



Recruitment variability and stochastic population growth of the soft-shell clam, *Mya arenaria*

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Abstract

Variability in recruitment is a striking feature of the life histories of most marine invertebrates and many fishes. The distribution of recruitment is typically lognormal rather than normal. It has been conjectured that such variation plays a major role in population growth of these species, but no complete stochastic demographic analysis has ever been reported. Here, we developed a set of deterministic and stochastic models for the clam, *Mya arenaria*. We constructed a size-classified, periodic matrix model to describe seasonal population dynamics, based on a mark-recapture study in Barnstable Harbor, MA, USA. In the deterministic model, an equilibrium recruitment rate of $ERR = 19.4$ recruits per adult was required to maintain constant population size. Periodic elasticity analysis showed that, at the ERR, fertility and larval survival accounted for 99% of the population growth rate λ . In a stochastic model with lognormally distributed recruitment, the stochastic growth rate $\log \lambda_s$ increased with increases in either $E(\log R)$ or $SD(\log R)$. The positive effect of $SD(\log R)$ is due to the highly skewed nature of the lognormal distribution. Variation in population size increases dramatically with increases in $SD(\log R)$, which makes it difficult to predict future population size. If variability in recruitment is high, quasi-extinction is nearly certain even when $\log \lambda_s$ is well above zero. Stochastic elasticity analysis shows that the contribution of adult growth and survival to λ_s increases dramatically when recruitment is variable. These results suggest that, for marine invertebrates with a lognormally distributed recruitment pattern, the amount of uncertainty in recruitment should be positively associated with adult life span.

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1. Introduction

Recruitment of offspring (defined as their survival to a specified age, size, or developmental stage) is a critical process in any population. Recruitment of marine invertebrates with planktonic larvae depends on survival in the plankton, finding an appropriate location

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to settle, and surviving from settlement to recruitment. These processes depend on multiple interacting biological and physical factors (Fraschetti et al., 2002; Gosselin and Qian 1997; Olafsson et al., 1994; Rumrill, 1990; Young et al., 1998). Stochasticity in environmental factors can lead to dramatic density-independent spatial and temporal variability in recruitment levels (e.g. in bivalves: Bachelet, 1986; Beukema et al., 2001; Goshima, 1982; Lima et al., 2000; Nakaoka, 1993; Pearson and Munro, 1991; Vahl, 1982). Environmental variability in recruitment is an integral part of the population dynamics of marine organisms.

Recruitment variability has been less studied for soft-substrate than for hard-substrate benthic fauna. The processes regulating recruitment seem to differ between these environments, and some authors have questioned the importance of recruitment variability in soft-substrate habitats (Ellien et al., 2000; Olafsson et al., 1994), although larval supply and post-settlement processes interact to create observed population structures (Lima et al., 2000). Often, conclusions about the importance of larval supply have been based on data relating the cohort strength of recruits to fluctuations in the adult population. A more powerful approach is to estimate the link between recruitment variability and population growth rate (Nakaoka, 1993, 1996, 1997; Noda and Nakao, 1996; Pfister, 1996). The shape of the recruitment distribution is an important but often neglected aspect of a stochastic model of recruitment (Nakaoka, 1997; Slade and Levenson, 1984).

In this paper, we examine the effects of recruitment variability on population growth of *Mya arenaria*, the soft-shell clam, using a stochastic matrix population model. *M. arenaria* is an important commercially harvested infaunal intertidal clam common in mudflats along the northeastern US. It lives for up to 12 years and spawns every year after about age two (Newell, 1991). A female *M. arenaria* may broadcast up to 10^6 eggs into the water column in the spring and the fall (Brousseau, 1978), but high mortality rates and larval transport can result in negligible larval settlement (Brousseau et al., 1982). Settlement and recruitment are extremely variable over time; Moller and Rosenberg (1983) and Beukema et al. (2001) reported coefficients of variation in *M. arenaria* recruitment of 143 (from 5 years of data) and 185 (from 27 years of data).

Interest in the management of this species has spurred several authors to formulate population

models. Brousseau and Baglivo (1984) used a matrix population model to calculate sensitivity of population growth rate to changes in vital rates, and matrix models have also been used to assess disease impact (Weinberg et al., 1997), and fisheries management strategies (Malinowski and Whitlatch, 1988). Brousseau and Baglivo (1984) and Malinowski and Whitlatch (1988) used their models to estimate an “equilibrium settlement rate” (ESR; given the distinction between settlement and recruitment, this might be better named the equilibrium recruitment rate, ERR), defined as the proportion of eggs spawned that must successfully survive their first year to maintain a constant population size (Vaughan and Saila, 1976). In the absence of independent measurement of recruitment, an analysis at the ESR provides information on the properties of a population at or near equilibrium. But, since the population is assumed to be at equilibrium in these models, equilibrium settlement rates but not population growth rates can be compared among sites, conditions, or studies. Brousseau et al. (1982) calculated that, for a Cape Anne, Massachusetts population of *M. arenaria*, only 0.0001% of eggs, which corresponds to about one recruit for every 10 adults, needed to survive each year to maintain constant population size. No settlers at all were detected in two out of the 3 years of their study, however, so in order to maintain the population, a much higher settlement must occur occasionally. None of the previous studies of *M. arenaria* have examined variation in recruitment, even though population growth and selection pressures are generally different between deterministic and stochastic models (Tuljapurkar, 1990; Caswell, 2001).

