounts for the possibility that harvested individuals may survive. The model can be used to estimate fishing mortality rates for stone crabs.

The model

Consider a closed population of large-sized individuals (large enough to lose both claws to fishing upon capture), in which catches are monitored for a short period of time. This time-period should be sufficiently short to ensure that declawed crabs will not have time to regenerate their claws. Claw regeneration in large stone crabs takes one year or more (Restrepo 1990), so this should not be a major constraint. The population dynamics during this time-period can be modeled by subdividing the population into harvestable and unharvestable crabs (those with and without legal-sized claws, respectively). Harvestable crabs may become unharvestable if they survive fishing; unharvestable crabs may not become harvestable within the time-interval, since it is assumed that claw regeneration does not occur.

Let

^hN, ^nN = population sizes (in numbers) of harvestable and unharvestable crabs,

F = rate of capture (assumed to be the same for both types of crabs),

^hM, ^nM = natural mortality rates for harvestable and unharvestable crabs, and,

S = fraction of harvestable crabs that survive claw removal and release (0 $\leqslant S \leqslant 1$).

For simplicity, assume that harvest and natural mortality rates remain fixed during the time-period. Note also that unharvestable crabs are immediately returned to the water upon capture so that their mortality due to capture is negligible. The differential equations describing the two-compartment model are

$$\frac{d^hN_t}{dt} = -(^hM + FS + F(1-S))\,^hN_t$$

$$= -(^hM + F)\,^hN_t, \text{ and} \quad (1a)$$

$$\frac{d^nN_t}{dt} = -\,^nM\,^nN_t + FS\,^hN_t. \quad (1b)$$

Equation (1a) is the standard mortality model and simply shows that crabs disappear from the population due to fishing and natural mortality. Losses due to fishing are $F\,^hN_t$. Of these, a fraction $(1-S)$ actually die, and a fraction (S) become part of the unharvestable population (Eq. 1b). Thus, F is a true fishing mortality only when S = 0.

Equation (1a) has the general solution

$$^hN_t = \,^hN_0\, e^{-(F + \,^hM)t}, \quad (2)$$

where $^hN_0$ is the population size at the beginning of the time-period ($t=0$). This solution can be substituted into Equation (1b) to solve it since, without claw regeneration, ^hN_t is independent of ^nN_t (i.e., by assumption, there is no transfer from the nonharvestable into the harvestable population):

$$\frac{d\,^nN_t}{dt} = -\,^nM\,^nN_t + FS\,^hN_0\ e^{-(F+\,^hM)t}. \qquad (3)$$

This is a first-order linear differential equation that can be solved with the integrating factor

$$e^{\int\,^nM\,dt} = e^{\,^nM\,t}.$$

Multiplying (3) throughout by this factor gives

$$\frac{d[e^{\,^nM\,t}\ ^nN_t]}{dt} = FS\,^hN_0\ e^{-(F+\,^hM-\,^nM)t}.$$

Integrating and letting $^nN_t = {}^nN_0$ at $t=0$ gives the solution to Equation (3):

$$^nN_t = \qquad (4)$$

$$\frac{FS\,^hN_0\ (1-e^{-(F+\,^hM-\,^nM)t})\ e^{-\,^nM\,t}}{F+\,^hM-\,^nM} + {}^nN_0\ e^{-\,^nM\,t}.$$

The dynamics explained by Equations (2) and (4) depend on six parameters ($^hN_0$, $^nN_0$, ^hM, ^nM, S, and F). The main usefulness of these two equations lies in simulation modeling (e.g., for yield-per-recruit analyses) in which parameters are given as inputs rather than estimated from fitting the equations to data. However, as shown below, the number of parameters can be reduced to three by taking the ratio $R = {}^nN_t/{}^hN_t$. Note that the ratio of the two population types is largely independent of the level of sampling intensity, provided that the availabilities of harvestable and unharvestable crabs to the sampling gear do not change. Obtaining estimates of either ^nN_t or ^hN_t alone would be a more difficult task which could involve tagging or detailed survey statistics (see Seber 1982 for a discussion on the estimation of abundance). Dividing Equation (4) by Equation (2) gives

