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POPULATION CYCLING IN SPACE-LIMITED ORGANISMS SUBJECT TO DENSITY-DEPENDENT PREDATION

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Abstract.—We present a population model with density-dependent disturbance. The model is motivated by, and is illustrated with, data on the percentage of space covered by barnacles on quadrats of rock in the intertidal zone. The autocorrelation function observed indicates population cycling. This autocorrelation function is predicted qualitatively and quantitatively by the detailed model we present. The general version of the model suggests the following rules regarding cycling in space-limited communities subject to density-dependent disturbances. These rules may apply to any space-limited community where a density-dependent disturbance reduces population densities to very low levels, like fire or wind for plant communities. We propose that the period of the cycle will be approximately equal to the time it takes the community to reach a critical density plus the average time between disturbance events when the density is above that critical density. The cycling will only be clear from autocorrelation data if the growth process is relatively consistent, there is a critical density (which the sessile organism reaches and passes) above which the probability of disturbance increases rapidly, and the time to reach the critical density is at least twice the average time between disturbance events.

Disturbance events are believed to be a critical feature of the population dynamics of sessile organisms (Sousa 1984). Many empirical studies have considered the influence of disturbance frequency and intensity on the community structure of space-limited organisms (Connell 1979; Denslow 1980; Sousa 1980; Paine and Levin 1981; Miller 1982; Keough 1984; Pickett and White 1985). The majority of these studies have focused on abiotic disturbances that act independently of the state of the community. Explaining species diversity has been the primary aim of many articles concerned with the impact of disturbances (Lubchenco 1978; Petraitis et al. 1989; Martinsen et al. 1990). In this article we present a simple model that focuses on the effect of density-dependent predation on the population dynamics of a single space-limited prey species. We show that this type of disturbance can cause local phase-forgetting (transfer of information decays with time) cycles in the population dynamics of the prey species. The theory presented here was motivated by data collected in an earlier study on the population dynamics of barnacles (Gaines and Roughgarden 1985).

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Consider a space-limited sessile organism that is censused at regular intervals by determining the amount of occupied space in a quadrat of fixed size. For example, in the earlier study (Gaines and Roughgarden 1985) a 34.6-cm^2 quadrat of rock was photographed every week and the percentage of the surface covered by one or more species of barnacle was measured. These data were collected (Gaines and Roughgarden 1985) for eight quadrats at Hopkins Marine Station, Monterey, California. From the time series of percent cover an autocorrelation function was calculated, which indicated statistically significant oscillations in the percentage of free space in four of the quadrats. The period of these oscillations ranged from 25 to 32 wk. Previous theoretical work suggested that this cyclical behavior is a consequence of the time lag induced by the age-structured sizes of the adult barnacles (Roughgarden et al. 1985; Bence and Nisbet 1989). However, attempts to quantitatively fit the observed data with this model have failed (J. Roughgarden, personal observation). The earlier study (Gaines and Roughgarden 1985) suggested that the cycles may be influenced by density-dependent predation by sea stars. Taking up this suggestion, we present a model in this article that attempts to explain the data collected in the earlier study (Gaines and Roughgarden 1985) in which the driving mechanisms for the fluctuations is density-dependent sea star predation on barnacles. The model addresses two topical issues in population biology. First, we believe that mathematical models that are tailored to address specific sorts of data and data collection may prove more useful to empiricists than more general models in which the variables (like total population size) and parameters (like carrying capacity) are not easily measured (Schoener 1986).