2. Methods

2.1. A deterministic model

We formulated a deterministic stage-classified, birth-pulse model with a pre-breeding census that projects the population from 1 year to the next by

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \quad (1)$$

where \mathbf{n} is a vector of stage abundances and \mathbf{A} is a constant projection matrix. We used an annual time step, but the matrix \mathbf{A} was constructed by multiplying

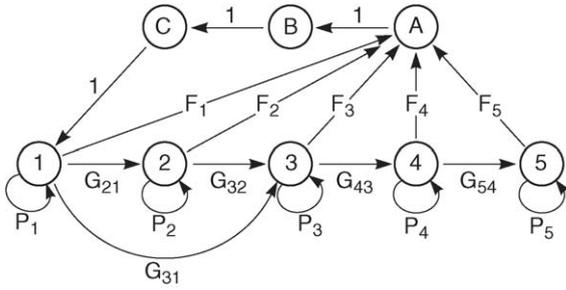


Fig. 1. The life cycle graph for *M. arenaria*. The circles indicate stages, and the arrows represent possible transitions: surviving and growing to a subsequent stage (G_{ij}), surviving and staying in the same stage (P_i), or fertility (F_i). Stages A, B, and C are dummy stages that produce the appropriate delay from reproduction to recruitment (see text).

four seasonal matrices:

$$\mathbf{A} = \mathbf{B}_{\text{spring}} \mathbf{B}_{\text{winter}} \mathbf{B}_{\text{fall}} \mathbf{B}_{\text{summer}} \quad (2)$$

$\mathbf{B}_{\text{spring}}$ describes growth, survival, and reproduction from March to June. The other matrices are similarly defined over 3-month intervals. This approach includes information on seasonal variation in vital rates into a model with an annual time step (Caswell, 2001).

Each of the seasonal matrices was size-classified, with classes 20–40 mm (stage 1); 40–50 mm (stage 2); 50–60 mm (stage 3); 60–70 mm (stage 4); and >70 mm (stage 5). The life cycle diagram (Fig. 1) shows the transitions possible from each season to the next using these parameters:

$$\mathbf{B}_h = \begin{pmatrix} 0 & 0 & 0 & F_1 & F_2 & F_3 & F_4 & F_5 \\ 1 & 0 & & & & & & \\ 0 & 1 & 0 & & & & & \\ & 0 & 1 & P_1 & & & & \\ & & 0 & G_{21} & P_2 & & & \\ & & & G_{31} & G_{32} & P_3 & & \\ & & & & 0 & G_{43} & P_4 & \\ & & & & & 0 & G_{54} & P_5 \end{pmatrix}, \quad (3)$$

$h = \text{spring, summer, } \dots$

The entries in the first row of \mathbf{B}_h are the fertilities, the entries on the diagonal are probabilities of surviving and staying in the same size class, the entries on the subdiagonals are probabilities of surviving and grow-

ing to larger size-classes. All other matrix entries are zero.

The stages A, B, and C are “placeholder stages” and are necessary because recruitment was defined as settlement and survival to age one, but the matrices project over a 3-month interval. In the absence of any information on seasonal survival of larvae or newly settled clams, the annual survival was incorporated into the F_i . The offspring then pass through stages A, B and C with probability one, arriving in stage one with the appropriate survival rate and at the proper time. Whether larval survival is incorporated into the F_i or allocated to the transitions between stages A, B, and C has no effect on population growth rate or its elasticity.

2.1.1. Parameter estimation

To estimate seasonal matrix parameters, growth and survival probabilities were measured in a mark-recapture study in Barnstable Harbor, Massachusetts (similar to Weinberg et al., 1997 and described in detail in Ripley, 1998). In March, 1995, 20 clams of each size class were collected from the intertidal mudflat and deployed in mesh bags. In June, September, and December, clams were removed from the bags, counted, measured, and redeployed. New clams were added at each sampling time to bring totals to 100 clams. Clams were counted and measured for the last time in March 1996.

Maximum likelihood estimates of the transition probabilities in \mathbf{B}_h were calculated as

$$\hat{b}_{ij} = \frac{t_{ij}}{n_j} \quad (4)$$

(Caswell, 2001), where t_{ij} is the number of clams starting the season in size class j and ending the season in size class i , and n_j is the number of clams in size class j deployed at the beginning of the season.

To calculate the fertilities, F_i , we used the “anonymous” reproduction method of allocating recruitment to size classes in proportion to their reproductive output (Caswell, 2001, p. 173). This method assumes that either the population is closed (larvae spawned by these adults recruit back to the same population) or that it is in equilibrium with a larger population with the same reproductive rate and size distribution. The F_i were calculated as $F_i = \phi_i R$, where ϕ_i is the proportion of population reproductive output contributed by size class i and R is the recruitment (number of stage 1 clams at

$t + 1$ per adult at t). To estimate the ϕ_i , the number of eggs per ripe female were counted from histological preparations of gonad samples, using standard stereological methods (Weibel, 1979). Samples were taken from five clams per size class in March, June, August and September 1995 because gametogenesis begins in the winter in Cape Cod populations of *M. arenaria*, and spawning occurs from March to September. Most reproduction occurs in the summer so we incorporated reproduction only in the June-to-August matrix. The ϕ_i were calculated from the mean number of eggs per ripe individual in stage i , Φ_i :

$$\phi_i = \frac{\Phi_i}{\sum_i \Phi_i}. \quad (5)$$

No ripe females in stage two were present in the samples taken. A value for stage two clams was calculated using clams collected in Quincy, Massachusetts (Ripley, 1998), which were nearly identical to those of Barnstable Harbor clams in other size classes.