$$R_t = a\ e^{bt} - c, \qquad (5)$$

where $\ R_t = \dfrac{^nN_t}{^hN_t},$

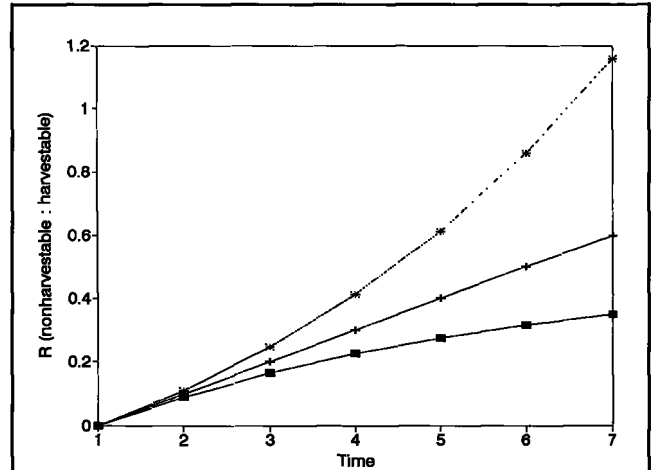$$a = \frac{FS}{F+\,^hM-\,^nM} + \frac{^nN_0}{^hN_0},$$

Figure 1
Expected trends in the ratio R (number of nonharvestable: harvestable stone crabs *Menippe mercenaria*) for three values of b in Eq. (5). Lower curve: b is negative and the trend exhibits convex curvature. Middle curve: b approaches zero and the trend is a straight line. Upper curve: b is positive and the trend is concave-upwards.
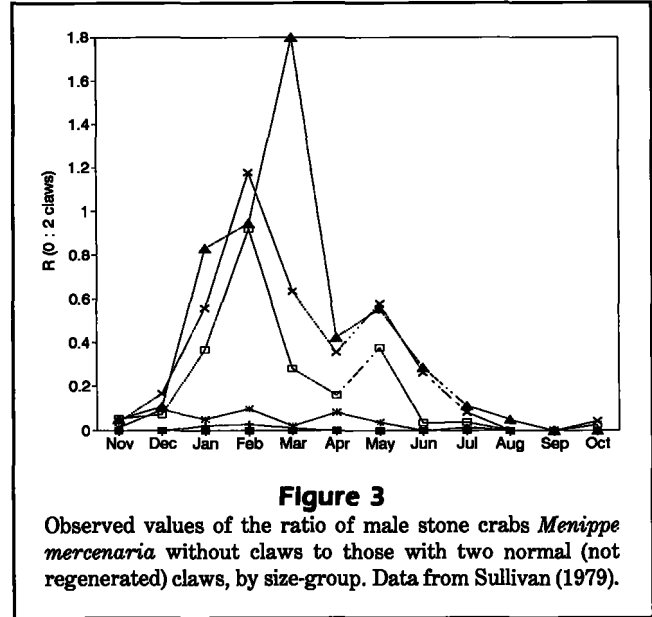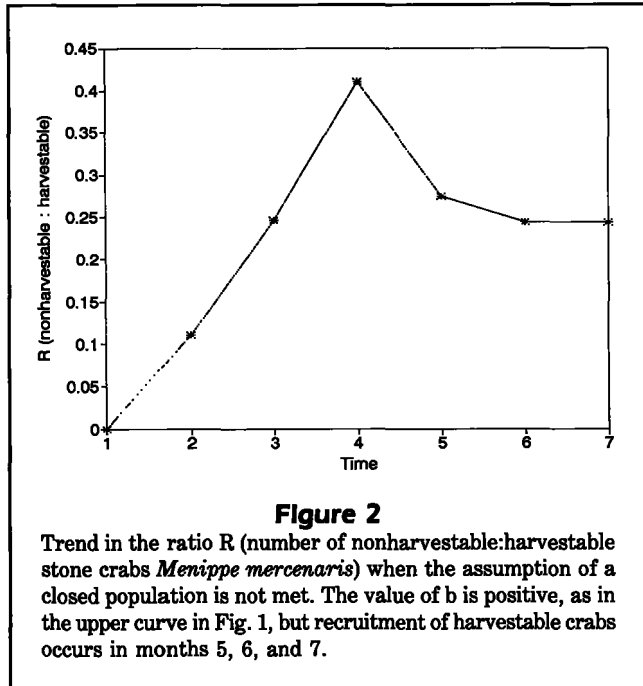
$$b = F + {}^hM - {}^nM,\ \text{and}$$

