LOVE, M. S., AND M. MOSER.
  1976. *Davisia reginae* sp. n. (Protozoa: Myxosporida) from four California marine fishes. J. Parasitol. 62:982-983.
  1983. A checklist of parasites of California, Oregon, and Washington marine and estuarine fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-777, 576 p.
LOVE, M. S., AND W. V. WESTPHAL.
  1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. Fish. Bull., U.S. 79:533-545.
MARGOLIS, L.
  1970. Nematode diseases of marine fishes. *In* S. F. Sniezko (editor), A symposium on diseases of fishes and shellfishes, p. 190-208. Am. Fish. Soc. Spec. Publ. 5.
MOSER, M., AND M. S. LOVE.
  1975. *Henneguya sebasta* sp. n. (Protozoa, Myxosporida) from California rockfish, *Sebastes* spp. J. Parasitol. 61:481-483.
MOSER, M., M. S. LOVE, AND L. A. JENSEN.
  1976. Myxosporida (Protozoa) in California rockfish, *Sebastes* spp. J. Parasitol. 62:690-692.
SEKERAK, A. D.
  1975. Parasites as indicators of populations and species of rockfishes (*Sebastes*: Scorpaenidae) of the Northeastern Pacific Ocean. Ph.D. Thesis, Univ. Calgary, Calgary, Alberta, 251 p.
SHOTTER, R. A.
  1973. Changes in the parasite fauna of whiting *Odontogadus merlangus* L. with age and sex of host, season, and from different areas in the vicinity of the Isle of Man. J. Fish Biol. 5:559-573.
TURNER, C. H., E. E. EBERT, AND R. R. GIVEN.
  1969. Man-made reef ecology. Calif. Dep. Fish Game, Fish Bull. 146, 221 p.
YAMAGUTI, S. M.
  1971. Synopsis of digenetic trematodes of vertebrates. Keigaku Publ. Tokyo, 1074 p.

MILTON S. LOVE
KIMBERLY SHRINER
PAMELA MORRIS

VANTUNA Research Group
Department of Biology
Occidental College
Los Angeles, CA 90041

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), Demetrius (1969), Emlen (1970), Goodman (1971), Keyfitz (1971), and Mertz (1971) have made contributions in the area. More recently, Caswell (1978) has given general formulae for the sensitivity of the population growth rate (λ) derived from a Leslie model, to changes in single life history parameters written as formulae involving eigenvectors of the Leslie matrix. The application of such analyses to the study of the population dynamics of commercially important species can provide useful information to those interested in resource management.

The work presented here describes the sensitivity of the population growth rate to changes in the settlement rate (Brousseau et al. 1982) and in the age-specific fecundity and survivorship rates of the soft-shell clam, *Mya arenaria*, using a modified Leslie matrix model and an extension of the sensitivity formulae derived by Caswell (1978). Predictions concerning the effect that changes in these life history parameters will have on λ and the implications of these results to the management of this species are discussed.

Results

Leslie Model

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

$$M = \begin{bmatrix} a_1 & a_2 & a_3 & \dots & a_{n-1} & a_n \\ r_s b_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & b_2 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & & b_{n-1} & 0 \end{bmatrix} \quad (1)$$

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_s and b_1. The factor r_s 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_1 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 λ. For this reason, we have studied sensitivities over a range of λ'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, λ, is the eigenvalue of M with maximum modulus. In general, λ 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 λ to a life history parameter is defined to be the derivative of λ with respect to that parameter.

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

$$Mv = \lambda v \qquad (2)$$

$$u'M = \lambda u' \qquad (3)$$

$$(u, v) = 1 \qquad (4)$$

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 λ. 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

$$u_1 = 1$$

$$u_i = \sum_{j=1}^{n} a_j b_{j-1} \dots b_i \lambda^{-(j-i+1)}, i > 1 \qquad (5)$$

and

$$v_1 = 1$$

$$v_i = \lambda^{-i} b_{i-1} \dots b_1 r_s, i > 1 \qquad (6)$$

and then normalize using Statement (4) above.

