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SENSITIVITY OF THE POPULATION GROWTH RATE TO CHANGES IN SINGLE LIFE HISTORY PARAMETERS: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA: PELECYPODA)

The question of sensitivity analyses in demographic studies was first addressed by Lewontin (1965), and since that time, Hamilton (1966), Demetrious (1969), Emlen (1970), Goodman (1971), Keyfizt (1971), and Mertz (1971) have made contributions in the area. More recently, Caswell (1978) has given general formulae for the sens-

**Results**

Leslie Model

The population of females is divided into *n* age classes. The Leslie matrix, *M*, has the following form:

\[
M = \begin{bmatrix}
a_1 & a_2 & a_3 & \ldots & a_{n-1} & a_n \\
r_1b_1 & 0 & 0 & \ldots & 0 & 0 \\
0 & b_2 & 0 & \ldots & 0 & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & 0 & \ldots & b_{n-1} & 0
\end{bmatrix}
\]

Here, *a*_i is the mean number of female eggs produced annually by a female in class *i* (age *i* - 1 to *i*); assuming a one-to-one sex ratio, *a*_i is one-half the total egg production. The parameter *b*_i is the probability of a clam in class *i* surviving to class 2, 3, ..., *n* - 1. The survivorship from age class 1 to age class 2 is divided into 2 factors, *r*_i and *b*_i. The factor *r*_i is the settlement rate or the probability that an egg will survive the planktonic larval stage and develop into a clam with a 2 mm shell length (0-2 mo of age); *b*_i is the probability that a clam with a 2 mm shell length will survive the remainder of the year (about 10 mo). If *x* is a column vector with *n* components such that *x*_i is the number of females in age class *i* immediately following spawning, then *Mx* represents the population 1 yr from now.

For benthic marine invertebrates possessing planktotrophic larval stages, the events surrounding metamorphosis and settlement are extremely
important for the development and maintenance of species populations. Settlement rates are notoriously variable in nature, however, making it impossible to determine a fixed \( r_s \) and hence a fixed \( \lambda \). For this reason, we have studied sensitivities over a range of \( \lambda \)'s (0.25-3.0). Values of \( a_i \) and \( b_i \) used for *Mya arenaria* are empirically derived (Brousseau 1978a, b).

### Sensitivity Formulae

The population growth rate, \( \lambda \), is the eigenvalue of \( M \) with maximum modulus. In general, \( \lambda \) is unique and is a positive real number. This follows from the Perron-Frobenius Theorem, which may be referenced, for example, in Demetrius (1969). The sensitivity of \( \lambda \) to a life history parameter is defined to be the derivative of \( \lambda \) with respect to that parameter.

Following Caswell (1978), let \( u \) and \( v \) be column vectors satisfying

\[
Mu = \lambda u
\]

\[
u'M = \lambda u'
\]

\[
(u, v) = 1
\]

where \( u' \) denotes the transpose of \( u \), and \((\cdot , \cdot)\) denotes inner product. Statement (2) indicates that \( v \) is a right eigenvector, while Statement (3) indicates that \( u \) is a left eigenvector, each associated with \( \lambda \). Statement (4) is used as a normalization device. While Statements (2) through (4) do not define \( u \) and \( v \) uniquely, they are sufficient to make the sensitivity formulae below well defined. Explicit calculations for the components of vectors \( u \) and \( v \) start with

\[
u_1 = 1
\]

\[
u_i = \sum_{j=1}^{n} a_j b_{j-1} \ldots b_i \lambda^{-(j-i+1)}, i > 1
\]

and

\[
v_1 = 1
\]

\[
v_i = \lambda^{-i} b_{i-1} \ldots b_1 r_s, i > 1
\]

and then normalize using Statement (4) above. With these definitions, Caswell (1978) shows

\[
d\lambda/dm_{ij} = u_i v_j, \quad i, j = 1 \ldots n,
\]

where \( m_{ij} \) is the parameter in the \( i,j \) position of the Leslie matrix \( M \), \( u_i \) is the \( i \)th component of vector \( u_1 \), and \( v_j \) is the \( j \)th component of vector \( v \).