$$c = \frac{FS}{F+\,^hM-\,^nM}.$$

Equation (5) shows that in a closed population and in the absence of claw regeneration, the ratio of nonharvestable to harvestable crabs should change exponentially with a concave, convex, or straight trend depending on the value of b. Consider a hypothetical population in which $^hN_0 = 1000$, $^nN_0 = 0.0$, $S = 0.5$, $F = 0.2$ per month, and $^hM = 0.2$ per month. When $^nM = 0.6$, $b = -0.2$, and R increases with convex curvature (Fig. 1, filled squares). When ^nM approaches 0.4, b approaches zero, and R increases linearly (Fig. 1, crosses). When $^nM = 0.2$ ($^nM = {}^hM$), b is positive and the trend in R is a concave-upwards curve (Fig. 1, asterisks). In practice, some of the model's assumptions may not be always met. For instance, if $^nM = 0.2$ per month and 250 crabs recruit to the harvestable stock at the beginning of months 5, 6, and 7, then the trend in R decreases starting in month 5, while fishing is still ongoing (Fig. 2).

Application of the model to a data set

No studies have been carried out in which the data necessary for the model have been collected. For this reason the estimates presented below are meant to

Figure 2

Trend in the ratio R (number of nonharvestable:harvestable stone crabs *Menippe mercenaris*) when the assumption of a closed population is not met. The value of b is positive, as in the upper curve in Fig. 1, but recruitment of harvestable crabs occurs in months 5, 6, and 7.

Figure 3

Observed values of the ratio of male stone crabs *Menippe mercenaria* without claws to those with two normal (not regenerated) claws, by size-group. Data from Sullivan (1979).

illustrate how the model can be applied. The data set I used (Sullivan 1979) was collected during 1975 and 1976 in an area where the fishery has been traditionally most intense. This data set contains detailed information on every individual captured, including carapace size, claw sizes, and claw status (presence/absence, regeneration stage, etc.).

The first step in analyzing the data is to define exactly how to categorize crabs in order to meet the assumption that unharvestable crabs do not become harvestable due to claw regeneration during the study period. One way to do so is as follows (Restrepo 1990): "Harvestable" crabs are those with two normal, legal-sized claws (normal claws are defined as those that have no signs of regeneration); "nonharvestable" are those without claws.

With this definition, all harvestable crabs that are caught will likely lose both claws and hence become part of the nonharvestable population if they survive. Conversely, crabs without any claws will not quickly become part of the harvestable population because it would take several regenerative molts (years) before their claws looked normal. Note that the definition above excludes from the analysis all crabs that have either one or two sublegal claws which could, through molting, become part of the harvestable population. In terms of meeting the model's assumptions, the above definition still poses a problem in that crabs with only one claw of legal size (which are relatively uncommon), whether normal or not, may become part of the nonharvestable stock upon declawing.

Figure 3 shows the observed trend in the ratio R [0 claws:2 normal claws] of male stone crabs from Sullivan's (1979) data, for several size-groups. (Female crabs are also harvested, but they are excluded from this analysis because few of them reach sizes at which both claws are of legal size.) Note that R is relatively constant and near zero for crabs <90mm in carapace width (CW) (Fig. 3). Based on claw size—carapace width relationships (Restrepo 1990), the smaller of the crabs' claws (the "pincer") becomes harvestable only when the carapace reaches 90mm in width. Thus males with two normal claws are not expected to lose both claws to fishing at sizes <90mmCW, a fact which is corroborated by Figure 3. Otherwise, R values for the smaller crabs would show larger deviations from the zero line in Figure 3. For this reason, the analyses were conducted with crabs >90mmCW (Fig. 4).

