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MUNRO'S METHOD FOR ESTIMATING INTERMOLT PERIODS OF TROPICAL DECAPODS IS ROBUST

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Crustacean growth is a discontinuous process in which body size increases only at the time of molting. Growth is usually described in terms of two components —the molt increment in size and the intermolt period (Botsford, 1985). For tropical decapods, Munro's (1974; 1983) method can be used to estimate the intermolt periods from mark-recapture data (Waugh, 1981; Davis, 1981; Hunt and Lyons, 1986).

Munro's method assumes that there is a lack of molting synchronicity in the population. This means that if an animal is randomly selected from the population at any time then the time that has elapsed since the animal last molted is a random variable (unobservable) with a uniform distribution. Observations that a species molts and reproduces throughout the year (e.g., see Lipcius (1985) and Sastry (1983)) could be considered as evidence in support of this assumption.

Suppose a group of animals in a length interval L are tagged, released, and recaptured Δt time units later. The proportion of animals which will have molted will be proportional to the length of time at liberty unless the animals have been at liberty for the full intermolt period (or longer)—in which case all of the animals will surely have molted (Fig. 1). Mathematically, the proportion of recaptured animals that have molted, for a given time interval at large, can be represented by

$$P_m = \text{proportion molting} = \begin{cases} \Delta t/C_L \ldots \Delta t < C_L \\ 1 \ldots \Delta t \geq C_L \end{cases}$$

where C_L is the length-specific intermolt period.

To estimate the intermolt time C_L for a given length interval using Munro's method one would analyze a collection of mark-recapture records as follows: 1—Divide the recaptures into groups according to the time at liberty, 2—Compute the proportion of animals in each group which has molted, and 3—The time it takes for one half of the animals to molt is equal to half of the intermolt period (Fig. 1).

Munro doubled the time at liberty at which half the animals had molted to arrive at an estimate of the intermolt period. Alternatively, it can be noted that if the proportion that have molted is regressed on the time at liberty, using just data from the ascending limb, then an estimate of the intermolt time would be given by the reciprocal of the slope. Theoretically, the line should pass through the origin.

Failures of Assumptions

Munro described only the assumption of no synchronicity for his method. As in all methods for estimating growth from tagging data, it must also be assumed that the type of tag used does not interfere with the normal growth process. In this section we identify and discuss two other assumptions which are implicit in the use of the method.

Individual Variability.—The method assumes that there is no individual variability in the intermolt period. Failure of this assumption leads to increased scatter about the regression line on the ascending limb. It also results in a smooth transition between the ascending limb and the horizontal line instead of a sharp angle (Fig. 1). To avoid bias, one should exclude data points which are close to the intersection of the ascending limb and the horizontal line (e.g., exclude points for which the proportion molting is greater than, say, 90%) if one wishes to use the regression method.

Note that variability in intermolt period can be created artificially; for example, by grouping animals over a wide range of lengths.

Tag Loss and Mortality.—Munro's method provides valid results in the presence of tag loss and mortality only if these are not concentrated at the time of molting. Although detailed information on crustacean tag loss is generally lacking, it appears that, depending on the type of tag used, the degree of tag loss at molting may be in excess of 10% (Cooper, 1970; Scarratt, 1970; Chittleborough, 1974; Davis, 1978). Also, animals may be more vulnerable to mortality factors at the time of molting than at other times (Edwards, 1962; Reilly and Saila, 1978; Conan, 1985).

If there is an increase in tag shedding or mortality at the time of molt, the result will be a lower estimate of the proportion molting since molted animals are removed from the sampled population. Suppose the proportion that retain their identity (*i.e.,* do not die or lose their tag at the time of molt) is denoted by PTR. Then instead of an estimate of

$$P_m = \frac{\text{number molted}}{\text{number molted} + \text{number not molted}}$$

one would obtain the erroneous estimate

$$P_m^* = \frac{\text{number molted} \times \text{PTR}}{\text{number molted} \times \text{PTR} + \text{number not molted}} .$$

That is, tag loss and mortality at the time of molting affect only the counts of molted animals and thus lower the observed proportion of molted animals. The combined effects of these factors is shown in Figure 2 for values of PTR equal to 0.8, 0.6, and 0.4.

To correct for tag loss and mortality, one can divide the observed number of molted animals by an estimate of PTR before calculating the proportion molted. Thus, the corrected value of P_m would be given by

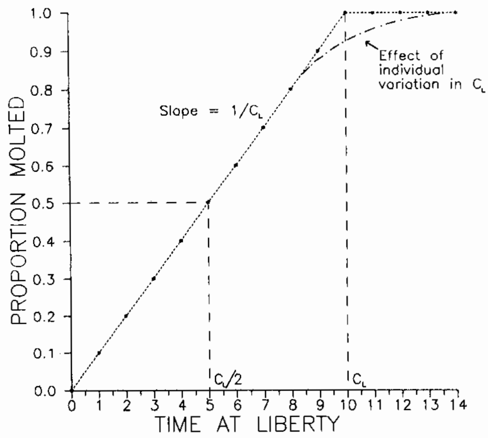
$$P_m(\text{correct}) = \frac{\text{observed number molted/PTR}}{\text{observed number molted/PTR} + \text{number not molted}} . \quad (1)$$

The corrected values of P_m would then be plotted against the midpoints of the times at liberty.