With these definitions, Caswell (1978) shows

$$d\lambda/dm_{ij} = u_i v_j, \quad i, j = 1 \dots n, \qquad (7)$$

where m_{ij} is the parameter in the i, j position of the Leslie matrix M, u_i is the ith component of vector u_1, and v_j is the jth 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

$$d\lambda/da_i = u_1 v_i, \quad i = 1, 2, \dots, n \qquad (8)$$

$$d\lambda/db_i = u_{i+1} v_i, \quad i = 2, 3, \dots, n-1 \qquad (9)$$

$$d\lambda/db_1 = r_s d\lambda/dm_{21} = r_s u_2 v_1 \qquad (10)$$

$$d\lambda/dr_s = b_1 d\lambda/dm_{21} = b_1 u_2 v_1. \qquad (11)$$

In particular, notice that λ 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 λ to vary. The settlement rate, r_s, then becomes a function of λ, specifically,

$$r_s = (\lambda - a_1)/(\lambda^{-1} a_2 b_1 + \lambda^{-2} a_3 b_2 b_1 + \dots + \lambda^{-n+1} a_n b_{n-1} \dots b_1), \qquad (12)$$

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

Relationships among the sensitivity formulae above have been derived by Demetrius (1969) and Caswell (1978). Of particular interest are

$$d\lambda/da_i > d\lambda/da_j, \quad i < j, \lambda > 1$$
$$d\lambda/da_i < d\lambda/da_j, \quad i < j, \lambda < 1 \qquad (13)$$

$$b_i d\lambda/db_i > b_j d\lambda/db_j, \quad i < j \qquad (14)$$

$$\frac{d\lambda/db_1}{d\lambda/da_1} = \frac{\lambda - a_1}{b_1}. \qquad (15)$$

Statement (13) can actually be made stronger, as proven by Demetrius (1969, Statement (8)); Statement (14), in the case $i = 1$, and Statement (15) follow from Demetrius (1969, Statement (11)) and Caswell (1978, Statement (22)); and Statements (5), (10), and (12) above.

Calculation of Sensitivity Values

Settlement Rate. —Using the data in Table 1, the sensitivity of the population growth rate of

TABLE 1.—Life history statistics used in the derivation of the Leslie matrix for *Mya arenaria* (data from Brousseau 1978a, b).

Age (yr)	Age class	Shell length (mm)	Fecundity[1] (a_i)	Probability of survival (b_i)
0-1	1	2.0-29.9	0.0	0.177
1-2	2	30.0-44.9	3,744.0	0.912
2-3	3	45.0-59.9	17,170.0	0.904
3-4	4	60.0-64.9	31,159.0	0.952
4-5	5	65.0-69.9	39,957.0	0.949
5-6	6	70.0-74.9	50,341.0	0.969
6-7	7	75.0-79.9	62,450.0	0.984
7+	8+	80.0-84.9	76,465.0	0.911

[1]Fecundity = number of female eggs produced per individual assuming a 1:1 sex ratio.

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 λ. As expected, r_s increases as the population growth rate increases, while the sensitivity of λ to changes in r_s decreases as λ increases. The population growth rate, λ, 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.

TABLE 2.—Sensitivity of various population growth rates (λ) to changes in the settlement rate (r_s). The intrinsic growth rate = log λ.

Population growth rate (λ)	Intrinsic growth rate	Settlement rate (r_s)	Sensitivity of λ to r_s
0.25	−1.386	6.535×10^{-12}	3.291×10^9
0.5	−0.693	1.700×10^{-8}	2.697×10^6
0.75	−0.288	1.139×10^{-6}	6.822×10^4
1.0	0.0	$[1]1.462 \times 10^{-5}$	8.562×10^3
1.25	0.223	7.320×10^{-5}	2.646×10^3
1.5	0.405	2.141×10^{-4}	1.307×10^3
1.75	0.560	4.618×10^{-4}	8.158×10^2
2.0	0.693	8.310×10^{-4}	5.765×10^2
3.0	1.099	3.702×10^{-3}	2.454×10^2

[1]r_s = Equilibrium settlement rate, $r_{s\,eq}$.