In the absence of an estimate of recruitment, we treated R as a free parameter and calculated population growth rate as a function of R , from which we estimated the ERR and the elasticity of λ at the ERR.

2.2. A stochastic model

The stochastic version of the matrix model includes variability in recruitment, and can be written

$$\mathbf{n}(t + 1) = \mathbf{A}_t \mathbf{n}(t) \quad (6)$$

where one or more elements of \mathbf{A}_t vary randomly over time. Specifying such a model requires a stochastic model for states of the environment and a rule associating vital rates with each environmental state so that matrices may be calculated (Caswell, 2001). For *M. arenaria*, the variability in recruitment (larval settlement and survival to age one) is orders of magnitude higher than variability in other matrix elements (Goshima, 1982). This variability is known to be important. Nakaoka (1997) found that it had a greater impact on population growth than did stochasticity in shell growth rates. Eigenvalue sensitivity to recruitment has also been shown to be higher than sensitivity to adult survival in a deterministic model for *M. arenaria* (Brousseau and Baglivo, 1984). Thus we chose to include variation only in recruitment.

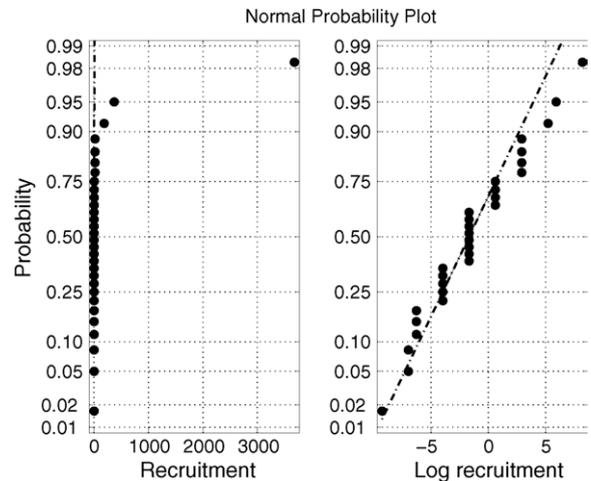


Fig. 2. Normal probability plots of recruitment (left) and log-transformed recruitment (right). Data are from Goshima (1982). Normally distributed data points would fall on the dashed line.

In the absence of evidence of a more complex pattern, we modelled recruitment, R , as varying independently from year to year. The distribution of R was estimated from a study by Goshima (1982) of *M. arenaria* in Japan. He provides densities of adults and of newly settled clams at five sites (less than 400 m apart) over 6 years. We estimated R as one-half the ratio of newly settled clams to adult clams (to nearest order of magnitude) at each time and site from Fig. 7 in Goshima (1982). If the plotted value for either young clam density or adult density was zero, we assumed that in twice the area one clam would be found, and so used 0.5 for our calculations. This was done to avoid division by, or taking the log of, zero. The division by two was necessary because we count only female offspring in the model. The resulting estimates of settlement range over seven orders of magnitude.

The settlement data are extremely variable, highly skewed, and much closer to a lognormal than a normal distribution (Fig. 2). The lognormal has often been used to describe the distribution of recruitment (Fogarty, 1993; Hennemuth et al., 1980). If survival from settlement to recruitment at age 1 is constant or is also lognormally distributed, then recruitment will be lognormal and we use the lognormal distribution throughout our calculations.

Many of our results reflect the properties of this distribution, so we summarize some of those here. The

lognormal distribution is right skewed, with a long tail of large values. If $Y = \log X$ is normally distributed, with mean $E(Y)$ and variance $V(Y)$, then X is lognormally distributed, with mean

$$E(X) = \exp\left(E(Y) + \frac{V(Y)}{2}\right) \tag{7}$$

Because the distribution is skewed, the mean $E(X)$ is a misleading measure of central tendency. A much better measure is the median, $M(X) = \exp(E(Y))$, which is also equal to the geometric mean of \mathbf{X} . As the variance $V(Y)$ increases, with the median $M(X)$ fixed, the distribution becomes more skewed, and that skew increases $E(X)$ according to (7).

In our calculations, we will vary both the overall “typical” level and the variability in recruitment. For the former calculations, we will vary $M(R) = E(\log R)$, keeping $V(\log R)$ constant. For the latter, we will fix $M(R)$ and vary $V(\log R)$. This is an appropriate model if the lognormal distribution (or something similar) actually describes the pattern of recruitment.

The matrices \mathbf{A}_t were constructed by randomly drawing R_t from an appropriate lognormal distribution; all other parameters were held constant. An example of a time-series of recruitment values generated by this process shows many years with low recruitment and a few years with high recruitment.

3. Deterministic model: analysis and results

The seasonal matrices, \mathbf{B}_h , are shown in Table 1. Survival probabilities are high, but growth is low, in the winter. In the summer, survival is low but growth is high. Spring conditions allow high growth and high survival, while in the fall, survival and growth are intermediate. The relative reproductive rates of the stages are $\phi_1 = 0.02$, $\phi_2 = 0.05$, $\phi_3 = 0.08$, $\phi_4 = 0.25$, and

$\phi_5 = 0.60$, demonstrating the strong size-dependence of reproductive output.

The population growth rate is the dominant eigenvalue λ of the annual matrix \mathbf{A} . The equilibrium recruitment rate (ERR) is the value of R at which $\lambda = 1$; we find numerically that ERR = 19.41 recruits per adult.