In some cases the raw data may not be available for correction. If all that is available is the estimate of the intermolt period, then an approximate correction would be given by

$$C_L(\text{correct}) = C_L(\text{uncorrected}) \times (1 + \text{PTR})/2.$$

This approximation is satisfactory when PTR is close to unity. However, it can be seen that when PTR is close to unity a correction is hardly needed.



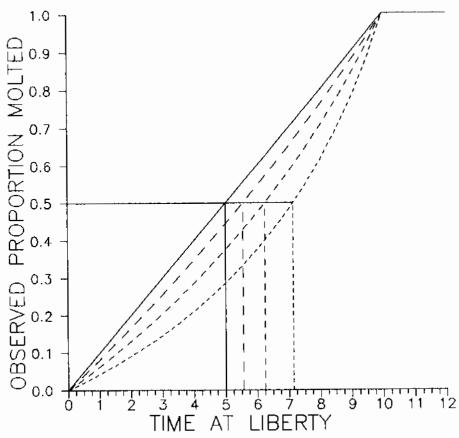


FIGURE 1 (Left). Relationship between proportion of recaptured animals which have molted, time at liberty, and intermolt period. When there is no individual variability in growth, the proportion of animals which have molted is a linear function of the time at liberty such that half the animals have molted after being at liberty for half the intermolt period; all animals have molted when at liberty for time exceeding the intermolt period (C_L). Individual variability in growth results in a departure from the linear relationship (dot-and-dash line).

FIGURE 2 (Right). Effect of the proportion which retain their identity (PTR, see text) on the relationship between the observed proportion of recaptured animals which have molted and the time at liberty. Solid line, PTR = 1.0; long dashes, PTR = 0.8; medium dashes, PTR = 0.6; short dashes, PTR = 0.4. Vertical lines show estimates of half the intermolt period under the assumption that half the animals have molted when time at liberty equals $C_L/2$.

EXAMPLE

We consider a hypothetical example which is based loosely on Munro's (1974; 1983) original data for spiny lobster (*Panulirus argus*). Without correcting the data for tag loss or mortality at the time of molting, one arrives at an estimate of half the intermolt period (i.e., $C_L/2$) of 45 d for one size class (Fig. 3, solid lines). Note that the S-shaped nature of the curve suggests failure of the assumptions of no tag loss/mortality at the time of molt and of no individual variability in growth. The S-shape could also be due to other factors such as combining data over a wide range of sizes or from males and females, or uninjured and injured animals, etc. We will assume that these alternative explanations have been investigated and ruled out as causes of the nonlinearity.

We corrected the data by using equation (1) and assuming values of PTR of 0.75 and 0.5 (Fig. 3). The resulting estimates of half of intermolt period are 41 and 36 d, respectively, which are 9% and 20% less than the uncorrected estimate.

DISCUSSION

We have identified two possible failures of assumption which can cause an error in the estimates of intermolt periods. These failures also cause the observations to depart from the theoretical linear relationship between proportion molted and time at liberty. Thus, the shape of the curve may be used to infer potential problems with the assumptions. In addition to Munro (1974), Waugh (1981) also observed an S-shaped curve. However, Waugh apparently felt the S-shaped form was to be expected as he fit a curvilinear model to the data rather than trying to correct for the nonlinearity.

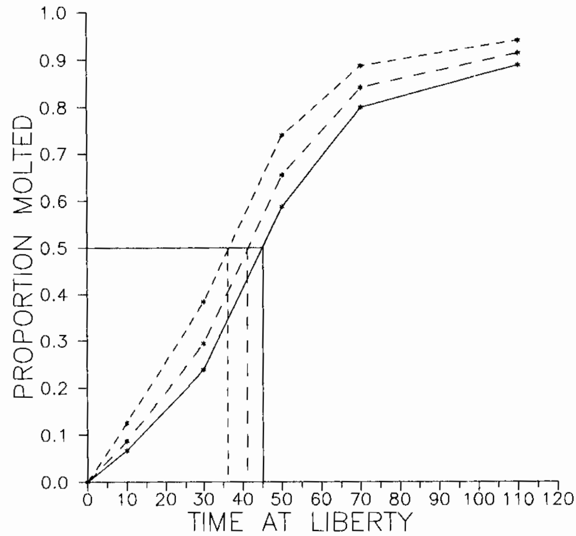


FIGURE 3. Hypothetical data (solid line) with corrections assuming PTR = 0.75 (long dashes) and PTR = 0.50 (short dashes). Vertical lines show estimates of half the intermolt period (i.e., $C_L/2$).

Corrections can be made for tag loss/mortality at the time of molting if these factors can be quantified. Failure to correct for this causes a positive bias. However, it is worth noting that Munro's technique appears to be quite robust to failures of the assumptions discussed here. Thus, in the example considered, a loss of 50% of the sampleable population at the time of molt would require only a 20% adjustment in the estimate.

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