Chapter 3

Age of sexual reproduction in *B. schlosseri*

The previous chapter discussed correlations among life history traits (growth, reproduction, mortality) of semelparous and iteroparous *B. schlosseri*. However, understanding the underlying causes for the correlations requires a model. This chapter first describes the progression of modeling techniques and then presents a model to study the age of first sexual reproduction in both morphs of *B. schlosseri*.

3.1 Comparative Studies

The comparative approach involves broad comparisons among similar groups of taxa (preferably conspecific populations) in different environments (Stearns 1976, Grosberg 1982). Where applicable, the comparative approach provides the best type of explanation for the basic life-history traits (Stearns 1976). However, an implicit assumption is that the environment is the primary cause of any differences in life-history traits. Also, different species or populations often have different genetic histories which can have a significant effect on the life-history traits (Grosberg 1982). Since both morphs of *B. schlosseri* live together in the same environment, the basic premise of the technique does not hold.
3.2 Genetic Models

Genetic models, as opposed to correlational studies, attempt to directly model the genetic influences on life-history traits. Many genes acting in combination likely determine life-history traits (Grosberg 1982, Stearns 1977). However, most genetic models examine only one locus. Three, apparently intractable, reasons disallow generalization to the multi-loci model required. First, two or more loci can have wildly nonlinear interactions (Wright 1968 cited in Stearns 1977). Second, the selective value of an allele can depend on the frequency of alleles at other loci (Wright 1968 cited in Stearns 1977). Finally, two sorts of evidence indicate that changes in only a few regulatory genes, rather than many structural changes, can establish large differences between species: (a) men and chimpanzees differ strongly in morphology, ecology, behavior, and life-history traits, yet the electrophoretically detectable structural loci are more similar between chimpanzee and men than between pairs of sibling fruit flies or mammals (King and Wilson 1975 cited in Stearns 1977); (b) serum albumins of frogs and placental mammals have evolved at the about the same rate while the chromosome number of mammals has changed 20 times faster than that of frogs, paralleling the much greater morphological diversity of mammals (Wilson et al. 1974 cited in Stearns 1977). The above complications will likely keep multi-loci genetic models unrealistic for a long time, perhaps forever (Stearns 1977). As discussed in section (2.2.1), no simple mode of genetic inheritance fits the data, thus making genetic modeling difficult.

An alternative technique, biometrical (or quantitative) genetics, provides a direct, although imprecise, method to study life-history. The biometrical approach compares the phenotypic resemblance among individuals of known relatedness. This allows the separation of the observed phenotypic variance into genetic and non-genetic (environmental) components. However, the technique has three major difficulties: (1) it does
not specify the genetics of inheritance and allows easy interpretation only of the additive
effects of alleles at different loci; (2) it assumes that phenotypic distributions satisfy a
normal distribution which is not true for threshold characters; (3) its results are specific
to the time, population, and environmental conditions in the study.

3.3 Life-History Theory

Yet another approach is life-history theory. It directly ignores the genetics but instead
models a basic tenet of evolution: survival of the fittest where fitness is a measure of the
expected number of descendents (Bell 1980; Stearns 1976).

3.3.1 The Characteristic Equation

Consider a population formed from the descendents of one organism. The growth rate
of that population will depend on its age structure and the probabilities of giving birth
and of dying at different ages. Assume a stable age distribution has been reached. Let
\( l_x \) = the probability of surviving to age \( x \), and \( b_x dx \) = the number of female progeny of
females of age \( x \) to \( x + dx \). Newborns at time \( t \) have parents of age \( k \) that were themselves
born at time \( t - k \) and survived to age \( k \). Thus, letting \( n_0(t) = \) the number of newborn
at time \( t \), we have

\[
n_0(t) = \int_0^\infty n_0(t - k) l_k b_k dk. \tag{3.1}
\]

If further we assume that the number of newborn progeny changes exponentially in time,
then

\[
n_0(t) = Ce^{rt}, \tag{3.2}
\]

where \( r \) = the intrinsic growth rate of the population. Fisher (1930), considering the
number of genes instead of the number of individuals, used the symbol \( m \) which he called
the Malthusian parameter. However, for consistency, I will use \( r \) throughout this thesis.
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Charlesworth (1973) showed that in an age-structured, diploid, random-mating population, any nonrecessive mutant which decreases $r$ will be eliminated by selection, while a mutant which increases $r$ will be selected. Thus, maximizing $r$ will also maximize the fitness of a population.

Substituting (3.2) into (3.1) yields

$$Ce^{rt} = \int_{0}^{\infty} Ce^{r(t-k)}l_k b_k dk,$$

$$1 = \int_{0}^{\infty} e^{-rk}l_k b_k dk. \quad (3.3)$$

The above equation, called Lotka's equation or the characteristic equation, was first derived by Lotka (1913) (also see Stearns (1976) for the derivation). The equation relates the mortality and fecundity schedule of a population in a stable age distribution with its intrinsic growth rate $r$. This equation is a basic tenet of most subsequent life history theoretical work (Stearns 1976).

### 3.3.2 Discrete forms of Characteristic Equation

Although (3.3) uses continuous time, organisms reproduce in discrete time intervals. A discrete form of (3.3), where the polling is done after mortality but before birth, is (Leslie 1948; Schaffer and Rosenzweig 1977)

$$1 = \sum_{x=0}^{\infty} \lambda^{-(x+1)} B_x l_x. \quad (3.4)$$

where

$\lambda$ = the intrinsic growth rate,

$B_x$ = the number of offspring produced by a $x$ year-old individual which themselves survive to the next breeding season,

$l_x$ = the mean survival rate to age $x$. 
Note that $\lambda = e^r$. Also, if $c_x$ is the probability that an $x$ year-old's new born progeny survives to the next breeding season, then $B_x = c_x b_x$. Thus, $B_x$ is the effective fecundity of an $x$ year-old individual (Schaffer 1974).

The life-history equation may also be stated in matrix form. Let $n_i(t)$ be the number of individuals of age between $i$ and $i + 1$ alive in the population at the beginning of the breeding season in year $t$. Define the vector $N(t)$ such that

$$
N(t) = \begin{pmatrix}
n_0(t) \\
n_1(t) \\
\vdots \\
n_m(t)
\end{pmatrix}
$$

where $m$ is the maximum age of the organism. Also, define $M(t)$, the population matrix, as

$$
M = \begin{bmatrix}
B_0 & B_1 & \ldots & B_{m-1} & B_m \\
p_0 & 0 & \ldots & 0 & 0 \\
0 & p_1 & \ldots & 0 & 0 \\
\vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & \ldots & p_{m-1} & 0
\end{bmatrix}
$$

where $p_i = l_{i+1}/l_i$ is the probability that an $i$ year-old survives to the next breeding season. We then have the relation

$$
N(t + 1) = MN(t).
$$

Note that the $\lambda$ from (3.4) is the dominant eigenvalue of $M$ (Leslie 1945). Thus, for most $M$ and any initial arbitrary age distribution we have that

$$
N(t) \propto \lambda^t N_1 \text{ as } t \to \infty,
$$
where $N_i$ is the associated eigenvector of $\lambda$ (Leslie 1945; Schaffer and Rosenzweig 1977). Existing life-history models assume that disturbances are always sufficiently infrequent that this limiting approximation is valid (Schaffer and Rosenzweig 1977).

### 3.3.3 Principle of Allocation

With no constraints on $l_k$ and $b_k$ in (3.3), the characteristic equation implies that the most fit organism imaginable (i.e., maximum $r$) starts to reproduce continuously immediately after birth and experiences no mortality. That no such creature exists implies that $l_k$ and $b_k$ cannot independently have any value. In real life, resources, or at least their uptake, are limited. Thus, organisms face a tradeoff of allocation of resources among activities (growth, maintenance, reproduction, etc.). The dominant doctrine of theoretical and experimental research into this tradeoff is the "principle of allocation" (Grosberg 1982). The principle of allocation's major prediction is that current reproduction imparts a cost in terms of subsequent survival and/or fecundity (Murphy 1968; Schaffer 1974; Schaffer and Rosenzweig 1977; reviewed in Stearns 1976, 1977, 1980). Energy not allocated to reproduction can presumably be used for other activities (growth, maintenance, predator avoidance, etc.) that enhance future reproduction.

### 3.3.4 Fisher's Reproductive Value

The tradeoffs limiting reproduction cause the value of reproduction to depend on the age class, as first shown by Fisher (1930). The idea is analogous to that of present value of money invested at compound interest. The reproductive value of a female at age $x$, denoted by $v_x$, is the average number of young the female can expect to have over the remainder of its life, discounted back to the present. It is given by

$$v_x = \frac{e^{rx}}{l_x} \int_x^\infty e^{-rt} l_x b_x dt.$$  (3.9)
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(Fisher 1930). In discrete form, it is

\[ v_x = \frac{\sum_{t=1}^{k} \lambda^{-t+1} l_t B_t}{l_x \lambda^{-x}}, \]

where \( k \) is the maximum age of a reproductive individual (Leslie 1948).

Reproductive value allows the characterization of different age classes as to their "worth" in terms of their contribution to the intrinsic growth rate of the population, \( r \). However, the reproductive value of a female is the present value of her future daughters only with a stable age distribution (Leslie 1948).

3.3.5 Cole's Model and Extensions

Cole

Differing reproductive values with age implies that the age of first reproduction and the reproductive effort are important considerations. If the reproductive value decreases quickly enough with age, then the optimal action would be for the organism to sacrifice itself to reproduce the maximum amount possible. Cole (1954) was the first to theoretically study the conditions under which this type of reproduction, called "semelparity" or big-bang reproduction, is superior to reproducing several times, called "iteroparity" or repeated reproduction (Cole 1954, Gadgil and Bossert 1970). For simplicity, in his study, he assumed that semelparity and iteroparity can be represented by annuals and perennials respectively. First, Cole discretized Lotka's equation (3.3) to get

\[ 1 = \sum_{x=\alpha}^{\omega} e^{-r_x} l_x b_x. \]

where \( \alpha \) and \( \omega \) are, respectively, the start and end of the reproductive period.

