Press, Ames, 593 p.
STEEDMAN, H. F. (editor).
1976. Zooplankton fixation and preservation. Monogr. Oceanogr. Methodol. 4, 350 p. The UNESCO Press, Paris.
SUMNER, F. B., R. C. OSBURN, AND L. J. COLE.
1911. A biological survey of the waters of Woods Hole and vicinity. Sect. 1—Physical and zoological. Bull. U.S. Bur. Fish. 31:1-442.
SUTCLIFFE, W. H., JR.
1957. An improved method for the determination of preserved plankton volumes. Limnol. Oceanogr. 2:295-296.
TRANTER, D. J.
1960. A method for determining zooplankton volumes. J. Cons. 25:272-278.
WIEBE, P. H., S. BOYD, AND J. L. COX.
1975. Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon. Fish. Bull., U.S. 73:777-786.
YENTSCH, C. S., AND J. F. HEBARD.
1957. A gauge for determining plankton volume by the mercury immersion method. J. Cons. 22:184-190.
ZAR, J. H.
1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J., 620 p.

JOSEPH KANE

Northeast Fisheries Center Narragansett Laboratory
National Marine Fisheries Service, NOAA
South Ferry Road, Narragansett, RI 02882.

ESTIMATION OF EQUILIBRIUM SETTLEMENT RATES FOR BENTHIC MARINE INVERTEBRATES: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA: PELECYPODA)

It is generally agreed that marine invertebrates possessing planktotrophic larval stages experience extremely high mortality during the early stages of their life history. In the settlement of benthic invertebrates, mortality occurs during three critical phases: 1) fertilization, 2) the free-swimming pelagic stage, and 3) the early postlarval attachment period. Since egg loss, larval recruitment, and early postlarval mortality may often be the limiting steps in the development and maintenance of marine benthic communities, it is of interest to ecologists to be able to make direct estimates of settlement rates in such populations.

It is often difficult, however, to obtain reasonable estimates of early life history stage mortality rates. The earliest attempt to determine such rates was made by Thorson (1966). Based on the standing crop of a population of *Venus* (= *Mercenaria*) *mercenaria*, he estimated that approximately 98.6% of the clams died during the postlarval period (stage 3) and that loss prior to this was probably much heavier. More recently, Muus (1973), in a study of 11 species of bivalves in the Oresund, Denmark, found postlarval mortality rates (stage 3) of 67-100% for all species; whereas Gledhill (1980) calculated larval mortality rates (stage 2) of 99.38% and 99.99% for two populations of *Mya arenaria* in Gloucester, Mass. None of these estimates, however, take into account the heavy mortality that occurs during stage 1, thereby overlooking the substantial loss occurring during the fertilization process itself.

In an attempt to overcome the difficulty in estimating early survival parameters empirically, Vaughan and Saila (1976) developed an indirect method using the Leslie matrix for determining mortality rates during the first year of life for the Atlantic bluefin tuna, *Thunnus thynnus*, assuming an equilibrium population. By expanding their treatment, as suggested by Van Winkle et al. (1978), it is possible to divide age class 1 into particular stages, thereby making the model appropriate for cases dealing with animals possessing more complex life cycles (i.e., those which include egg, larvae, postlarval juveniles, etc.). In the case of benthic invertebrates with free-swimming larval stages, this method can be used to calculate mortality rates during settlement for any species population for which demographic parameters are available. Such theoretical estimates are of special interest for two reasons. First, the equilibrium settlement rate (r_s) value can be compared with field-determined estimates; second, the value may be useful in the prediction of future age structures in natural populations.

This paper describes the indirect method for estimating the settlement rate based on age-specific fecundity and survivorship rates and discusses its application to a commercially important species of bivalve, *Mya arenaria.*

Results

Leslie Matrix

Matrix methods for analyzing age-structured populations were developed by Leslie (1945,

1948) and subsequently used in numerous studies of human and animal populations. In the present setting, the Leslie matrix takes the form:

$$L(r_s) = \begin{bmatrix} a_1 & a_2 & a_3 \ldots a_{n-1} & a_n \\ r_s b_1 & 0 & 0 \ldots 0 & 0 \\ 0 & b_2 & 0 \ldots 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & b_{n-1} & 0. \end{bmatrix}$$

Here, a_i is the number of female eggs produced annually by a female *Mya arenaria* in class i (age $i-1$ to i), and b_i is the probability of a clam in class $i-1$ surviving to class i for $i \geqq 2$. The survivorship from age-class 1 to age-class 2 (P_o in the notation of Vaughan and Saila (1976)) has been divided into two factors, r_s and b_1. The factor r_s is the settlement rate, or the probability that an egg will 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).

The intrinsic growth rate is an increasing function of the settlement rate, r_s. Therefore, the equilibrium value, $r_{s_{eq}}$, $0 < r_{s_{eq}} < 1$, can be calculated for the population assuming steady state conditions. Since the values of a_i and b_i have been determined the *Mya arenaria* (Brousseau 1978a, b), $r_{s_{eq}}$ can be determined for this species. Similar calculations are described by Vaughan and Saila (1976) and Van Winkle et al. (1978).