Second, our approach addresses the issue of scale in population processes. The unit of interest in population dynamics has traditionally been the individual, with birth and death acting on each individual independently of its neighbors. When a process of interest acts on a larger scale, groups of individuals in the case of sea star predation, the classical approach may not explain the dynamic behavior of the system at that scale. Hence, because sea star predation operates on groups of individuals and the barnacle cover in the immediate vicinity appears to be the cue for predation events, we use the dependent variable—occupied space in a small quadrat in the intertidal zone. This choice of dependent variable appears to be most relevant to the scale of the predation phenomenon. This scale cannot, however, hope to accurately address processes occurring at the level of the individual. Phenomena that influence larger spatial scales, for example, settlement events along a length of coastline, are likewise ignored. Because of the way in which the data were collected, we believe that the model presented below currently provides the most plausible explanation for the local population cycles observed during the earlier study (Gaines and Roughgarden 1985). If the data had been collected at a much larger, or much smaller spatial scale, then population cycles might not have been observed. It is worth noting that it was fortuitous that the scale of the quadrats and the scale of the sea star predation are similar.

In the first section we argue for a simple expression for the period of the population cycles. We then formulate a model of the probability density function of percent occupied space as a continuous random variable that increases linearly with time in the absence of sea star predation. This model is used to approximate an expression for the period of the autocorrelation function and the rate at which the autocorrelation function period should decay. The general theory presented in this section is applicable to any situation in which a density-dependent disturbance affects space-limited prey (see, e.g., Andrew and Jones 1990). The second section introduces the discrete state space analogue of the model and uses a Markov chain approach to numerically evaluate the autocorrelation function. This provides numerical support for the arguments in the first section and a framework for modeling more specific situations.

The most important result of the first two sections is that the period of the cycle in percent covered space is equal to the time it takes bare rock to attain a density at which there is heavy predation, plus the mean time between predation events. In the final section we modify the discrete state space model to incorporate two details of the earlier study data (Gaines and Roughgarden 1985), a nonlinear rate of increase in the amount of space covered by barnacles in the absence of predation and a more complex relationship between predation frequency and barnacle density. This last section is intended to mimic the processes driving the population cycles observed during the earlier study (Gaines and Roughgarden 1985) more accurately. With realistic parameters the theory provides a surprisingly good quantitative fit to the autocorrelation data.

THE PERIOD OF THE POPULATION CYCLE AND A CONTINUOUS STATE SPACE MODEL OF THE PROBABILITY DENSITY FUNCTION

In the absence of predation assume that the amount of occupied space rises linearly at rate g. Sea stars arrive at the patch and consume all individuals in the quadrat if, and only if, the amount of occupied space is at or above a critical value, c.

This kind of predation follows logically from an optimal diet model of foraging behavior in which the prey item is the quadrat and its quality is the density of prey in the quadrat (Charnov 1976). If the density of prey is below a threshold value it is more profitable for the predator to feed elsewhere. If the density is above a threshold value then the predator remains and consumes all the prey in the quadrat, and the amount of occupied space returns to zero.

For simplicity we will assume that the arrival of predators is a Poisson process that occurs at rate d, therefore the mean (and standard deviation) of the interarrival time (time between predator arrivals) is $1/d$.

The period of the population cycle, T, described by this process is defined by the following equation:

$$T = c/g + 1/d, \tag{1}$$

because for each patch the period of the cycle in percent cover is the time it takes the process to move from 100% free space to the critical percent cover, plus the mean time between predation events. (Alternatively, this is the average time it takes occupied space to change from a given percent cover back to that

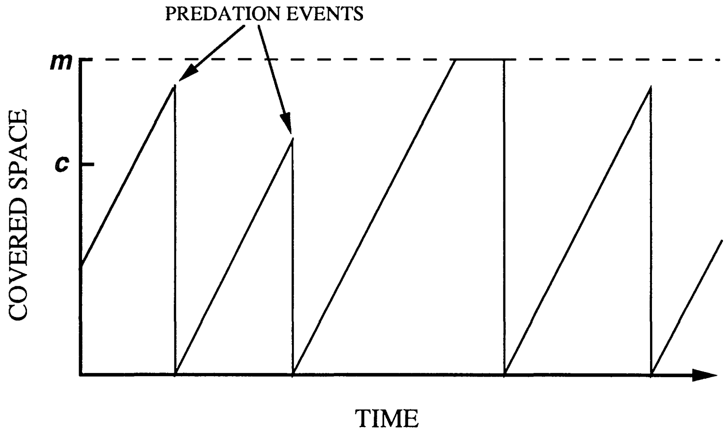

FIG. 1.—Example of fluctuations in the amount of space occupied by a sessile organism subject to density-dependent predation. The critical threshold above which predation occurs is marked *c*. The maximum amount of space that can be occupied is denoted *m*.