Consider an organism that begins producing at the age of \( \alpha \) with a constant mean litter size of \( b \). Also, assume zero mortality from birth to age \( \omega \) so that \( l_x = 1 \) for \( 1 \leq x \leq \omega \).
\( \omega \). In the case of semelparity with reproduction at the first time step only, \( \omega = \alpha = 1 \) so (3.11) becomes \( e^r = b \) which gives

\[
 r = \ln b. \tag{3.12}
\]

The most extreme case of iteroparity would be each organism producing \( b \) offspring each year for eternity. In this case, \( \alpha = 1 \) and \( \omega \to \infty \) so (3.11) results in

\[
 r = \ln(b + 1). \tag{3.13}
\]

Comparing (3.12) to (3.13) led Cole (1954) to make the famous statement (called "Cole's paradox"):

For an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproduction habit would be exactly equivalent to adding one individual to the average litter size (p.118).

Most organisms, especially those with large litters, could presumably easily evolve to produce one more progeny. Thus, why does iteroparity exist? Cole (1954) provided a partial answer to this problem by studying the effect of delayed age at first reproduction on the proportionate increase in \( r \) in going from a semelparous to an infinite iteroparous life history. As the age of first reproduction increases, so does the percentage gain from iteroparity (Cole 1954; Fig. 2) implying that iteroparity would be favoured in organisms with longer prereproductive periods.

However, in Cole's (1954) analysis some of the assumptions, particularly the lack of mortality and infinite life span, are highly unrealistic. Later researchers expanded this basic model by making the assumptions more tenable or by creating more general models with Cole's model as a special case.
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Gadgil and Bossert

Gadgil and Bossert (1970) criticized Cole's assumption of no mortality. With a large litter size, mortality during the first year of life would be relatively higher than later on. Assuming that an annual organism just basically replaces itself after its first reproduction, they stated that

\[ l_1 b_1 \sim 1. \]  \hfill (3.14)

For an annual species, this gives

\[ 1 = e^{-r} l_1 b_1, \]

\[ r = \ln(l_1 b_1). \]  \hfill (3.15)

For a perennial, assuming constant litter size and no mortality beyond the first time step, (3.15) gives \( l_x b_x = l_1 b_1 \approx 1 \) for all ages. The discretized characteristic equation (3.11) yields

\[ r = \ln(l_1 b_1 + 1). \]  \hfill (3.16)

Using (3.14), (3.16) becomes

\[ r \sim \ln(2l_1 b_1). \]  \hfill (3.17)

Thus, Gadgil and Bossert (1970) suggested that Cole's result be modified to read:

For an annual species the absolute gain in the Malthusian parameter which could be achieved by changing to the perennial reproductive habit would be approximately equivalent to doubling the average litter size (p.11).

However, Stearns (1976) pointed out that their semelparous (annual) and iteroparous (perennial) organisms are not comparable since the semelparous population is just replacing itself \( (r = 0) \) while the iteroparous population is growing rapidly \( (r = \ln 2 \approx 0.69) \).
Gadgil and Bossert’s argument of the annual organism just barely replacing itself applied to perennials actually leads to the equation

$$1 = \sum_{x=1}^{\infty} l_x b_x.$$

Finally, if the semelparous organism were to double its average litter size without affecting mortality (highly unlikely in real life), then the basic assumption (3.14) would no longer hold!

Gadgil and Bossert also studied the result using computer simulation, finding that in all cases examined the reproductive effort increases with age. However, Fagen (1972) constructed a model where the reproductive effort at first decreased! This shows the potential danger of trying to generalize from computer studies.

Bryant

Bryant (1971) criticized Gadgil and Bossert (1970) for using a special case ($r = 0$) to establish a general result. Also, the result in (3.16) shows that the benefit of iteroparity is equivalent to adding one to the effective litter size. This actually makes it a special case of Cole’s result. If a general mortality term is used instead of just mortality in the first time period, then the annual species needs to add less than or equal to 1 to the effective litter size to match the iteroparous advantage.

Bryant (1971) considered an example with the survivorship being exponentially distributed, $l_x = e^{-ux}$, where $u$ is the mortality rate. The result for an annual species is $r = \ln(b) - u$ and for a perennial it is $r = \ln(b + 1) - u$. Thus, Cole’s statement still holds for this example.
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Charnov and Schaffer

Charnov and Schaffer (1973) expanded on previous work by considering variation in adult and juvenile mortality. They considered two species: one annual and the other perennial. Both reproduce once at the end of the year and produce $B_a$ and $B_p$ progeny, respectively. Both the annual and perennial offspring have a survivorship the first year of $C$. The perennial has an adult survivorship of $P$ per year.

The relation between the number of individuals next year $N(t+1)$ and the number of individuals this year $N(t)$ for the annual species is:

$$N(t + 1) = B_a CN(t)$$

(3.18)

while for the perennial species it is:

$$N(t + 1) = B_p CN(t) + PN(t)$$

$$= (B_p C + P)N(t).$$

(3.19)

If both populations increased at the same rate, then we would have $B_a C = B_p C + P$ or

$$B_a = B_p + P/C.$$  

(3.20)

Cole's (1954) and Bryant's (1971) results are special cases of the above equation with $P = C = 1$ and $P = C < 1$ respectively. Thus, Charnov and Schaffer (1973) suggested that Cole's result be modified to read:

For an annual species, the absolute gain in intrinsic population growth rate that can be achieved by changing to the perennial habit would be exactly equivalent to adding $P/C$ individuals to the average litter size.

Usually $P \gg C$ (for examples, see Deevey 1947 or Caughley 1966 (cited in Charnov and Schaffer 1973)). In these environments, the evolution of iteroparity is likely.
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Charnov and Schaffer (1973) next considered prereproductive time where the age of first reproduction is in year $K$ ($K > 1$). The resulting equation is

$$\frac{B_i}{B_s} = 1 - \frac{P}{\lambda} = R_i \quad (3.21)$$

where $B_i$ and $B_s$ are the iteroparous and semelparous clutch sizes, respectively. Prereproductive time, $K$, affects $R$ only through its effect on $\lambda$. Iteroparity is favored by low $R$. Actually, (3.20) and (3.21) are different forms of the same equation (Young 1981) showing that prereproductive time does not qualitatively change the life-history results.

Young

Young (1981) created a more general model that included Cole’s (1954) and Charnov and Schaffer’s (1973) results as special cases. The model allows for prereproductive time, between reproduction time, and adult survivorship to vary independently of one another. Senescence for the iteroparous life type is included by a maximum number of reproductive episodes before death. It is assumed that the intrinsic growth rate ($\lambda$), and juvenile survivorship and prereproductive development time (PDT) are the same for both genotypes. The yearly juvenile survivorship need not be constant, but the proportion of offspring that survive to reproductive age is assumed to be constant. Finally, Young (1981) assumed a stable age distribution. The resulting model simplifies to:

$$\frac{B_s}{B_i} = \frac{1 - (P/\lambda)^x}{1 - (P/\lambda)Z} \quad (3.22)$$

where

$x = \text{maximum number of reproductive episodes before senescence.}$

$Z = \text{time between reproductive episodes.}$

Assuming that $P/\lambda < 1$ and letting $Z = 1$ and $x \to \infty$ in (3.22) results in Charnov and Schaffer’s equation (3.21).
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Discussion

Cole's model prediction that iteroparity would be favoured in organisms with longer pre-reproductive times applies to B. schlosseri. However, even the more general assumptions of Young's model do not fit B. schlosseri very well. For example, mortality is assumed to be solely a function of the age of the organism, but, as shown in Fig. 3.4, the mortality rate also depends strongly on the time of year. The next section discusses several models that add the effects of environmental change.

3.3.6 Stochastic Models

Cohen

Cohen (1966) constructed a long-term growth rate optimization model that accounted for a randomly varying environment. In particular, he modeled an annual plant. The seeds can germinate the next year, with the resulting plants producing seeds according to environmental conditions, or the seeds can lay dormant, but with a certain portion decaying. The number of seeds present is defined by the recursive relationship

\[ S_{t+1} = S_t - S_t G - D(S_t - S_t G) + G Y_t S_t. \]  

(3.23)

where

\( S_t = \) the number of seeds at time \( t \),

\( G = \) the fraction that germinates each year,

\( D = \) the fraction that decays each year,

\( Y_t = \) the average number of seeds per germinated seedling. It is assumed to be a random variable depending on environmental conditions but independently of the population density.
Figure 3.4: The proportion of a cohort of field colonies that survives from settlement to sexual maturity. Open bars show semelparous survival and solid bars show iteroparous survival. The caption and figure are from Fig. 5, Grosberg 1988.
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Over a sequence of $N$ steps, this becomes
\[ S_N = S_0 \prod_i [(1 - G)(1 - D) + GY_i]^{n_i}, \tag{3.24} \]
where $n_i$ is the number of times that a particular $Y_i$ occurred during the $N$ steps. Taking logarithms, dividing by $N$, and letting $N \to \infty$ results in
\[ \lim_{N \to \infty} \frac{\log S_N}{N} = \sum_i P_i \log [(1 - G)(1 - D) + GY_i] \tag{3.25} \]
where $P_i$ is the probability associated with $Y_i$ and $\lim(\log S_N/N)$ is the mathematical expectation of the specific growth rate of the seed population.