To explore the effect of perturbations on λ , we calculated the elasticities (i.e. proportional sensitivities) of λ to the entries of the seasonal matrices. The elasticity matrix for season h is

$$\mathbf{E}_{\mathbf{B}_h} = \left(\frac{b_{ij}^{(h)}}{\lambda} \frac{\partial \lambda}{\partial b_{ij}^{(h)}} \right) \tag{8}$$

where $b_{ij}^{(h)}$ is the (i, j) entry of \mathbf{B}_h (Caswell and Trevisan, 1994). The entries of $\mathbf{E}_{\mathbf{B}_h}$ give the proportional change in λ resulting from a small proportional change in b_{ij} in season h . Because the elasticities sum to one within each season, the elasticity of λ to $b_{ij}^{(h)}$ can be interpreted as the proportional contribution of $b_{ij}^{(h)}$ to population growth.

Elasticities depend (weakly) on the parameter values, so we calculated them from the matrices at the ERR. The results thus apply to populations with growth rates close to $\lambda = 1$, although the elasticity patterns for values as low as $\lambda = 0.6$ and as high as $\lambda = 1.4$ are nearly indistinguishable from those at the ERR (results not shown here). Calculations for periodic elasticities are detailed in Caswell and Trevisan (1994) and (Caswell 2001, Chapter 13).

The results of the elasticity analysis are shown in Fig. 3. In the summer, when spawning occurs, elasticities are highest for fertilities. In the other seasons, the highest elasticity is for survival of the cohort of juveniles growing from one placeholder stage to the next. In no season are the elasticities to adult growth and survival parameters high. In terms of contributions to population growth, this population relies on repro-

Table 1

Seasonal projection matrices \mathbf{B}_h , h = summer, . . . , spring. Only parameters in the lower right 5×5 corner of the 8×8 matrix are displayed here: P_i (on the diagonal) and $G_{i,j}$ (on the subdiagonal) for stages 1–5

Summer					Fall					Winter					Spring				
0	0	0	0	0	0.11	0	0	0	0	0.71	0	0	0	0	0	0	0	0	0
0.1	0.06	0	0	0	0.33	0.23	0	0	0	0.21	0.82	0	0	0	0.87	0.18	0	0	0
0.3	0.18	0	0	0	0	0.23	0.69	0	0	0.07	0.18	0.79	0	0	0.13	0.65	0.41	0	0
0	0	0.21	0.19	0	0	0	0	0.14	0	0	0	0.11	0.89	0	0	0	0.35	0.63	0
0	0	0	0.1	0.26	0	0	0	0	0.45	0	0	0	0.06	0.95	0	0	0	0	0.05

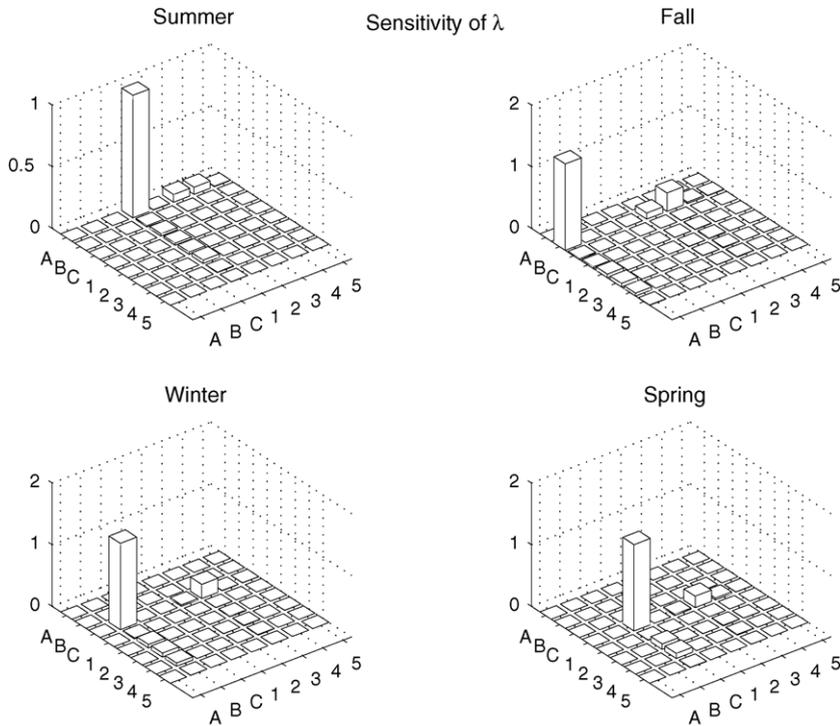


Fig. 3. Elasticity of the deterministic population growth rate λ to changes in the entries of the seasonal matrices \mathbf{B}_h . The elasticities are calculated at the equilibrium recruitment rate ERR.

duction, settlement, and recruitment. The growth and survival of adults make negligible contributions to λ . As we will show in the next section, this conclusion depends critically on the constancy of recruitment.

4. Stochastic model: analysis and results

4.1. Population growth rate

Population growth in a stochastic environment is described by the stochastic growth rate

$$\log \lambda_s = \lim_{T \rightarrow \infty} \frac{1}{T} \log \|\mathbf{A}_{T-1} \cdots \mathbf{A}_1 \mathbf{A}_0\| \quad (9)$$

Subject to mild restrictions on the matrices and the model of the environment, $\log \lambda_s$ is the long-term average growth rate of every realization with probability one (Furstenberg and Kesten, 1960; Cohen, 1976; Tuljapurkar and Orzack, 1980; Caswell, 2001, Chapter 14), and measures fitness in stochastic life history mod-

els (Tuljapurkar, 1990). If $\log \lambda_s \leq 0$ the population will eventually decline toward extinction (with probability 1) and if $\log \lambda_s \geq 0$ the population will eventually increase.