The trend in the observed R values (Fig. 4, filled squares) is reminiscent of that in Figure 2: it appears to increase concavely upwards from November to February, suggesting that $^nM < {}^hM + F$, and it then decreases starting in March. This decline is possibly a consequence of recruitment of large crabs with normal claws into the fishing grounds, suggesting a failure of the closed-population assumption. Empirical evidence for a similar recruitment peak of large males in the spring was found by Ehrhardt et al. (1990) in Everglades National Park. In addition to recruitment, the decline in R after February could also be attributed to declawed crabs being removed from the study site in greater numbers after this month (some vessels may remove the claws at the end of the day as they travel from the fishing grounds to port). Because of these
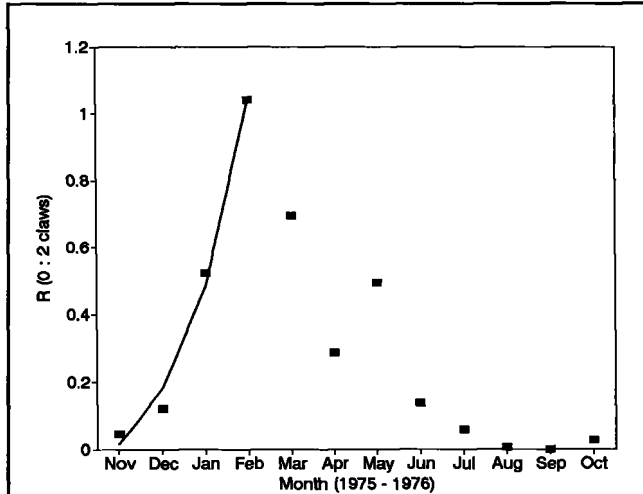
Figure 4
Grouped values from Fig. 3 for crabs ⩾ 90 mm CW (symbols). Solid line: fit of Eq. (5) to the first four observations (estimates of fitted parameters are given in Table 1).

Table 1
Parameter estimates and correlation matrix obtained by fitting Equation (5) to Sullivan's (1979) data on stone crab *Menippe mercenaria*.

Parameter	Estimate	SE	â	b̂	ĉ
				Correlation with	
a	0.191	0.175	1.000		
b	0.618	0.252	−0.994	1.000	
c	0.175	0.229	0.972	−0.949	1.000

problems, only the first four data points in the series were used to estimate the parameters in Equation (5).

The least-squares parameter estimates, standard errors and correlation matrix are given in Table 1 (fit shown in Fig. 4). Note that the errors and correlations are extremely high, owing to the small amount of data used (4 data points to estimate 3 parameters). From these estimates, the following are obtained:

$$\frac{{}^{n}N_0}{{}^{h}N_0} = \hat{a} - \hat{c} = 0.016$$

$$FS = \hat{c}\,\hat{b} = 0.109$$

$$F + {}^{h}M - {}^{n}M = \hat{b} = 0.618.$$

Thus by fitting Equation (5) to the data, the relevant parameters that are estimated are the initial ratio

(which could be measured directly, anyway) and the product FS. Due to the indeterminacy in the estimates of FS and $F + {}^{h}M - {}^{n}M$, auxiliary information is required before the harvest rate (F) can be deduced. One possibility is to assume that the natural mortalities of clawed and clawless crabs are identical. If so, then $F = \hat{b}$ and $S = \hat{c}$. This would result in $F = 0.618$/month and $S = 17.6\%$; instantaneous mortality due to fishing would be $F(1-S) = 0.51$/month. If ${}^{n}M > {}^{h}M$ as suggested by Bert et al. (1978), then the value of F will be less than that estimated by $\hat{b}$. Note that $F = \hat{b} = 0.618$/month translates into about 4.3/year (during a 7-month fishing season), which appears to be unreasonably high, giving indirect support to Bert et al.'s (1978) contention.

Conclusions

An application of the model to estimate current exploitation rates has not been carried out. As shown in the previous section, the data required to do so are relatively simple (crab size, number of claws, and type of claws) but cannot be obtained from the fishery landing statistics. Therefore, a research sampling program would have to be set up to monitor the population and obtain an estimate using the model. Such a sampling program should give consideration to the following requirements:

1 The areal coverage should be large enough to ensure that declawed crabs are not removed from the study site by the fishing vessels.
2 Time-periods when recruitment, immigration, or emigration take place should not be included in the analyses.
3 Counts of both harvestable and nonharvestable individuals should be made periodically (e.g., weekly) so the counts represent the number of individuals at a particular time, rather than the average number of individuals during a long time-period as was done in the preceding section.
4 To avoid imprecision and parameter correlations such as those in Table 1, a large number of R values should be available for parameter estimation.

Acknowledgments

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