Analysis of (3.25) indicates that a necessary condition for $G_{max} < 1$ (where $G_{max}$ is the value of $G$ giving maximum growth) is
\[ \bar{Y} \left(1 - \frac{\sigma_Y^2}{\bar{Y}^2}\right) < 1 - D. \tag{3.26} \]
Thus, it becomes advantageous to postpone the germination of some fraction of the seeds only when the variance of the yield becomes large enough in relation to the mean yield and the viability of the seeds. If instead of seeds germinating, one considers progeny reproducing, then this analysis shows that iteroparity is favored in a variable environment. The spreading of reproduction over time to enhance the chance of reproducing during a favourable period is known as "bet-hedging" (Cohen 1966).

Murphy

Using computer simulation, Murphy (1968) found that under conditions of uncertain survival of prereproductives and relatively stable survival of organisms during the reproductive stage, iteroparity is advantageous. This is true both with respect to competition between species and within a freely interbreeding population. Conversely, either high or variable adult mortality encourages early reproduction, high fecundity, and few reproductive periods or even only one.
Schaffer

Schaffer (1974) showed that if, in constant environments, repeated breeding (iteroparity) is the optimal reproductive strategy, environmentally induced variation in reproductive success favors reductions in per capita reproductive output. Conversely, variations in postbreeding survival among adults favor greater investments in breeding. However, the principal issue is the age-specificity of the fluctuations (i.e., do they principally affect immature adults?).

3.3.7 Discussion

Unfortunately, these stochastic models do not allow the specification of an arbitrary temporal variation, thereby seriously limiting their usefulness. The basic result of these models is that iteroparity is favoured in more variable environments. However, since the B. schlosseri semelparous and iteroparous morphs live together, their environments, including any variability, are essentially identical. Also, the range of survival to first reproduction, as shown in Fig. 3.4, is from .04 to .23 for iteroparous morphs and .03 to .24 for semelparous morphs suggesting that the morphs do not experience a large difference in the degree of changes in mortality.

Life-history theory is predicated on the assumption that mortality and sexual reproduction are based solely on age. However, for most clonal organisms, including Botryllus schlosseri, this is an inappropriate assumption. Studies have shown that postzygotic age is at best weakly correlated with the development, behaviour, and reproductive success of clonal organisms (Jackson 1985). Partial mortality among genets decouples age and size. Thus, a small individual can be old and likewise a large individual can be young (Grosberg 1982). However, neither age nor size is necessarily an accurate predictor of the start of sexual reproduction. Rather, the onset is determined by a complex interaction
between intrinsic factors such as age, size, and physical condition and extrinsic factors such as density, food availability, physical disturbance, and season (Harvell and Grosberg 1988). Thus, a stochastic, state-based modeling technique is needed to model the important characteristics of *B. schlosseri*. Dynamic programming, as described below, is used here.

3.4 Dynamic Programming

3.4.1 Definition and Assumptions

Dynamic programming is a stochastic, state-based modeling approach that allows one to consider dynamic behaviour in organisms. It has several components. First is the specification of the organism's "state". A state variable represents any characteristic of an organism that affects its fitness (Mangel and Clark 1988). Basically, the technique views an animal choosing the behavioural option that will maximize its fitness based on its current state. However, it is not being suggested that an organism actually consciously solves the optimization problem. Rather, the organism is assumed to "breed true" so that by natural selection the behavioural sequence with the greatest fitness will predominate (Houston and McNamara 1988).

In its common discrete form (for continuous time dynamic programming, see Mangel 1985; Bertsekas 1976), dynamic programming divides time, $t$, into discrete units from 1 to $T$, where $T$ is the final time step in the calculations. The basic concept is the *lifetime fitness function* $F$, defined for $1 \leq t \leq T$ as (Mangel and Clark 1988):

$$F(x,t,T) = \max E \left\{ \sum_{j=t}^{T-1} R(X(j), A(j), j, w(j)) + \phi(X(T)) | X(t) = x \right\} \quad (3.27)$$

with the maximization taken over possible values of actions $A(j), j = t, t+1, \ldots, T-1$ and
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\( X(t) = \) the state (possibly multi-dimensional) of the organism at time \( t \),
\( x = \) the current state of the organism,
\( A = \) the set of possible actions of the organism,
\( R = \) the reward function that denotes the increase in fitness (i.e. current reproduction) from a given action,
\( w = \) a random variable (such as the environment) that affects the state or reward function,
\( \phi = \) the terminal fitness function that denotes the fitness of the organism after the last time step.

The equation for updating \( X \) for \( t < T \) is (Mangel and Clark 1988):

\[
X(t + 1) = G(X(t), A(t), t, w(t)), \tag{3.28}
\]

where \( G \) includes the state dynamics and constraints as appropriate.

3.4.2 Solution Techniques

From (3.27), we have

\[
F(x, T, T) = \phi(x). \tag{3.29}
\]

Next, consider \( t = T - 1 \). Assuming that \( w_1 = w(T - 1) \) and \( x = X(T - 1) \), then (3.28) becomes

\[
X(T) = G(x, A, T - 1, w_1). \tag{3.30}
\]

Thus, (3.27) gives

\[
F(x, T - 1, T) = \max_A E_w \{ R(x, A, T - 1, w_1) + F(G(x, A, T - 1, w_1), T, T) \}, \tag{3.31}
\]

where \( E_w \) is the expectation over values of \( w \). By repeating the above procedure, we get for \( t = T - 1, T - 2, \ldots, 1 \) that

\[
F(x, t, T) = \max_A E_w \{ R(x, A, t, w) + F(G(x, A, t, w), t + 1, T) \}. \tag{3.32}
\]
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This is the general dynamic programming equation (Mangel and Clark 1988) that is normally used in actually computing a solution. Note that the solution is calculated iteratively backwards in time. As Kierkegaard (Bertsekas 1987) said "Life can only be understood going backwards, but it must be lived forwards."

Each iteration provides both the maximal future fitness, \( F(x, t, T) \), and the optimal strategy \( A^* = A^*(x, t) \). The optimal strategy depends on both the current state, \( x \), and the time \( t \). This strategy specification, called feedback control policy (Mangel and Clark 1988), allows the organism to dynamically determine the optimal action. However, the question of whether strategies that use the entire previous state history can be superior to strategies that use just the current state naturally arises. The answer is no (Bertsekas 1978; also see Mangel and Clark 1988 for the case of fixed \( n \) previous states). The intuitive reason is that the previous state history is implicitly accounted for in the current state value (Mangel and Clark 1988).

The maximization of fitness from time \( t \) forward in (3.32) is similar to Fisher's (1930) idea of reproductive value. In fact, the life-history equation is a special case of the dynamic programming technique but without the state dynamics. For example, Mangel (1987) shows how to reformulate the equation for the value of future reproduction from age \( a \), \( V(a) \):

\[
V(a) = e^{ra} \sum_{t=a}^{w} (l_t m_t / l_a) e^{-rt}
\]

to allow the use of dynamic programming.

3.4.3 Advantages and Disadvantages

Dynamic programming is more than just another technique to solve life-history equations since it widely applicable to many different problems in biology (see Mangel and Clark 1988). Being state-based, it uses more biologically relevant parameters than other
modeling techniques (Mangel and Clark 1988). Also, dynamic programming has the additional flexibility of modeling behavioral responses to environmental fluctuations and uncertainty. Integrating the results of actions with qualitatively different effects on fitness into a common currency allows the easy comparison of different behavioural alternatives. Dynamic programming can easily handle difficult constraints like integer or discrete sets (Bertsekas 1987). In the calculation procedure, for each time step and each state value, the optimal action and the corresponding fitness value are calculated. This makes the globally optimal solution readily available.

The flexibility of dynamic programming, however, may create problems. In an attempt to try modeling nature’s intricacies, researchers often devise complex models that are incomprehensible. Unfortunately, it is difficult to prevent people from abusing powerful scientific techniques (Clark 1989).

As the dimension of the state space increases, the solutions, both numerical and analytical, of the dynamic optimization problems increase in difficulty. Called the curse of dimensionality, it is an inherent feature of all dynamic optimization problems (Bellman 1957; Mangel and Clark 1988; Houston and McNamara 1988). For example, in the algorithm given in (3.32), the fitness is calculated for all state variable values and all times. Thus, assuming that each variable has the same number of possible values, the procedure requires an order of \( T \cdot A \cdot V^N \) calculations and \( V^N \) storage. Here \( T \) is the number of time steps, \( A \) is the number of actions, \( V \) is the number of state variables and \( N \) is the number of possible values. Thus, as the number of state variables, \( V \), increases, the number of calculations and storage requirements grows very rapidly (Mangel and Clark 1988).

Gradient-based optimization methods allow the use of more state variables than dynamic programming. However, the use of gradient methods entails several disadvantages.
The major limitation is that the methods do not give feedback control that can incorporate observations of random events as they become available. Also, the optimization model must be computed repeatedly for each different set of initial values. In comparison, with dynamic programming a single computation of the model gives the optimal policies for a range of initial values of the state variables and for all possible values of the random variables, such as the weather. Also, dynamic programming models incorporate fixed costs directly without extra computation (Shoemaker 1981).

A potentially limiting factor in dynamic programming is the use of discrete time steps. Note that only a single state transition and a single behavioural decision occurs in each time unit. Nonetheless, even in cases where state transitions occur at random times, it is usually possible to use discrete-time dynamic programming by choosing a sufficiently short time unit (Mangel and Clark 1988). However, the number of calculations increases linearly with $T$ so computational time limitations might limit the reduction of the time step.

Often, models that gain realism by adding more parameters or interactions between parameters (dynamic programming does both) end up telling us more and more about less and less. In other words, they become less general (comment by E. Smith in Houston and McNamara 1988, p.150). Nonetheless, any principles revealed by the model can be checked for generality against a variety of data or even with different models.