In the long run, the logarithm of population size $N(t)$ is normally distributed with mean $t \log \lambda_s$ and variance $t \sigma^2$. Thus, the parameter σ^2 measures the rate at which the variance of $\log N(t)$ increases. In models such as ours, with environments independent and identically distributed, σ^2 can be estimated as

$$\sigma^2 = 2(\log \mu - \log \lambda_s) \quad (10)$$

where $\log \mu$, the growth rate of the mean population, is the log of the dominant eigenvalue of the average projection matrix.

Fig. 4 shows the dependence of $\log \lambda_s$ on recruitment and on the variability of recruitment. These values were calculated using (9) with $T = 20,000$. Combinations of $E(\log R)$ and $SD(\log R)$ that lead to a stationary population ($\log \lambda_s = 0$) are contoured on Fig. 4.

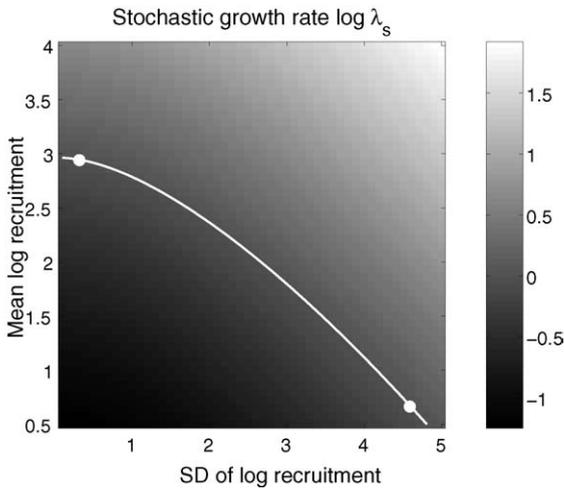


Fig. 4. The stochastic growth rate $\log \lambda_s$ as a function of $SD(\log R)$ and $E(\log R)$. The contour indicates combinations of $SD(\log R)$ and $E(\log R)$ for which $\log \lambda_s = 0$. The solid circles on the contour indicate parameter combinations used for the stochastic elasticity calculations shown in Fig. 7.

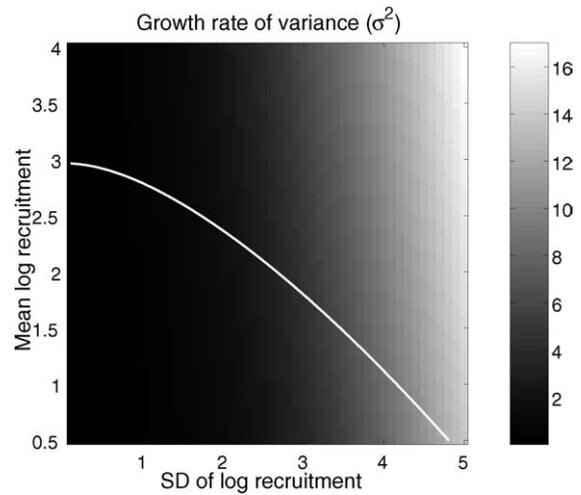


Fig. 5. The growth rate σ^2 of the variance in the log of population size, as a function of $SD(\log R)$ and $E(\log R)$. The contour indicates combinations of $SD(\log R)$ and $E(\log R)$ for which $\log \lambda_s = 0$.

The stochastic growth rate increases with increases in both $E(\log R)$ and $SD(\log R)$. It is not surprising that population growth increases with a higher median level of recruitment. It is no surprise that the growth rate should increase with increases in the typical recruitment level. But the positive response to variability is not necessarily expected. It is a direct consequence of the lognormality of R ; it would not occur if R were normally distributed, for example. The skewness of the lognormal means that increasing variability while holding the median fixed produces rare large recruitment events. These rare episodic events (which are typical of data on recruitment in marine organisms) can support positive long-term population growth.

The parameter σ^2 measures the rate of divergence of trajectories starting from a given initial condition. Since asymptotically

$$V(\log N(t)) = \sigma^2 t \tag{11}$$

the higher the value of σ^2 , the more rapidly uncertainty in population size increases with time. Fig. 5 shows σ^2 as a function of $E(\log R)$ and $SD(\log R)$. While σ^2 increases slightly with $E(\log R)$, it is determined mostly by the variability of R . The values for σ^2 are very large. As a point of reference, if $\sigma^2 = 2$, the 95% confidence

interval on population size after only 10 years spans seven orders of magnitude. This implies that even moderate levels of recruitment variability make it impossible to predict future population size with any certainty. Any such prediction would have to be statistical in nature.

4.2. Quasi-extinction probability

Although the population will eventually increase if $\log \lambda_s > 1$, stochasticity will lead to short-term temporary population declines. A decline to a proportion θ of the initial population size is called quasi-extinction (Ginzburg et al., 1982). The probability of this event is

$$P_q(\theta) = \begin{cases} 1 & \text{if } \log \lambda_s \leq 0 \\ \exp\left(\frac{2 \log \lambda_s \log \theta}{\sigma^2}\right) & \text{if } \log \lambda_s > 0 \end{cases} \tag{12}$$

Fig. 6 shows the probability of quasi-extinction for $\theta = 0.1$; that is, the probability that a population will decline to 10% of its initial size. When recruitment variability is low, P_q drops abruptly from 1 to near 0 when $\log \lambda_s$ becomes positive. But when variability is higher ($SD(\log R) > 2$), P_q remains close to 1 even when $\log \lambda_s$ is well above zero. This emphasizes