Of course, the components of \( M \) of interest to us are those in the first row (the fecundity parameters) and those in the main subdiagonal (the survivorship parameters). Further, since position \( m_{21} \) equals \( r_s b_1 \) in our notation, the sensitivity formulae become

\[
d\lambda/dai = u_1 v_i, \quad i = 1, 2, \ldots, n
\]

\[
d\lambda/db_i = u_{i+1} v_i, \quad i = 2, 3, \ldots, n - 1
\]

\[
d\lambda/db_1 = r_s d\lambda/dm_{21} = r_s u_2 v_1
\]

\[
d\lambda/dr_s = b_1 d\lambda/dm_{21} = b_1 u_2 v_1.
\]

In particular, notice that \( \lambda \) is not equally sensitive to \( r_s \) and \( b_1 \) unless the two values are equal.

For the present study, we hold \( a_i \) and \( b_i \) fixed and allow \( \lambda \) to vary. The settlement rate, \( r_s \), then becomes a function of \( \lambda \), specifically,

\[
r_s = (\lambda - a_1)/(\lambda^{-1} a_2 b_1 + \lambda^{-2} a_3 b_2 b_1 + \ldots + \lambda^{-n+1} a_n b_{n-1} \ldots b_1),
\]

and is used in the Leslie matrix, \( M \). We then compute \( u \) and \( v \) satisfying Statements (2)-(4) for the given \( \lambda \), and the sensitivity values Statements (8)-(11).

### Calculation of Sensitivity Values

**Settlement Rate.** Using the data in Table 1, the sensitivity of the population growth rate of
Mya arenaria to changes in the settlement rate ($r_s$) can be calculated. Results are summarized in Table 2 for a range of values of $\lambda$. As expected, $r_s$ increases as the population growth rate increases, while the sensitivity of $\lambda$ to changes in $r_s$ decreases as $\lambda$ increases. The population growth rate, $\lambda$, is far more sensitive to changes in $r_s$ than it is to changes in any other single life history parameter. A further discussion of this point is given below.

The sensitivity of $\lambda$ to changes in survivorship parameters other than $r_s$ is illustrated in Figure 2, where it is evident that $\lambda$ is more sensitive to changes in $b_1$, the survivorship of an individual from 2 mo to 1 yr of age, than to other values of $b_i$ for $i > 1$. As above, these curves illustrate a general result. Since $b_1$ is $> b_i$ for $i > 1$ in the Mya arenaria model, $d\lambda/db_1$ is $> d\lambda/db_i$ using Statement (14).

By comparing Figures 1 and 2, it seems evident that the population growth rate is more sensitive to changes in survivorship than to changes in fecundity. This result may be made precise if the population is actually growing ($\lambda > 1$), since using Statements (13) and (15) it follows that $d\lambda/db_1$ is $> d\lambda/db_i$ for all values of $i$. Finally, by examining Statements (10) and (11), it is clear that $\lambda$ is more sensitive to $r_s$ than to $b_1$ for the Mya arenaria model as long as $r_s$ is $< b_1$. Hence, $\lambda$ is more sensitive to $r_s$ than to all other survivorship parameters, and, at least for growing populations, more sensitive to changes in $r_s$ than to any other fecundity parameter as well.

**Discussion**

Fisher (1958) in his fundamental theorem of

![FECUNDITY](image)

**FIGURE 1.**—Sensitivity of a range of $\lambda$'s (0.25-3.0) to changes in the fecundity ($a_i$) of Mya arenaria in each age class. The first age class is not included since Mya arenaria are not mature until after the first year of age.
natural selection states that natural selection will favor genotypes which increase the population growth rate, \( \lambda \). Since the \( \lambda \) for a population is based on the life history parameters of age-specific fecundity and survivorship, the greater the sensitivity of \( \lambda \) to changes in a particular life history value, the greater the potential for effecting evolutionary change through that parameter.