3.5 The Model

3.5.1 Background Information and Assumptions

In all the previous optimization models listed, the implicit assumption of only a single mode of reproduction is often violated by clonal organisms (Caswell 1985). Most clonal organisms reproduce both sexually and asexually. This raises the question of whether
the basic unit of selection is the single zooid or the whole colony. Asexual reproduction ensures a common genetic ancestry among all the zooids. It thus acts like growth in non-clonal organisms. Apart from somatic mutations and extrachromosomal factors, all zooids are identical genetically. Urbanek (1973) states that it is widely accepted that somatic mutations have rather minor evolutionary value. Also, mutations do not usually result in instantaneous speciation “because the gametes carrying the new mutation are not reproductively isolated from those carrying the ‘parental’ growth gene” (Mayr 1963; 1970 p. 251 cited in Urbanek 1973). Also, Boardman (1973) asserts that somatic mutations are probably of negligible phenotypic expression in most groups. Thus, I will ignore the effects of somatic mutations in the model.

*Botryllus schlosseri* rarely propagate clonally. Grosberg (1982, 1988) only saw two colonies fragment among more than 3,000 studied. Thus, the vast majority of colonies start from a sexually produced larva. The basic unit of selection would therefore be the colony. As such, the fitness of a colonial organism is measured, as with non-colonial organisms, by the relative numbers of descendent colonies (or genes) that it contributes to future generations (Harper 1985).

Although the age of first sexual reproduction is determined by a complex interaction of many factors, internal and external, the model will consider only the morph type, size, age, and time, since those seem to be the most important factors (Grosberg 1982, 1988).

The value of offspring depends on the age of reproduction. For example, early reproduction in a growing population leads to a proportionately greater contribution to population growth (Lewontin 1965 (cited in Grosberg 1982)). Although the population of *Botryllus schlosseri* is not on average growing over the years, the iteroparous and semelparous morphs have seasonally specific periods of population growth and decline. However, the standard dynamic programming model (see eq. 3.4) considers the fitness being the total expected lifetime reproductive output. In the model, I equate fitness to
something similar to Fisher’s (1930) reproductive value; I assume that the most fit organism leaves the largest number of descendents at time $T$ in the limiting case as $T \to \infty$. However, this definition is not appropriate in stochastic environments (e.g., Cohen 1966; Stearns 1977; Mangel and Clark 1988; Yoshimura and Clark 1991). I have no data or evidence for significant yearly changes at Eel Pond. Thus, apart from seasonal changes, the model ignores environmental stochasticity.

Section (2.1) describes the synchronization of the asexual and sexual cycles. Thus, all times are given in units of generations.

As described in section (2.3), the growth rate until sexual reproduction is approximately exponential. However, for both iteroparous and semelparous colonies, the growth rate decreases several generations before sexual reproduction (Fig. 3.5 - for iteroparous colonies, this decrease is most noticeable in the 1 August graph). The model assumes that the colony stores energy for reproduction during the generation just before reproduction, resulting in no growth then. Also, as described in section (2.3), Brunetti and Copello (1978) found that the growth rate fell in later generations until it stabilized around a constant value. Although some, or even all, of this growth decrease could result from production of sexual organs, the model allows the growth rate to change at a fixed age, and then drop at a fixed rate for several generations until it reaches 1.0 at a defined maximum size.

The length of a generation varies inversely with the water temperature (Fig. 3.6). At Woods Hole, over the reproductive period, the water temperature roughly increases linearly until August and then linearly decreases (Grosberg, personal communication). Fig. 3.7 shows a May to mid-November growing season. Thus, I assumed the approximate temperature and generation length schedule shown in Table 3.2, resulting in the dates for each generation given in Table 3.3.

Mortality depends on many factors, with the most important ones for Botryllus
Figure 3.5: Growth trajectories of eight cohorts (each composed of 10 colonies). The solid circles show trajectories for semelparous colonies; the open circles show trajectories for iteroparous colonies. The caption and figure are taken from Fig. 3, Grosberg 1988.
Figure 3.6: The relationship between the mean duration of an asexual generation and temperature. The error bars denote ranges. The caption and figure are taken from Fig. 2, Grosberg 1982.
Figure 3.7: The seasonal mean daily settlement of *B. schlosseri* per 100 cm² plate. The caption and figure are taken from Fig. 5, Grosberg 1982.
schlosseri being size, age, time, and sexual reproduction. The effect of sexual reproduction on mortality in iteroparous colonies is ignored since I don't have any data to use. I assume that the other three factors act independently, so that total survival is the product of survival from each of these factors. So that time-dependent mortality would be non-negative, I used the mortality schedule at the time of maximum survivorship to define the time dependent mortality. For iteroparous colonies, this is the time period September 1-15 while for semelparous colonies it is September 16-30 (Fig. 3.4). Since per zooid mortality is almost constant, mortality due to all zooids dying from chance events decreases almost exponentially with increasing size (Grosberg, personal communication; Jackson 1985; Harvell and Grosberg 1988). However, large, sexually mature colonies also have a large mortality due to an age effect. Table 2.1 gives the life-history table for iteroparous morphs. The semelparous colonies' life table up to sexual maturity can be obtained from Fig. 3.4. Determining the optimal age of first sexual reproduction requires knowledge of the mortality if the colony does not reproduce at its usual age. However, that information is not known for semelparous colonies since they invariably die after a single reproductive episode. I assume that mortality in older colonies is due to a cumulative effect of metabolism. This is implied for several reasons: (a) high growth rates in iteroparous colonies are correlated with fewer clutches being produced (Grosberg

Table 3.2: Temperature and generation length schedule.

<table>
<thead>
<tr>
<th>Month</th>
<th>Temp. (°C)</th>
<th>Gen. Length (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>June</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>July</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td>Aug.</td>
<td>25</td>
<td>5</td>
</tr>
<tr>
<td>Sep.</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td>Oct.</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>Nov.</td>
<td>10</td>
<td>18</td>
</tr>
</tbody>
</table>
Table 3.3: Approximate dates for the end of each generation.

<table>
<thead>
<tr>
<th>Gen. #</th>
<th>Date End</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>May 18</td>
</tr>
<tr>
<td>2</td>
<td>June 5</td>
</tr>
<tr>
<td>3</td>
<td>June 14</td>
</tr>
<tr>
<td>4</td>
<td>June 23</td>
</tr>
<tr>
<td>5</td>
<td>June 29</td>
</tr>
<tr>
<td>6</td>
<td>July 5</td>
</tr>
<tr>
<td>7</td>
<td>July 11</td>
</tr>
<tr>
<td>8</td>
<td>July 17</td>
</tr>
<tr>
<td>9</td>
<td>July 23</td>
</tr>
<tr>
<td>10</td>
<td>July 29</td>
</tr>
<tr>
<td>11</td>
<td>August 3</td>
</tr>
<tr>
<td>12</td>
<td>August 8</td>
</tr>
<tr>
<td>13</td>
<td>August 13</td>
</tr>
<tr>
<td>14</td>
<td>August 18</td>
</tr>
<tr>
<td>15</td>
<td>August 23</td>
</tr>
<tr>
<td>16</td>
<td>August 28</td>
</tr>
<tr>
<td>17</td>
<td>September 2</td>
</tr>
<tr>
<td>18</td>
<td>September 8</td>
</tr>
<tr>
<td>19</td>
<td>September 14</td>
</tr>
<tr>
<td>20</td>
<td>September 20</td>
</tr>
<tr>
<td>21</td>
<td>September 26</td>
</tr>
<tr>
<td>22</td>
<td>October 2</td>
</tr>
<tr>
<td>23</td>
<td>October 11</td>
</tr>
<tr>
<td>24</td>
<td>October 20</td>
</tr>
<tr>
<td>25</td>
<td>October 29</td>
</tr>
<tr>
<td>26</td>
<td>November 15</td>
</tr>
</tbody>
</table>
1982); (b) the mortality increase in sexually mature colonies is imputed to weakening from abnormally elevated metabolic activity (Brunetti 1974); (c) as shown in Fig. 3.5, overwintering colonies, with a low metabolic rate in early spring, live longer than colonies that do not overwinter; (d) Starving colonies grow more slowly and live longer (Grosberg 1982). Since semelparous colonies grow at almost double the rate of iteroparous colonies, and semelparous colonies first reproduce at about age 6, for age 6 on, I used the combination of 2 iteroparous age-dependent mortality values, starting at age 9, the usual minimum age for sexual reproduction. The numbers are undoubtedly inaccurate, but I believe that the idea of increasing mortality is correct so the modeling results will give useful qualitative information. Mortality of both iteroparous and semelparous planktonic larvae is unknown (Grosberg, personal communication). Thus, without anything else to use, I assume that planktonic survivorship is proportional to the corresponding survival to sexual maturity (Fig. 3.4), with the proportionality constant being such that \( r \approx 0 \).

After overwintering, colonies have different mortality and growth patterns. First, about 90% of semelparous and iteroparous colonies survive the winter (Grosberg 1982, 1988). Also, the growth rate is less than one for about 4 generations and then it is slightly greater than one for about 3 generations before the growth rate returns to approximately the pre-winter amount (see Fig. 3.5). A lack of food causes this early spring growth retardation (Grosberg, personal communication). From the Fig. 3.5 data for the September to October cohorts for the first 4 generations after winter, I noticed that, for both semelparous and iteroparous colonies, the rate of size decrease (i.e. size of colony at time \( t - 1 \) divided by the size of the colony at time \( t \)) is very nearly a linear function of the logarithm of the size of the colony. In particular, I found that \( y \approx .167x + .45 \) where \( y \) is the rate of size decrease and \( x \) is the natural logarithm of the colony size in number of zooids. I don't know any theoretical reason why a relationship of this nature should hold, but qualitatively it makes sense since larger colonies (larger \( x \)) will, under
starvation conditions, be able to obtain more food from the meager supply passing by, but less per zooid. Larger colonies decreasing in size more quickly than smaller colonies means that all the colonies' sizes tend towards the equilibrium size (i.e. $y = 1$). Grosberg (personal communication) has said that after winter, colonies "reset" to the same size basically regardless of age. Although the data in Fig. 3.5 only covers roughly the range of 50 to 400 zooids, without other information, I extrapolated the size reduction equation to all colony sizes. This means that the equilibrium point, $y = 1$, occurs for a colony of about 27 zooids. Thus, if the equation were to also apply to colonies started during the early spring, then their growth rates, especially for semelparous colonies, would be severely curtailed. However, Fig. 3.5 and 2.3 shows that the growth rate is near normal, although Fig. 2.3 shows that a portion of the June 1-15 colonies had average growth rates (buds/zooid) between 0.5 and 1.5. I can only assume that somehow, such as through good location, the young colonies can get enough to eat. For the fifth to seventh generations of slow growth, I assume, based on the Oct. 1 cohort data in Fig. 3.5, that the growth rate increases by .3 compared to that predicted for the same size in the first four generations.