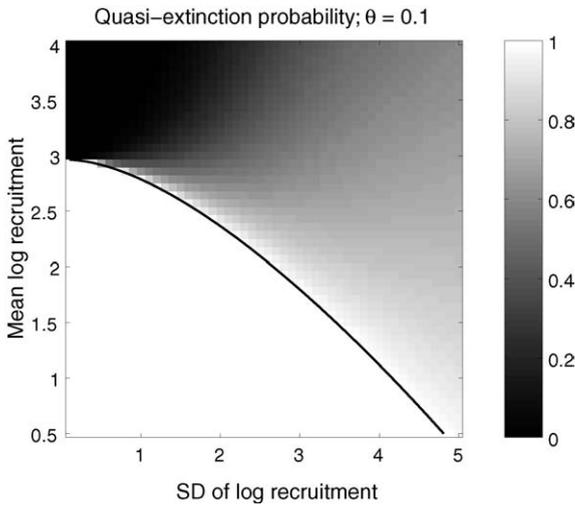


Fig. 6. The quasi extinction probability $P_q(\theta)$ for $\theta = 0.1$, as a function of $SD(\log R)$ and $E(\log R)$. The contour indicates combinations of $SD(\log R)$ and $E(\log R)$ for which $\log \lambda_s = 0$.

the highly fluctuating nature of this population, except when recruitment variability is very low.

4.3. Elasticity analysis

To evaluate the effects of demographic perturbations in a stochastic environment, we need to calculate the elasticities of the stochastic growth rate λ_s . The elasticities of λ_s to the entries of the annual matrix \mathbf{A} in (2), i.e.

$$\frac{\partial a_{ij}}{\partial \lambda_s} \frac{\partial \lambda_s}{\partial a_{ij}}$$

could be calculated directly using Tuljapurkar’s algorithm (Tuljapurkar, 1990). But the entries of \mathbf{A} are complicated mixtures of survival, growth, and reproductive parameters from the seasonal matrices, and changes in the a_{ij} have no simple biological interpretation (Caswell and Trevisan, 1994). Instead, we want the stochastic analogue of the seasonal elasticity matrix (8):

$$\mathbf{E}_{\mathbf{B}_h}^{(\text{stoch})} = \left(\frac{b_{ij}^{(h)}}{\lambda_s} \frac{\partial \lambda_s}{\partial b_{ij}^{(h)}} \right), \quad h = \text{spring}, \dots \tag{13}$$

Table 2

Proportional contributions to population growth rate from classes of matrix elements

	Environment		
	Constant	Low variability	High variability
Reproduction	0.25	0.15	0.11
Larval survival	0.74	0.45	0.34
Adult survival and growth	0.01	0.41	0.55

Values in a constant environment are elasticities of λ , calculated at the ERR, to the matrix entries. Values in low and high variability environments are elasticities of λ_s , calculated at the points on the ERR contour in Fig. 4, to the matrix entries.

The entries of $\mathbf{E}_{\mathbf{B}_h}^{(\text{stoch})}$ give the proportional sensitivity of λ_s to a proportional change in the (i, j) entry of the matrix for season h , keeping all other parameters fixed. These elasticities sum to 1 within each season, so they can be interpreted (with care) as the contributions of the corresponding parameter to stochastic population growth. The extension of Tuljapurkar’s formula needed for this calculation is given by Caswell (2005).

The deterministic elasticities were evaluated at the ERR in Fig. 3. Corresponding stochastic results could be obtained using any combination of $E(\log R)$ and $SD(\log R)$ along the $\log \lambda_s = 0$ contour in Fig. 4. We selected two such points, one corresponding to high $E(\log R)$ and low variability, the other to low $E(\log R)$ and high variability (Fig. 4). Fig. 7 shows the resulting elasticities.

Comparing Figs. 3 and 7 reveals a striking pattern. In a constant environment, the survival and growth of adult clams make almost no contribution to population growth (Fig. 3). As recruitment variability increases, the contributions of adult survival and growth become larger, and the contributions of reproduction and larval survival become smaller (Fig. 7). Summing the relevant elasticities and dividing by four gives the proportional contribution of each type of matrix element to population growth rate (Table 2). In a stochastic environment, *M. arenaria* relies about equally on the survival and growth of adults and the reproduction and survival of larvae.

5. Discussion

Due to its highly skewed distribution, recruitment variability increases the stochastic population growth