Fecundity and Other Survivorship Rates. —The sensitivity of λ to changes in fecundity are illustrated in Figure 1. Under equilibrium conditions ($\lambda = 1.0$), sensitivity to fecundity changes over the reproductive life span of the individual are slight. If the population is actually growing ($\lambda > 1.0$), the magnitude of the sensitivity to changes in the fecundity decreases with increasing age, while the reverse is true if the population is actually declining ($\lambda < 1.0$). This follows from Statement (13). For declining populations this is probably due to the combined effects of an increasing reproductive value with increasing age and a shift in the age structure to older individuals as the population declines.

The sensitivity of λ to changes in survivorship parameters other than r_s is illustrated in Figure 2, where it is evident that λ 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_i is $> b_1$ 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 $> d\lambda/da_i$ for all values of i. Finally, by examining Statements (10) and (11), it is clear that λ is more sensitive to r_s than to b_1 for the *Mya arenaria* model as long as r_s is $< b_1$. Hence, λ 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.
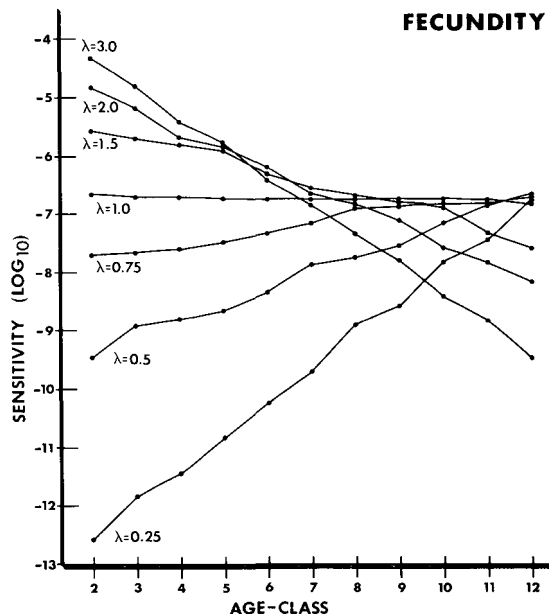
Discussion

Fisher (1958) in his fundamental theorem of

FIGURE 1.—Sensitivity of a range of λ'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; λ. Since the λ for a population is based on the life history parameters of age-specific fecundity and survivorship, the greater the sensitivity of λ 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; λ is relatively insensitive to changes in egg production. The most interesting results of the sensitivity analyses are produced by changes in the survivorship parameters.
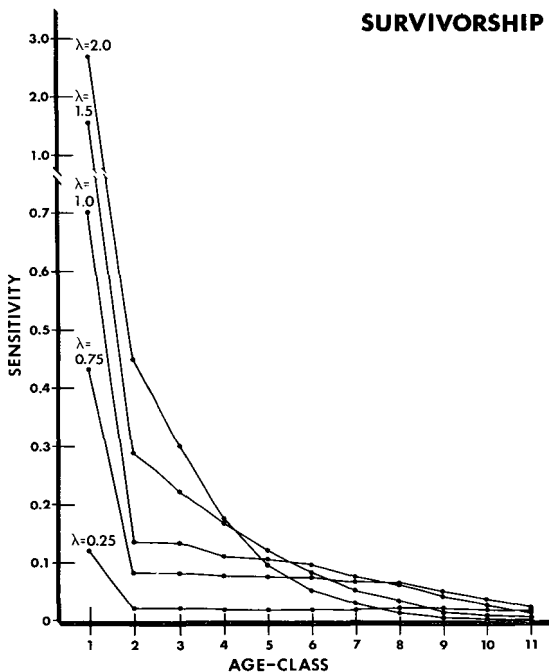
Based on our analyses, two important generalizations can be made regarding the sensitivity of λ. First, whenever $r_s < b_1 < b_i$, the population growth rate will be more sensitive to changes in r_s than to changes in any of the other survivorship parameters. Second, in growing populations, i.e., where $\lambda > 1$, λ 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