As mentioned previously, I assume that the age dependent mortality depends on the cumulative metabolic rate. Since overwintering colonies live about 6 or 7 generations longer (Grosberg 1982 (Table 5)) and there is about a 7 generation period when colony size is decreasing or not increasing much, I assume that the effective age for age dependent mortality increases in proportion to the metabolic amount over the maintenance amount.

Although Grosberg (1982) states that iteroparous colonies continue to sexually reproduce every generation once they begin, this is not necessarily true after overwintering (Grosberg, personal communication). Thus, the model does not require that iteroparous colonies continue reproducing once they start on the likelihood that, apart from after winter, it is optimal for them to do so anyway.
As stated earlier, the model assumes that there is no growth during the generation before reproduction as the colony stores energy. For overwintering colonies, although they are starving, there is no significant decrease in fecundity (Grosberg 1982 (Table 5)). Instead, the model assumes, on energetic considerations, that the growth rate during a generation of reproduction would be the non-reproduction growth rate divided by the normal growth rate. This would be consistent with the growth stoppage before reproduction in non-overwintering colonies.

3.5.2 Equation and Parameter Values

As stated earlier, the purpose of the model is to predict the optimal age of first sexual reproduction. The dynamic programming technique assumes that this age depends on maximizing the "fitness" $F$ given by:

$$F(s, a, t) = [1 - m(s, a_e, t)] \max\{F(s_1, a + 1, t_n),
$$

$$rF(s_2, a + 1, t_n) + \beta ksp(t_n)F(1, 0, t_n)\}.$$  \hspace{1cm} (3.33)

where the first maximand corresponds to the decision "grow" and the second to "reproduce". The variables and parameters are described on the following pages.
Chapter 3. *Age of sexual reproduction in* *B. schlosseri*

<table>
<thead>
<tr>
<th>Variable</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>s</em></td>
<td>Size of colony in number of zooids.</td>
</tr>
<tr>
<td><em>a</em></td>
<td>Age of colony in number of asexual generations.</td>
</tr>
<tr>
<td><em>t</em></td>
<td>Time of the year in asexual generations.</td>
</tr>
</tbody>
</table>
| \(F(s,a,t)\) | The maximum discounted expected future reproduction of a colony of size *s*, age *a* and at time *t*. Thus, \(F(1,0,t_n)\) is the maximum discounted expected future reproduction of a new colony at time *t*.
<p>| (m(s,a_e,t)) | The mortality of the colonies given by the relation (1 - m(s,a_e,t) = (1 - m_s(s))(1 - m_a(a_e))(1 - m_t(t))) (see below and parameter table). |
| <em>a_e</em>     | The effective age. As discussed previously, I assume that this depends on the cumulative metabolic rate above maintenance level. Thus, if the colony has positive growth potential at the current time <em>t</em>, then for the next generation, <em>a_e</em> increases by ((\text{growth potential for size } s \text{ at time } t) / (\text{maximum growth potential for size } s \text{ at any time})). With negative growth potential, <em>a_e</em> remains constant. In the computer program, <em>a_e</em> is calculated from the colony size at each time step from the colony’s start to the current time. |
| <em>s_1, s_2</em> | Size of the colony, in number of zooids, if the colony does not or does reproduce (respectively) (see [1] below). |
| <em>t_n</em>     | The next asexual generation. If <em>t</em> &lt; <em>T_v</em> (see parameter table), then <em>t_n</em> = <em>t</em> + 1, else <em>t_n</em> = 1. |
| <em>p(t_n)</em>  | The time dependent survivorship factor of the planktonic larvae. Since I have no data for this, I assume that it is equivalent to (1 - m_t(t)) (see parameter table below). |</p>
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Interpretation</th>
<th>Assumed Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r$</td>
<td>Colony type</td>
<td>0 (semelparous)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1 (iteroparous)</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Number of embryos per zooid (average from June 15 to Sep. 15 data in Table 5, Grosberg 1982)</td>
<td>10.10 (semelparous)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.24 (iteroparous)</td>
</tr>
<tr>
<td>$k$</td>
<td>The basic survival factor of planktonic larvae</td>
<td>.001 and .002</td>
</tr>
<tr>
<td>$T_y$</td>
<td>The number of asexual generations in a year</td>
<td>26</td>
</tr>
<tr>
<td>$m_s(s)$</td>
<td>Size dependent mortality (see [2])</td>
<td>.75 .25 .01 0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(for semelparous colonies)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.61 .37 .13 .02 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(for iteroparous colonies)</td>
</tr>
<tr>
<td>$m_s(a_s)$</td>
<td>Age dependent mortality (see [3])</td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0 .09 .40 .81 1.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(for semelparous colonies)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.03 .07 .07 .36 .52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.60 1.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(for iteroparous colonies)</td>
</tr>
</tbody>
</table>
Chapter 3. Age of sexual reproduction in B. schlosseri 60

\( m_t(t) \)  Time dependent mortality (see [4])

\[
\begin{array}{cccccc}
0.02 & 0.02 & 0.02 & 0.03 & 0.04 \\
0.05 & 0.07 & 0.11 & 0.15 & 0.17 \\
0.18 & 0.18 & 0.18 & 0.22 & 0.26 \\
0.22 & 0.18 & 0.13 & 0.08 & 0.03 \\
0 & 0 & 0 & 0 & 0 \\
0 & & & & & (for semelparous colonies) \\
0.12 & 0.14 & 0.16 & 0.18 & 0.16 \\
0.13 & 0.10 & 0.08 & 0.05 & 0.04 \\
0.04 & 0.01 & 0.01 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 \\
0 & & & & & (for iteroparous colonies)
\end{array}
\]

Notes:

[1] For times of normal growth (generations 8-26 for all colonies and generations 1-7 for colonies started the same year), \( s_1 = \alpha s \). For overwintering colonies during the first four generations, as discussed earlier, \( y = 0.167x + 0.45 \) where \( y = \frac{s_1}{s} \) and \( x = \ln s \). This gives \( s_1 = s(0.167\ln s + 0.45) \). For generations 5 to 7, the growth rate increases by \( 0.3 \) so we have \( \frac{1}{y} = \frac{1}{0.167\ln s + 0.45} + 0.3 \) which gives \( s_1 = s \left( \frac{0.167\ln s + 0.45}{0.065\ln s + 0.135} \right) \). In all cases, \( s_2 = \frac{\alpha}{\alpha} \).

[2] I used the assumption that size dependent mortality decreases exponentially with size. The values listed were obtained from using \( \alpha = 2.03 \) and a survival rate of 0.207 to sexual maturity (Grosberg 1988) for the iteroparous colonies and \( \alpha = 3.88 \) and a survival rate of 0.218 to sexual maturity (Grosberg 1988) for the semelparous colonies. The values given are for the size indices as described in the “Methods” section below.
Table 2.1 was used to determine the per generation age dependent mortality for iteroparous colonies. Each semelparous age dependent mortality was obtained by combining 2 iteroparous age dependent mortality values on the assumption, as discussed earlier, that the age dependent mortality is due to cumulative metabolic activity with that of semelparous colonies being roughly double that of iteroparous colonies.

The mortality to the age of first sexual reproduction relative to its maximum value, as given in Fig. 3.4, is used to determine the time dependent mortality. This mortality is assumed to occur equally over 9 generations for iteroparous colonies and over 6 generations for semelparous colonies. The values for the generations are interpolated from the cohort values given in Fig. 3.4.