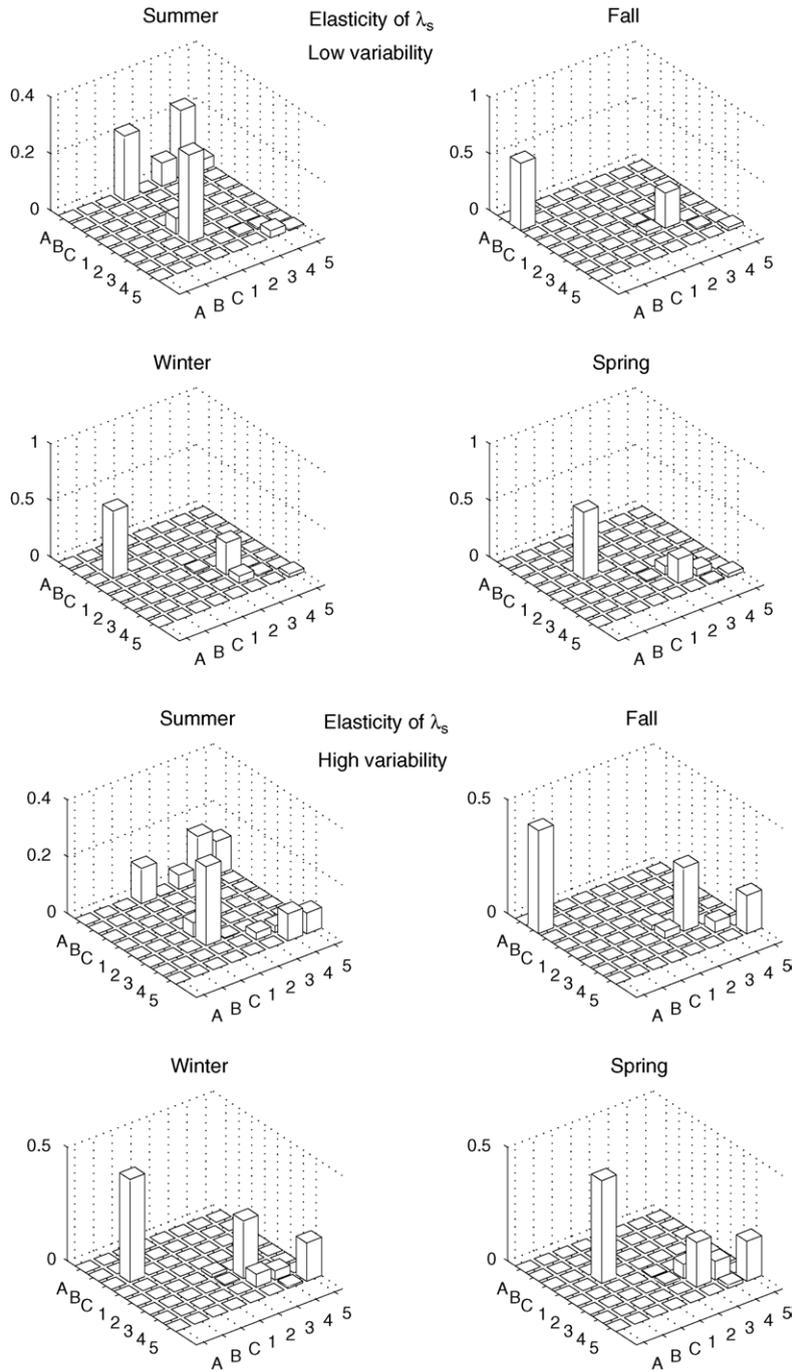


Fig. 7. The elasticity of the stochastic growth rate λ_s to changes in the entries of the seasonal matrices \mathbf{B}_h , $h = \text{summer}, \dots, \text{spring}$. Elasticities are calculated at the points indicated on the $\log \lambda_s = 0$ contour in Fig. 4. Above: low $SD(\log R)$, high $E(\log R)$. Below: high $SD(\log R)$, low $E(\log r)$.

rate, and such variability might be a critical factor determining population performance. Observed large standing stocks of *M. arenaria* may be due to one good year of recruitment, but the population persists because clams live long enough that another good recruitment event is likely to occur before they die. This phenomenon has also been observed for a subtidal snail, *Umbonium costatum* (Noda and Nakao, 1996). In that study, positive population growth was dependent on 1 year out of eight with unusually high recruitment success. Fogarty (1993) examined recruitment distributions in fish and concluded that, when recruitment was distributed lognormally, the occasional strong year-class would predominate the adult population. Adult survival through variation in the environment has been termed a storage effect and is recognized as a bet-hedging strategy (Warner and Chesson, 1985; Stearns, 1992).

Although there is debate as to what distribution (normal, lognormal, beta, gamma, etc.) best describes recruitment of marine invertebrates and fish (Shelton, 1992; Taillie et al., 1995), many observed distributions are certainly closer to lognormal than to normal. Nakaoka (1997) found that recruitment in the clam *Yoldia notabilis*, which is similar in life history to *M. arenaria*, fitted a lognormal distribution more closely than a normal distribution. Many other authors have reported massive recruitment in 1 or 2 years out of the several studied, also suggesting a strongly skewed pattern (e.g. Caffey, 1985; Coe, 1956; Beukema et al., 2001; Loosanoff, 1964; Noda and Nakao, 1996).

Our results do not contradict the well-known negative relationship between stochastic growth rate and variability in vital rates when the *mean*, rather than the median, is kept fixed (Efford, 2001; Tuljapurkar, 1990). In our model, increasing recruitment variability while keeping the median recruitment fixed increases $\log \lambda_s$. Because the lognormal distribution is skewed, this manipulation also increases the mean. This increase is not an artifact; it is a real biological property of skewed distributions like the lognormal, and seems paradoxical only because of an excessive familiarity with the normal distribution. If one kept the mean recruitment fixed while increasing the variability, the median would decline, and the mean would become a more and more atypical value.

In a variable environment, there exists a continuum of values of $E(\log R)$ and $SD(\log R)$ that lead to a

stationary population ($\log \lambda_s = 0$). The location of a population on this continuum determines the pattern of elasticities. In a constant environment, 99% of the elasticity of λ is accounted for by fertility and juvenile survival. However, as variability increases, the fate of adults makes a larger and larger contribution. Our results agree with those of Jonsson and Ebenman (2001), who also found that elasticity to adult survival was higher than to fertility in iteroparous life histories under variability. Managers of shellfish populations could use this information to help achieve sustainable harvest by setting maximum rather than minimum size limits for harvest, especially in situations with high variation in recruitment.