Calculation of Equilibrium Settlement Rate and Stable Age Structure

Under conditions of the Perron-Frobenius Theorem, the population will reach an equilibrium state (starting with any initial reproducing population) if $\lambda = 1$ is the dominant eigenvalue of $L(r_s)$. Thus, $r_{s_{eq}}$ is the unique solution to the equation

$$|L(r_s) - \mathrm{I}| = 0.$$

By induction on the size of the matrix (n),

$$|L(r_s) - \mathrm{I}| = \pm(1 - a_1 - r_s b_1 a_2 - r_s b_1 b_2 a_3 - \ldots - r_s b_1 b_2 \ldots b_{n-1} a_n).$$

The required settlement rate is given by:

$$r_{s_{eq}} = \frac{1 - a_1}{b_1 a_2 + b_1 b_2 a_3 + \ldots + b_1 b_2 \ldots b_{n-1} a_n} .$$

Using the data in Table 1, the required settlement rate for *Mya arenaria* is $r_{s_{eq}} = 0.001462\%$ or 1 egg out of about 68,400 survive to 2 mm. Thus 1 egg out of 384,000 must survive the first year to maintain a steady population. Errors of up to 5% in the fecundity and survivorship values will yield equilibrium settlement rates of between 0.000983% (1 egg in 101,700 surviving to 2 mm size) and 0.00218% (1 egg in 45,800 surviving to 2 mm size). In addition, the eigenvector corresponding to the eigenvalue $\lambda = 1$ gives the stable age structure for the population. Postsettlement population structures were determined for only the $r_{s_{eq}}$ calculated above. The results are given in Table 2.

TABLE 1.—Life history statistics used in the derivation of the Leslie Matrix for *Mya arenaria*. (Data from Brousseau 1978b.)

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	62,460.0	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.

TABLE 2.—Calculated stable age structures for the population of *Mya arenaria*, based on the entire population and the adult population (≤ 30 mm) only.

Age class	Percent of entire population	Percent of adult population (≤ 30)
[1]1	42	
2	7	12
3	7	12
4	6	10
5	6	10
6	5	9
7	5	9
8	5	9
9	5	9
10	4	7
11	4	7
12	4	7

[1] This age class represents clams 2-29.9 mm in shell length.

Discussion

In his classic work on marine invertebrate communities, Thorson (1950) stated the definitive "number of eggs and larvae produced per pair of adult animals per lifetime to maintain the population is...one pair of larvae." More simply, to remain at equilibrium, a replacement rate of one must be maintained. For a population of *Mya* *arenaria* possessing the life history statistics given above, 1 out of about 790,000 eggs produced during the lifetime of an individual must survive to ensure continuance of the population.

However, variable recruitment and high postlarval mortality tend to be the general rule among temperate and boreal marine invertebrates, especially the bivalves. At the Jones River in Gloucester, the tidal flat received a heavy set of young *Mya arenaria* in 1973 (Brousseau 1978a, b). Based on crude estimates of stock density, age-specific fecundity, and the density of the resultant spatfall, the settlement rate was 0.0498%, or about 34 times larger than the calculated $r_{s_{\mathrm{eq}}}$. During the two subsequent years, on the other hand, this site received only a limited spatfall, which, coupled with high postlarval mortality, resulted in settlement rates of 0.0%. Under such fluctuating conditions, therefore, the settlement history of a population takes on added significance.

In addition to being of theoretical interest, determination of the equilibrium settlement rate for a commercially important species may be of value in its harvesting management as well. Although the impact of repeated exploitation is difficult to assess given the uncertainties of environmental conditions, continued harvesting on tidal flats receiving annual settlement rates below equilibrium may prove to be extremely harmful to the resident population.

Literature Cited

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.

GLEDHILL, C.

1980. The influence of established infauna on recruitment of the soft-shell clam, *Mya arenaria* L. M.S. Thesis, Univ. Massachusetts, Amherst, 40 p.

LESLIE, P. H.

1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

1948. Some further notes on the use of matrices in population mathematics. Biometrika 35:213-245.

MUUS, K.

1973. Settling, growth and mortality of young bivalves in the Oresund. Ophelia 12:79-116.

THORSON, G.

1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. (Camb.) 25:1-45.

1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3:267-293.

VAN WINKLE, W., D. L. DEANGELIS, AND S. R. BLUM.

1978. A density-dependent function for fishing mortality rate and a method of determining elements of a Leslie matrix with density-dependent parameters. Trans. Am. Fish. Soc. 107:395-401.

VAUGHAN, D. S., AND S. B. SAILA.

1976. A method for determining mortality rates using the Leslie matrix. Trans. Am. Fish. Soc. 105:380-383.

DIANE J. BROUSSEAU

Department of Biology
Fairfield University
Fairfield, CT 06430

JENNY A. BAGLIVO
GEORGE E. LANG, JR.

Department of Mathematics
Fairfield University
Fairfield, CT 06430

GROWTH OF JUVENILE RED SNAPPER *LUTJANUS CAMPECHANUS*, IN THE NORTHWESTERN GULF OF MEXICO[1]

The red snapper, *Lutjanus campechanus*, has received considerable attention in the past due to its importance as a commercial and sport fish in the Gulf of Mexico. Most published material deals with the fishery and is summarized in Carpenter (1965). Few major papers have dealt with the natural history of red snapper.

Moseley (1965) reported on growth, reproduction, and food habits of red snapper taken by trawl and handline off the Texas coast. He determined age and growth rate from scales by assuming that growth checks were produced during the spawning season. Bradley and Bryan (1975) also sampled red snapper along the middle Texas coast with trawl and hook and line. They were unable to distinguish age classes by length frequencies and attributed that to an extended spawning season. Futch and Bruger (1976) used otolith readings to determine age and growth of red snapper off the coast of Florida.

This paper presents new information on growth of young snapper and relates that information to their occurrence on an artificial reef.

---

[1] University of Texas Marine Science Contribution No. 519.