Equation Analysis

Equation (3.33) has two important features. First, all terms contain the function $F$. Also, unlike the standard dynamic programming equation (3.27), no final time $T$ is used. Instead, (3.33) uses the implicit limiting behaviour as $T \to \infty$. But, unless the year-to-year growth rate is exactly 1, $\lim_{T \to \infty} F(s, a, t; T) = 0$ or $\infty$. Assuming a stable age and size distribution exists (at least on a year-to-year basis), then for $T \to \infty$, the distribution of progeny of a colony of any size and age will approach the stable age and size distribution. The only possible difference among different colonies will be the relative numbers of progeny in each class. In other words, $\lim_{T \to \infty} F(s, a, t; T)/F(1, 0, t; T) = L(s, a, t)$ for some finite function $L$. Thus, dividing (3.33) by $F(1, 0, t_n)$ results in:

$$F'(s, a, t) = [1 - m(s, a, t)] \max\{F'(s_1, a + 1, t_n),$$

$$rf'(s_2, a + 1, t_n) + \beta ksp(t_n)\}$$

(3.34)

where $F'(s, a, t_1) = F(s, a, t_1)/F(1, 0, t_n)$ for $t_1 = t, t_n$. Now, as $T \to \infty$, $F' \to L$. For simplicity, I have dropped the prime in the rest of the paper.
Approximations and Correlations With Previous Work

Equation (3.34) is in general too complex for analytic study and must be solved using a computer. However, knowledge about the behaviour of the equations can be gained from studying several simplifications to the equation. First, ignore the after winter size change, time dependence in mortality, and assume \( a_e = a \). Thus, size can be determined from the age so let \( m_s(a)m_s(s) = m(a) \). This gives (from (3.34)):

\[
F(s, a, t) = [1 - m(a)] \max\{F(s_1, a + 1, t_n),
\]
\[
rF(s_2, a + 1, t_n) + \beta ks\}. \tag{3.35}
\]

Assume that the organism first reproduces from some age \( a_1 \) to its maximum age \( A \) (\( a_1 = A \) for semelparous colonies). Let \( p_o(a) = 1 - m(a) \). Then the reproductive value of the organism at age \( a_1 \) will be

\[
F(s, a_1, t) = \beta ks p_s(a_1)\{1 + p_s(a_1 + 1) + p_s(a_1 + 1) \cdot p_s(a_1 + 2) + \ldots + p_s(a_1 + 1) \cdot p_s(a_1 + 2) \ldots p_s(A)\} \tag{3.36}
\]

Since \( l_x = \prod_{i=1}^x p_s(i) \), the equation can be rewritten as:

\[
F(s, a_1, t) = \beta ks \sum_{i=a_1}^A l_i/l_{i-1} \tag{3.37}
\]

which is basically the same as Fisher's equation for reproductive value in discrete form (3.10). If the organism does not reproduce at time \( a_1 \) but instead grows (at exponential rate \( \alpha \)) and then reproduces at the next time step, the result is:

\[
F(x, a_1, t) = \beta ks a p_s(a_1) \sum_{i=a_1+1}^A l_i/l_{a_1} \tag{3.38}
\]

The age of first sexual reproduction is the maximum \( a_1 \) for which the right hand side of (3.37) is greater than that of (3.38). Thus, for the iteroparous morph, the resulting
inequality simplifies to:

\[ 1 > (\alpha - 1) \sum_{i=a_1+1}^{A} l_i/l_{a_1} \]  

(3.39)

while for the semelparous colonies it becomes:

\[ 1 > \alpha p_a(a_1) \]  

(3.40)

This shows, interestingly, that the value of $\beta k$ does not seem to have an influence. Using the $m_a$ and $m_s$ values given in the previous section, for iteroparous colonies with $\alpha = 2.03$, (3.39) gives $a_1 = 12$, while for semelparous colonies with $\alpha = 3.88$, (3.40) gives $a_1 = 10$. The actual values are 11.5 and 6.2 as given in the 2X and 3X feeding levels in Table 4 of Grosberg (1988). While the iteroparous value is quite reasonable, the semelparous value is too high. Equation (3.40) requires that $p_a(a_1) < 1/\alpha$ which means that the mortality must become high at about 7 generations. However, this is only an approximation, and there are other considerations, so I will continue using my current assumptions since I don't know the actual mortality values.

Consider another approximation. As before, ignore the time dependent mortality. Let $T$ be some large time to consider and let $t$ be the current time. Define $\eta = [F(1, 0, t; T)]^{1/(T-t)}$ = the geometric average reproduction rate of the organism per unit time. Assume that this rate applies for all times $t$. Finally, assume that at age $a$, $s = \alpha^a$. If the organism first reproduces at age $a = a_1$, then from equation (3.34) we have:

\[ F(1, 0, t; T) = \beta k \alpha^{a_1} \sum_{a=a_1}^{A} l_a F(1, 0, t+a; T). \]  

(3.41)

Using $\eta$ gives

\[ \eta^{T-t} = \beta k \alpha^{a_1} \sum_{a=a_1}^{A} l_a \eta^{T-(t-a)}. \]  

(3.42)

Dividing both sides by $\eta^{T-A-t}$ gives

\[ \eta^A = \beta k \alpha^{a_1} \sum_{a=a_1}^{A} l_a \eta^{A-a}. \]  

(3.43)
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This is a polynomial of degree $A$ in $\eta$ with the optimal age of reproduction being the value of $a_1$ that optimizes $\eta$. Unlike (3.39), the value of $\beta k$ does affect the result. Consider the special case of only one reproduction (semelparous). Then (3.43) simplifies to

$$\eta = \alpha(\beta kl_{a_1})^{1/a_1}. \quad (3.44)$$

Thus, the value of $\alpha$ is just a scaling factor for the reproductive value and does not affect the decision of when to reproduce! For iteroparous colonies with $\alpha = 2.03$, the age of first sexual reproduction is 13 for $k = .001$ and .002. For semelparous colonies the value is 8, also for both $k$ values. Note that for both iteroparous and semelparous morphs, a factor of 2 change in $k$ does not change the optimal age of first sexual reproduction, so $k$ does not appear to be an important consideration. Also, although the semelparous value is closer to 6.2 compared to the first simplification, it is still significantly larger.

**Methods**

Since iteroparous colonies can contain up to 1000 zooids, the computer memory required to solve (3.34) directly (several megabytes) is too large to implement on most microcomputers. Instead, since for most of the time the growth is exponential at the constant rate $\alpha$, in (3.34), the $s$ in $F$ is replaced by $x$ giving

$$F''(x, a, t) = \max\{F''(x_1, a + 1, t_n), rF''(x_2, a + 1, t_n) + \beta ksp(t_n)\} \quad (3.45)$$

where $x, x_1, x_2$ are indicators of the size equivalent to the age of a similarly sized colony that has not reproduced sexually or gone through a winter. Thus, during the initial growth phase at rate $\alpha$, we have $s = \alpha^x$ or, equivalently, $x = \log_\alpha s$. Since only fitness values corresponding to integral values of $x$ are stored, only 24 values of $x$ are required. For convenience, I drop the double prime throughout the rest of the thesis.
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Equation (3.45) is solved using an iterative technique. Initial values are assigned to $F(x, a, T_y)$ for all $x, a$. Then, (3.45) is used repeatedly to solve for the previous time steps. After each time step is solved, the fitness values are scaled (i.e. divided by $F(0, 0, t)$). When the beginning of the year ($t = 1$) is reached, during the next iteration the end of the previous year ($t = T_y$) is calculated. After a full year backwards is calculated, the values at time $t$ are compared to the values at the same time $t$, but for the next year. Since the model does not account for year-to-year fluctuations in the environment, at steady state the scaled fitness values on a year to year basis should be the same. Of course, steady state will never be reached in the model, so the model assumes that steady state is effectively reached when the absolute relative difference in the fitness values from one year to the next are all less than a small value ($\epsilon$) and the decision (to reproduce or not to reproduce) does not change between the years.

However, convergence is not very fast due to oscillatory behaviour in the fitness values. I used a technique, called "relaxation", to speed convergence. Relaxation, often used in fluid dynamics equations (e.g. see Mitchell & Griffiths (1980)), is a form of linear interpolation between the previous and current values. If $f'_n$ is the $n$th relaxed value obtained, and $f_{n+1}$ is the value obtained from the iteration equations using the value $f'_n$, then we have

$$f'_{n+1} = f'_n + \omega(f_{n+1} - f'_n).$$

where $\omega$ is the relaxation parameter. For $\omega > 1$, it is called over-relaxation, for $\omega < 1$, it is called under-relaxation, and for $\omega = 1$, it is equivalent to not using relaxation at all.

In overwintering organisms, the decrease and then increase in size results in non-integral values of $x$. Since I only store fitness values corresponding to integral values of $x$ and the growth is exponential, I use exponential interpolation. For example, let $x < g$ (the size index when the growth rate is reduced). Also, let $x_i = \text{int}(x)$ and $x_f = x - x_i$. 

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Then, \( F(x, a, t) = F(x_i, a, t)^{1-s_j} F(x_i + 1, a, t)^{s_j} \).

Field Data for Comparison

Fig. 2.3 shows the frequency distributions of various life-history parameters over the year. Although the data are not separated on a semelparous/iteroparous basis, there is a definite dichotomy in the number of embryos per zooid with no colonies having between 4.0 and 8.0 embryos per zooid. I assume that the colonies with less than 4.0 embryos per zooid are iteroparous and those with more than 8.0 are semelparous. Since Fig. 2.2 shows that in general semelparous and iteroparous have non-overlapping life history parameters, I assumed that the lowest ages of first sexual reproduction are semelparous and the highest ones are iteroparous. Thus, I calculated the approximate frequency distributions as given in Fig. 3.8 with the data summarized in Fig. 3.9. Several patterns become evident. First, the age of first sexual reproduction rises in the July cohort (about generation 8) for iteroparous colonies and in August (about generation 13) for semelparous colonies. Secondly, the age of first sexual reproduction decreases for both morphs in early September (about generation 17). Finally, in late September (about generation 20), the age of first sexual reproduction greatly increases, also for both morphs.