Previous analyses of deterministic models (Brousseau et al., 1982; Malinowski and Whitlatch, 1988) have likely underestimated the potential for growth in *M. arenaria* populations. Equilibrium settlement rates have been used to estimate larval survival, under the assumption that the population is in equilibrium (Vaughan and Sails, 1976; Brousseau et al., 1982). Given the importance of variation in recruitment demonstrated here, we believe that calculation of ESR provides little information on settlement impact on population structure and is probably useless for shellfish management. Furthermore, because variability in recruitment makes population size dramatically less predictable and increases the risk of population crashes, estimating recruitment variability is critical for fisheries planning. The large values of σ^2 observed in this population also show that such planning will be essentially statistical in nature, because the population is inherently unpredictable even a short time in the future.

Further research is needed to characterize recruitment dynamics of marine invertebrates, to describe year-to-year and spatial variability more completely. Characterizing how recruitment varies with different developmental modes, such as planktotrophic, lecithotrophic, or brooded larvae, will also be helpful to understanding marine invertebrate population dynamics. Our model incorporated fertility, survival in the plankton, and survival to age 1 year into one variable parameter (R). It would be interesting to investigate the relative contributions to variability from the three components separately, since there is evidence for several marine invertebrates that cohort strength in soft-substrate environments is determined

by post-settlement processes rather than by larval supply (Ellien et al. 1999; Flach, 2003; Olafsson et al., 1994).

Our results suggest that the advantage of broadcasting larvae may not be solely in greater dispersal (Palmer and Strathmann, 1981; Strathmann and Strathmann, 1982), but also in sporadic large recruitment successes. For animals with a life span long enough to sustain populations through several years with no settlement, broadcast spawning is a gamble with potentially big payoffs. It is possible that broadcast spawning evolved because of, rather than in spite of, its variability. Alternatively, the low parental investment of energy into planktonic larvae, which leads to variability in settlement, may have selected for long life span. Our results suggest that the skewness of the recruitment distribution might be related to the reproductive life span of the organism. In other words, adults should live long enough that there is a high probability of a successful recruitment event occurring during their life span. This idea was proposed by Murphy (1968) for clupeid fish, discounted by Roff (1981) and resurrected by Longhurst (2002), but has not been investigated for marine invertebrates.

5.1. Comparison to other modelling studies

Several aspects of our analysis are unique in comparison to other stochastic demographic analyses (reviewed by Nakaoka, 1996; Caswell, 2001; Fieberg and Ellner, 2001). We use a seasonal stochastic model to include processes operating throughout the year, and introduce the elasticity analysis of the stochastic growth rate to seasonal perturbations (see also Smith et al., 2005). This lets us document the effects of recruitment variability on the contributions of adult and juvenile vital rates to population growth and persistence. Our results have implications for management of shellfish populations and for our understanding of effects of environmental variability in marine habitats. Recent studies of population viability analysis have emphasized the importance of choices made in modelling environmental stochasticity. Wichmann et al. (2003), for example, have shown that extinction risk depends on the pattern of periodicity in fluctuating environments, and our results emphasize the importance of connections between the variance and the expectation of recruitment. A better understanding of the types of environmental

stochasticity to which small populations are subject is critical to understanding extinction risk.

Although recruitment plays a key role in our analysis, this is not a “model of recruitment,” but rather a model of population dynamics in which, of all the biological processes involved (survival, development, individual growth, fertility) we have chosen to focus on stochasticity in recruitment and its effects on population growth and on the elasticity of population growth. Two related approaches, both of which involve recruitment, but which ask quite different questions, are prominent in the literature.

First, Roughgarden and colleagues (e.g., Roughgarden et al., 1985, 1988, 1993; Possingham and Roughgarden, 1990; Alexander and Roughgarden, 1996; Shkedy and Roughgarden, 1997; Connolly and Roughgarden, 1998, 1999) have examined the effects of recruitment on competition for space, especially in species that (unlike *M. arenaria*) live on hard substrates. These models include both discrete-time and continuous-time formulations. They separate planktonic larvae from benthic adults, and may include age or size (Pascual and Caswell, 1991) structure within the adult component. They have been extended to include advection and diffusion processes that determine the transport of larvae (Roughgarden et al., 1988; Possingham and Roughgarden, 1990; Alexander and Roughgarden, 1996; Shkedy and Roughgarden, 1997; Connolly and Roughgarden, 1998, 1999). In these models, recruitment is determined by an interaction between the availability of larvae (determined by reproduction and by larval transport) and the availability of space for settlement (determined by the growth of settled adults). Stochastic variation in larval availability has not been explored in these models, although Roughgarden et al. (1993) included stochastic disturbances and Shkedy and Roughgarden (1997) explored consequences of fluctuations in upwelling processes.

A second set of questions arises from considering benthic populations on a scale such that recruitment is completely independent of local reproductive processes. Such recruitment-subsidized populations can be described by matrix models with inputs (Hughes, 1990; Hughes and Tanner, 2000; Pfister, 1996). These models can provide no insight into the role of larval production, since it is assumed to happen elsewhere, but they do predict adult population size and struc-

ture as a function of larval input. Attention to date in these studies has focused on the equilibrium population densities resulting from a balance of constant recruitment and the constant mortality of the settled individuals. The results of fluctuating recruitment levels, and to mixtures of local and subsidized recruitment, are only beginning to be examined (Caswell, unpublished data).

We believe that stochastic, seasonal matrix population models provide a powerful tool for addressing the demographic consequences of recruitment, but no single modelling approach can capture all the effects of recruitment (or, indeed, any other biological process) on population dynamics.

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