Existing evidence indicates that population growth rate is more sensitive to changes in survival rates than to changes in reproductive output. Cole (1954) reached this conclusion when he suggested that in species with repeated reproduction and relatively large litter size, there is little selection pressure favoring increased fecundity. Similarly, Caswell (1978) using Hartshorn's (1975) data for Pentaclethra macroloba, a tropical rain forest tree, illustrates by the use of models, that, for this species, population growth rate is more sensitive to changes in growth and survival than to changes in fecundity. The data reported here for Mya arenaria follow the same pattern; \( \lambda \) is relatively insensitive to changes in egg production. The most interesting results of the sensitivity analyses are produced by changes in the survivorship parameters.

Based on our analyses, two important generalizations can be made regarding the sensitivity of \( \lambda \). First, whenever \( r_s < b_1 < b_i \), the population growth rate will be more sensitive to changes in \( r_s \) than to changes in any of the other survivorship parameters. Second, in growing populations, i.e., where \( \lambda > 1 \), \( \lambda \) is always most sensitive to changes in the settlement rate. In terms of Deevey's (1947) categorization of generalized survivorship curves, the relationship \( r_s < b_1 < b_i \) is probably operative in most Type III curves, which are characterized by extremely heavy mortality early in life. Consequently, these generalizations are of interest since the types of life history features exhibited by Mya arenaria are likely to be common to other species of marine organisms, many of which are also commercially important.

On a more practical level, the ability to identify those life history stages to which the population growth rate is most sensitive may serve as a useful tool in directing the efforts of those interested in shellfish management. For instance, the models described here indicate that larval settlement is the most critical stage in Mya arenaria's life history. Developing a better understanding of the factors surrounding metamorphosis and settlement and implementing a method for inducing spatfall would probably be the single most effective way to increase clam yields.

Another area for consideration centers around the survivorship of the first year class. Since the population growth rate of Mya arenaria is also very sensitive to changes in the \( b_1 \) parameter, a second way to increase clam productivity is to improve the survivorship of clams 2 mo to 1 yr of age (ca. 2-25 mm shell length). This age class corresponds to that postlarval stage in Mya arenaria which is the most vulnerable to both biotic (predation) and abiotic (wash-out, temperature and salinity fluctuations) factors in the environment.

The practice of transplanting juvenile Mya arenaria from one flat to another has been used by managers since the turn of the century (Belding 1930) in efforts to 1) replenish depleted clam beds or 2) reduce densities in "overcrowded" beds. Currently, there is a renewed interest in this procedure\(^1\) even though in the past, these efforts have met with varying degrees of success (Belding 1930; Turner 1951; Smith et al. 1955). The

\( ^1 \)D. E. Wallace, Director, Department of Marine Resources, State of Maine, Boothbay Harbor, ME 04538, pers. commun. April 1983.
reasons may be related to the vulnerability of juveniles as discussed above.

To insure success with transplanting techniques, it is essential to reduce mortality among transplanted clams either by protecting them from significant sources of mortality in the field or by retaining them in protective “nurseries” until they pass this critical phase. Past attempts to protect juveniles in the field by building fences to exclude predators have proven costly, difficult to carry out, and unreliable (Smith et al. 1955). More promising are recent advances in aquaculture techniques for commercially important bivalves. By employing “nurseries” for the young and field “grow-out” procedures for adults, sources of juvenile mortality can be reduced while still utilizing natural sources of food during the greater part of the individual’s growth period.

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THE OCCURRENCE OF PISCINE ERYTHROCYTIC NECROSIS (PEN) IN THE SEA LAMPREY, PETROMYZON MARINUS, FROM SEVERAL MAINE LOCALITIES

The sea lamprey, Petromyzon marinus, is an anadromous fish found in the North Atlantic Ocean from Iceland and northern Europe to northwestern Africa, and from the Grand Banks and the Gulf of St. Lawrence to Florida (Hubbs and Lagler 1949). The sea lamprey has adopted an entirely freshwater life cycle in the Great Lakes where it has seriously depleted fish populations (Everhart 1976).

The lamprey feeds on other fishes by hanging on with its sucking mouth. Once attached, it...