Another possible check on the modeling results is correlation with the larval settlement rate (Fig. 3.7). As shown, little settlement occurs at the beginning (May) and end (November) of the growing season. Instead of smooth changes, definite peaks occur. Over the two years of data, these peaks seem to occur at about the same times: mid to late June, late July, late August, early September, and mid October. Also, most of the peaks are about the same size except for the one in late July which is at least 4 or 5 times as large. Unfortunately, the morph specific larval settlement is not given. However, the increase in the proportion of iteroparous colonies in late July (Fig. 3.8) indicates that a lot of the large peak then is likely due to iteroparous settlement.
Figure 3.8: Frequency distributions of age at first sexual reproduction for semelparous and iteroparous colonies. This data is adapted from Fig. 2.3. Hashed bars represent data from 1979 cohorts; open bars represent data from 1980 cohorts.
Figure 3.9: Field data summaries of Fig. 3.8. The x-axis is the time of year that the colonies began. The central line is the mean, the vertical lines are the error bars and the outside dashed lines are the upper and lower bounds.
Variable Model Parameters

In the model, I assume that the value of $k$ is such that the intrinsic growth rate of the population, $r$, $\approx 0$. For the iteroparous morph, Table 2.1 gives the September 1-15 period survivorship and fecundity figures. Fig. 3.8 shows that for that period about 40% started sexual reproduction during generations 9 and 10, 40% started during generations 11 and 12, and finally about 20% started sexual reproduction during generation 13. Thus, in each later generation from 9 to 13, roughly an additional 20% of remaining start sexual reproduction. Therefore, we have $[.207(1596)(.2) + .201(1932)(.4) + .186(2318)(.6) + .173(1957)(.8) + .110(1843) + .053(1639) + .021(1704)]k \approx 1$ which gives $k \approx .0012$. For the semelparous morph, from Grosberg (1988), the maximal survival is about .218 with a mean fecundity of 2267 embryos. Thus, $(.218)(2267)k \approx 1$ which gives $k \approx .0020$. This is about 70% higher than the estimated $k$ for the iteroparous morph. Grosberg (1982) states that no reason is evident to believe that larval behaviour differs between semelparous and iteroparous larvae so the $k$ values should be roughly the same. Although the semelparous morph value is likely more accurate, in case the iteroparous morph’s $k$ value is lower, I modeled $k = .001$ and .002 to examine the effect.

I modeled 18 cases for both $k$ values and for both semelparous and iteroparous morphs for a total of 72 cases, with the results given in Fig. 3.10-3.21. The 18 cases examine the influence of the following factors: growth rate decrease after winter, growth rate, maximum size, and different numbers of generations at the maximum growth rate and to reach the maximum size. From Grosberg (1982) (Table 5), for iteroparous colonies, the growth rate ranged from 1.90 to 2.14 with an average of 2.03 buds/zoooid while for semelparous colonies, the growth rate ranged from 3.23 to 4.16 with an average of 3.88 buds/zoooid. The cases cover the minimum, average, and maximum values of $\alpha$ for both morphs. Grosberg (1982) states that semelparous morphs normally only grow to a
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maximum of about 250 zooids and iteroparous to about 800 before sexually reproducing. I used these values as the low maximum size. Fig. 3.5 shows that some semelparous colonies can reach sizes of about 500 zooids and iteroparous morphs can reach sizes of about 1000 zooids. I used these as the medium maximum values. Finally, Fig. 3.5 shows that for the July 15 cohort, a couple of semelparous colonies reached sizes of at least 800 zooids. In case iteroparous colonies do not reach their absolute maximum size even at 1000, I tried using 1300 zooids. These values (800 and 1300) were used as the high maximum size. From Fig. 3.5, the growth rate levels off, on average, at about 200 zooids for semelparous colonies and at about 500 zooids for iteroparous colonies. Thus, the age at which the growth rate changed was calculated as that which was closest to those sizes. The number of generations over which the growth rate linearly decreases to 1.0 is loosely based on reaching maximum size at the latest age that sexual reproduction first occurs.

3.5.3 The Model Cases

The 18 cases are summarized below:

<table>
<thead>
<tr>
<th>Cases</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)-(c)</td>
<td>No after winter growth decrease</td>
</tr>
<tr>
<td>(d)-(f)</td>
<td>As (a)-(c) but with after winter growth decrease</td>
</tr>
<tr>
<td>(g)-(i)</td>
<td>As (d)-(f) but with low $\alpha$ and varying max. size</td>
</tr>
<tr>
<td>(j)-(l)</td>
<td>As (g)-(i) but with medium $\alpha$</td>
</tr>
<tr>
<td>(m)-(o)</td>
<td>As (j)-(l) but with a different # of generations for growth rate decrease</td>
</tr>
<tr>
<td>(p)-(r)</td>
<td>As (m)-(o) but with high $\alpha$</td>
</tr>
</tbody>
</table>

Each case is presented in the figures as 2 superimposed graphs with 8 variables below presented numerically and graphically. On the graphs, the y-axis is age in asexual generations and the x-axis is the time of year, in asexual generations, that the colony started.
Figure 3.10: Iteroparous colony first sexual reproduction age cases (a) to (f) with $k = .001$ (see sec. 3.5.3 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. The left side has no winter effect while the right side has a winter effect. $\alpha$ values increase going down the page.
Figure 3.11: Semelparous colony first sexual reproduction age cases (a) to (f) with \( k = .001 \) (see sec. 3.5.3 for details). The \( x \)-axis is the time of year the colony started; the \( y \)-axis is the age of first sexual reproduction. The left side has no winter effect while the right side has a winter effect. \( \alpha \) values increase going down the page.
Figure 3.12: Iteroparous colony first sexual reproduction age cases (g) to (l) with $k = 0.001$ (see sec. 3.5.3 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. The left side has $\alpha = 1.9$ while the right side has $\alpha = 2.03$. The maximum colony size limit values increase going down the page.
Figure 3.13: Semelparous colony first sexual reproduction age cases (g) to (l) with $k = .001$ (see sec. 3.5.3 for details). The x-axis is the time of year the colony started; the y-axis is the age of first sexual reproduction. The left side has $\alpha = 3.23$ while the right side has $\alpha = 3.88$. The maximum colony size limit values increase going down the page.
Figure 3.14: Iteroparous colony first sexual reproduction age cases (m) to (r) with $k = .001$ (see sec. 3.5.3 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. The left side has $\alpha = 2.03$ while the right side has $\alpha = 2.14$. The maximum colony size limit values increase going down the page.
Figure 3.15: Semelparous colony first sexual reproduction age cases (m) to (r) with $k = .001$ (see sec. 3.5.3 for details). The x-axis is the time of year the colony started; the y-axis is the age of first sexual reproduction. The left side has $\alpha = 3.88$ while the right side has $\alpha = 4.16$. The maximum colony size limit values increase going down the page.
Figure 3.16: Iteroparous colony first sexual reproduction age cases (a) to (f) with $k = 0.002$ (see sec. 3.5.3 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. The left side has no winter effect while the right side has a winter effect. $\alpha$ values increase going down the page.
Figure 3.17: Semelparous colony first sexual reproduction age cases (a) to (f) with $k = .002$ (see sec. 3.5.3 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. The left side has no winter effect while the right side has a winter effect. $\alpha$ values increase going down the page.
Figure 3.18: Iteroparous colony first sexual reproduction age cases (g) to (l) with $k = .002$ (see sec. 3.5.3 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. The left side has $\alpha = 1.9$ while the right side has $\alpha = 2.03$. The maximum colony size limit values increase going down the page.
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Figure 3.19: Semelparous colony first sexual reproduction age cases (g) to (l) with $k = .002$ (see sec. 3.5.3 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. The left side has $\alpha = 3.23$ while the right side has $\alpha = 3.88$. The maximum colony size limit values increase going down the page.
Figure 3.20: Iteroparous colony first sexual reproduction age cases (m) to (r) with \( k = .002 \) (see sec. 3.5.3 for details). The \( x \)-axis is the time of year the colony started; the \( y \)-axis is the age of first sexual reproduction. The left side has \( \alpha = 2.03 \) while the right side has \( \alpha = 2.14 \). The maximum colony size limit values increase going down the page.
Figure 3.21: Semelparous colony first sexual reproduction age cases (m) to (r) with $k = .002$ (see sec. 3.5.3 for details). The x-axis is the time of year the colony started; the y-axis is the age of first sexual reproduction. The left side has $\alpha = 3.88$ while the right side has $\alpha = 4.16$. The maximum colony size limit values increase going down the page.
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The dashed line is the average age of first sexual reproduction from the field data (as given in more detail in Fig. 3.9) and the line with the dots is the model results. Below these graphs, on the left are four input variables and on the right are four output variables. Beside each variable is a box with a central vertical line and an asterisk. The vertical line designates the average or expected value for that variable while the asterisk denotes its actual value. The input variables use a linear scale while the output variables use a logarithmic scale with a factor of 10 difference between the central line and the edge of the box. If the value is outside this range, it is placed at the edge. The input variables are the base growth rate ($\alpha$), the maximum size limit, the generation $\#$ at which the growth rate first changes, and finally the number of generations over which the growth rate decreases linearly to 1.0. For the output variables, the first one is the yearly colony population growth rate (expected value is of course 1.0). Once the age of first sexual reproduction was calculated, forward iteration was used to calculate the densities of colonies, and thus the yearly change in densities (i.e. the yearly population growth rate). The next three output variables are, respectively, the minimum, average, and maximum colony sizes over the year (the central line designates the expected average value of 695.6 zooids for iteroparous colonies and 224.7 zooids for semelparous colonies (Grosberg 1982)).

All the computer runs used the small convergence criterion of $\epsilon = .001$ to try ensuring accurate modeling results. For iteroparous cases (a)-(c), I did not use relaxation. For semelparous cases (a)-(c), I used $\omega = .9$ since some cases did not converge otherwise. For semelparous case (g) with $k = .002$, the solution would not converge regardless of the value of $\omega$. Finally, I used $\omega = .8$ which gave a maximum difference of .011 after 400 iterations. For all the remaining 65 cases, I used $\omega = .73$ with all of them converging within 400 iterations.
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Analysis of Results

In the following analysis, when I talk about the age of colonies varying over the year, I mean the age of first sexual reproduction varying over the time of year that the colony started. Also, each new set of cases will discuss the differences with the previous set of cases.

First, consider \( k = .001 \) (Fig. 3.10-3.15). Cases (a)-(c) show very little fluctuation in the age over the year. The rise, dip, rise from field data is not evident for any one of these. Also, the resulting larval settlement curves would be smooth, rather than have large peaks as shown in Fig. 3.7. The annual growth rate is way too high for all except Fig. 3.10(a). Finally, the colony sizes are all too large, especially for the semelparous morphs.