FIGURE 2.—Sensitivity of a range of λ's (0.25-2.0) to changes in the survivorship (b_i) of *Mya arenaria* in each age class.

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.

Literature Cited

BELDING, D. L.
1930. The soft-shelled clam fishery of Massachusetts. Mass. Dep. Conserv., Div. Fish Game, Mar. Fish. Serv. 1, 65 p.

BROUSSEAU, D. J.
1978a. Spawning cycle, fecundity, and recruitment in a population of soft-shell clam, *Mya arenaria*, from Cape Ann, Massachusetts. Fish. Bull., U.S. 76:155-166.
1978b. Population dynamics of the soft-shell clam *Mya arenaria*. Mar. Biol. (Berl.) 50:63-71.

BROUSSEAU, D. J., J. A. BAGLIVO, AND G. E. LANG, JR.
1982. Estimation of equilibrium settlement rates for benthic marine invertebrates: its application to *Mya arenaria* (Mollusca: Pelecypoda). Fish. Bull., U.S. 80:642-644.

CASWELL, H.
1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Pop. Biol. 14:215-230.

COLE, L. C.
1954. The population consequences of life history phenomena. Q. Rev. Biol. 29:103-137.

DEEVEY, E. S., JR.
1947. Life history tables for natural population of animals. Q. Rev. Biol. 22:283-314.

DEMETRIUS, L.
1969. The sensitivity of population growth rate to perturbations in the life cycle components. Math. Biosci. 4:129-136.

EMLEN, J. M.
1970. Age specificity and ecological theory. Ecology 51:588-601.

FISHER, R. A.
1958. The genetical theory of natural selection. 2d ed. Dover, N.Y., 291 p.

GOODMAN, L. A.
1971. On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates. Theor. Pop. Biol. 2:339-354.

HAMILTON, W. D.
1966. The moulding of senescence by natural selection. J. Theor. Biol. 12:12-45.

HARTSHORN, G. S.
1975. A matrix model of tree population dynamics. *In* F. B. Golley and E. Medina (editors), Tropical ecological systems: trends in terrestrial and aquatic research, p. 41-51. Springer-Verlag, N.Y.

KEYFITZ, N.
1971. Linkages of intrinsic to age-specific rates. J. Am. Stat. Assoc. 66:275-281.

LEWONTIN, R. C.
1965. Selection for colonizing ability. *In* H. G. Baker and G. L. Stebbins (editors), The genetics of colonizing species, p. 77-94. Acad. Press, N.Y.

MERTZ, D. B.
1971. Life history phenomena in increasing and decreasing populations. *In* G. P. Patil, E. C. Pielou, and W. E. Waters (editors), Statistical ecology, Vol. 2, p. 361-399. Penn. State Univ. Press, University Park, Pa.

SMITH, O. R., J. P. BAPTIST, AND E. CHIN.
1955. Experimental farming of the soft-shell clam, *Mya arenaria*, in Massachusetts, 1949-1953. Commer. Fish. Rev. 17(6):1-16.

TURNER, H. J.
1951. Fourth report on investigations on the shellfisheries of Massachusetts. Mass. Div. Mar. Fish. (Woods Hole Oceanogr. Inst. Coll. Reprints, Contrib. No. 615.)

DIANE J. BROUSSEAU

Department of Biology
Fairfield University
Fairfield, CT 06430

JENNY A. BAGLIVO

Department of Mathematics
Fairfield University
Fairfield, CT 06430

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