Cases (d)-(f), with a growth rate reduction after winter, shows large variations over the year that correspond very roughly to field data. However, for the iteroparous / semelparous morphs, the July / August (respectively) peaks occur about 3-4 generations too soon (about 1 month). Also, the late September dip, then rise, is greatly exaggerated in the iteroparous morph and to a lesser extent in the semelparous morph. This is because the model predicts that colonies started over a fairly wide period in the late summer and early fall will reproduce in the early spring, which is not true. However, the main problem with this model is that allowing the growth to continue unabated results in too large colony sizes, especially for semelparous colonies.

Cases (g)-(i), with a size limitation introduced, have ages of first sexual reproduction that correspond much more closely to field data. With iteroparous colonies, as the maximum size increases, the age of first sexual reproduction increases but the fall rise in age occurs earlier, up to 5 generations too early. The July peak can be roughly seen a few generations early in Fig. 3.11(h). Since only the first integral value of the age when
reproducing becomes favoured over not reproducing is shown, the “real” age when this switch occurs would be somewhat lower. Thus, the age shown is the “real” age truncated up. This tends to obscure some of the details of how this age changes over the year. The growth rates are too low and sizes too small, although case (i) has sizes that are close to that expected. For the semelparous colonies, in case (g), the ages follow the field data quite closely, with a slight rise around generation 8 and generation 15, with a dip around generation 20 followed by a sharp rise at generation 22. However, the sizes are somewhat low and the growth rate is way too low. Cases (h) and (i) show that, given the chance, the colonies will grow to much larger sizes, but even then the population growth rate is still way too low.

Cases (j)-(l) show the results from using the average growth rate. Compared to the left side, the ages are somewhat lower but very similar, but case (l), for both iteroparous and semelparous colonies, has the September rise occurring one generation later. The population growth rate is higher because reaching reproduction size at even slightly lower ages means there is less mortality before reproduction.

Cases (m)-(o) show the effect of having a longer period of time after the growth rate is reduced before the maximum size is reached. For iteroparous colonies, the age stayed the same or went down slightly since each generation of growth means one less generation of reproduction so it is better to reproduce if the growth rate is fairly low. On the other hand, the semelparous colonies’ age either stayed the same or increased. With only one reproduction episode, the colonies will try to maximize their size until very slow growth and/or high mortality make it unprofitable. For iteroparous colonies, the population growth rate and colony sizes are lower, while for semelparous colonies it is true only for all sizes but the largest, 800 zooïds.

Finally, cases (p)-(r) show the results for the highest growth rate. The results change
little except that iteroparous colonies have a more steep decline before the rise in September. The growth rates and sizes are larger but very similar also.

Now, compare \( k = .001 \) (Fig. 3.10-3.15) to \( k = .002 \) (Fig. 3.16-3.21). The ages of first sexual reproduction are, on the whole, very similar. However, for many cases the rise in age before winter is 1 or 2 generations later making it more accurate for iteroparous colonies but less accurate for semelparous colonies. For the iteroparous cases, the population growth rate increases by about a factor of 4 while for the semelparous cases it increases by a range of factors from 8 to 16. For iteroparous cases, the factor of 4 increase is due to about 2 full generations living over the year, while for semelparous colonies, the factor of 8 is due to 3 or 4 full generations living over the year. The larger factor increase (up to 16) is due to the colonies reproducing a generation earlier which avoids the high mortality imposed by the model for later generations.

Although with \( k = .002 \) the yearly growth rate for iteroparous colonies is close to the expected value of 1.0, for semelparous colonies it is too low for the most realistic cases (i.e. where the maximum size is 250 zooids). In fact, it is too low by a factor of 20 to 40. This is caused by the extra mortality imposed by the model at later ages which makes the densities too low. Assuming about 4 generations per year, this means that the density is too low by a factor of 2 to 2.5. Since \( k = .002 \) is fairly accurate for semelparous colonies, this indicates that the mortality values do not rise sharply with age in semelparous colonies. This corresponds to Grosberg (1982) who states that semelparous colonies continued to live as long as he prevented sexual reproduction by removing their oocytes at each asexual generation.

On the whole, the model results predict the qualitative, and even quantitative, patterns of age of first sexual reproduction, especially for the iteroparous morph. Since cases (a)-(c) did not show these qualitative features, it implies that the after winter growth rate change is responsible. Thus, since the current conditions are not responsible, the
colonies can somehow tell the time of year. With the synchronization of the asexual generation length to the water temperature, the current value and changes in the water temperature is the likely method used, although the photoperiod is another possibility. Also, the model allows one to suggest the cause for the changes in the age of first sexual reproduction. The dip in age in early September is for colonies that reproduce in early spring before their size is greatly reduced. The large rise in age in late September is due to the colonies waiting until they regain some of their size after winter before reproducing. The rise in age in July for iteroparous colonies is to avoid reproducing during the period in early September when the age goes down.

For both semelparous and iteroparous colonies, $k \approx 0.002$ as expected, although it might be a bit lower for iteroparous colonies. In particular, for iteroparous colonies, the most realistic maximum size is 1300 zooids, while for semelparous colonies it is close to 250 zooids. Thus, although iteroparous colonies do not usually grow to very close or up to their maximum sizes since they want to be able to reproduce for many generations, semelparous colonies always tried to grow to, or at least near, their maximum sizes before reproducing, even despite increased mortality. This would explain why with little substrate semelparous colonies grow into folds despite the extra risk of being torn off (Grosberg 1982). Thus, size is very important for determining the age of reproduction in semelparous colonies, as confirmed by the starvation, substrate, and embryo removal experiments in Grosberg (1982).

Finally, except for during the first 7 generations after winter, once an iteroparous colony began sexual reproduction, it continued each generation until death. Thus, Grosberg's (1982, 1988) observation to that effect could be due to it being the optimal thing to do rather than a physical constraint.

However, even over the range of parameters studied, the variance in field data shown in Fig. 3.9, particularly for the iteroparous colonies, is not reproduced in the results.
Possible causes for this are natural individual variation and the model not accounting for spatial heterogeneity since I have no data for it. However, the colonies are sessile so their growth and mortality depends on the suitability of their location which can vary greatly over their habitat.

3.5.4 Density and Reproduction Amounts

As mentioned previously, once the age of first sexual reproduction is found, forward iteration is used to obtain the density and reproduction amounts at each time of the year. Fig. 3.22 shows these values for iteroparous colonies and Fig. 3.23 shows it for semelparous colonies. In Fig. 3.22, there is an internal peak about generation 15 (Aug. 23). However, the major peak is at the end of the year and early part of the next year. Thus, although the ages of first sexual reproduction are fairly accurate compared to the average, the reproduction data is not. Part of the reason is that in real life the age of first sexual reproduction is spread over a range rather than concentrated in the average. Secondly, it is likely that spatial effects make a large difference. As mentioned previously, although overwintering colonies are starving in early spring, it appears that their offspring, to a large extent, do not. Thus, since the progeny tend to locate close to the parental colony (Grosberg 1982), colonies probably only reproduce if the local conditions are favourable. Fig. 3.23 (semelparous colonies) shows 3 peaks at generations 12 (Aug. 8), 19 (Sep. 14) and 25 (Oct. 29). In these cases, the reproduction is in a yearly cycle. Comparing Fig. 3.22 and 3.23 with Fig. 3.7, it is difficult to make any comparisons with any degree of confidence. Density-dependence and the range of ages of first sexual reproduction are important in determining the amount of reproduction during each time step.
Figure 3.22: Iteroparous colony density and rep. amounts, cases (i), (l), and (r) with $k = .002$. The x-axis is the time of year the colony started.
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Figure 3.23: Semelparous colony density and rep. amounts, cases (g), (j), and (p) with $k = .002$. The $x$-axis is the time of year the colony started.
3.5.5 Lack of Time Dependent Mortality

From the earlier discussion, it appears that the growth rate change after winter is the primary factor controlling the age of first sexual reproduction changes over the year. However, it is possible that it could be due to a combination of the growth rate change after winter and the time dependent mortality. Fig. 3.24 shows the effect of removing the time dependent mortality for several iteroparous and semelparous cases. The ages are almost identical, with the only major difference being that the population growth rate is much higher.

3.5.6 Conclusions and Possible Enhancements

The relatively good agreement between the field data and the model results allows several conclusions. First, each morph’s life history characteristics, particularly the age of first sexual reproduction, is near equilibrium. The after winter growth rate change causes fluctuations in the age of first sexual reproduction throughout the year for both the semelparous and the iteroparous morphs. Thus, the model suggests that the colonies can tell the time of year. Apart from during the first seven generations for overwintering colonies, iteroparous colonies continue reproducing every generation, as noted by Grosberg (1982), not necessarily due to an energetic or physical constraint, but simply because it is optimal for them to do so. However, although average values of the age of first sexual reproduction are predicted quite accurately, the full range of values (Fig. 3.8, 3.9) cannot be predicted primarily because of a lack of spatial heterogeneity in the model.

An interesting enhancement to the model, that could help understand why each morph reproduces in the amount that it does and also why intermediate morphs are so rare, would be to find the optimal amount of reproduction as well. However, the effect of
Figure 3.24: Age of first sexual reproduction, using $k = .002$, without time dependent mortality (see sec. 3.5.5 for details). The $x$-axis is the time of year the colony started; the $y$-axis is the age of first sexual reproduction. Left side: iteroparous cases (i), (l), (r); right side: semelparous cases (g), (j), (p). $\alpha$ values increase going down the page.
varying amounts of reproduction on mortality and growth rate of the next generation are not known. Before a successful attempt can be made at this model, more information needs to be known about *B. schlosseri*, starting with the potential mortality of older semelparous colonies.

The next chapter will examine various theories about the coexistence of species that occupy the same niche and their applicability to *B. schlosseri*. The use of the dynamic programming technique in solving this problem will also be discussed.