same percent cover.) Increasing the critical percent cover, decreasing the rate at which covered space increases, and decreasing the predation rate will all cause the period of the cycle to increase. Because of the stochastic nature of the arrival of sea star, the population cycles are phase forgetting. The crucial result is that density-dependent predation on groups of sessile space-limited organism may cause phase-forgetting cycles in local population density in the absence of age structure and/or time delays (see Roughgarden et al. 1985; Bence and Nisbet 1989).

Although this heuristic argument yields a period for the population cycle, it does not tell us the likelihood of seeing that period in autocorrelation data, and it ignores the fact there is a limit to the amount of percent cover that can be occupied, namely, 100%. To address these problems consider the following model of the probability density function of the amount of occupied space.

Let $X(t)$ (where t denotes time) be a random variable that represents the percentage of the quadrat covered by the sessile organism. Let the percent cover increase linearly at rate g in the absence of predation to some maximum percent cover m. An example of the way in which the random variable $X(t)$ behaves is sketched in figure 1. The probability density function $p(x, t)$ can be written as the sum of a function $\hat{p}(x, t)$ that describes the distribution for $0 \leq x(t) < m$ and a probability mass $p_m(t)$ that is concentrated at the maximum value m, $p(x, t) = \hat{p}(x, t) + p_m(t)\delta(x - m)$, where $\delta(x)$ is the Dirac delta function.

In Appendix A we show that our assumptions lead to the following equations for the probability density of $x(t)$,

$$\partial p(x, t)/\partial t + g\partial p(x, t)/\partial x = 0 \qquad \text{for } 0 \leq x < c \tag{2a}$$

$$\partial p(x, t)/\partial t + g\partial p(x, t)/\partial x = -dp(x, t) \qquad \text{for } c \leq x < m \tag{2b}$$

$$dp_m(t)/dt = gp(m, t) - dp_m(t), \tag{2c}$$

with boundary condition

$$p(0, t) = (d/g)\left[p_m(t) + \int_c^m p(x, t)\,dx\right]. \tag{2d}$$

Note that the transient behavior of $p(x, t)$ determines the transient behavior of the autocorrelation function of $x(t)$. Therefore, the temporal pattern of change in percent cover is reflected in the transient properties of $p(x, t)$, which we now explore.

Period and Decay Rate of the Autocorrelation Function

If the probability of reaching the maximum state is small, $p_m(t)$ is small, and equation (2) reduces to

$$\partial p(x, t)/\partial t + g\partial p(x, t)/\partial x = 0 \qquad \text{for } 0 \leq x < c \tag{3a}$$

$$\partial p(x, t)/\partial t + g\partial p(x, t)/\partial x = -dp(x, t) \quad \text{for } x \geq c\,, \tag{3b}$$

with boundary condition

$$p(0, t) = (d/g)\int_c^\infty p(x, t)\,dx\,. \tag{3c}$$

Given that the density of barnacles will cycle periodically, it is of interest to get an impression of the likelihood the cycles will be observed in autocorrelation functions derived from field data. In Appendix B we use equation (3) to find the rate at which the autocorrelation function decays. Before considering this result it is instructive to consider four special cases.

1. d is very large. If d is very large then the percent cover increases to the critical value, then falls almost instantaneously to zero. This results in cycles of period c/g and the cycles will be phase remembering; the autocorrelation function will not decay to zero.
2. $c = 0$. In this case the percent cover is subject to random density-independent mortality. The autocorrelation function decays rapidly to zero and no cycling occurs.
3. d is very small. Under these circumstances the predation rate is too low, the cycles are phase forgetting, and the autocorrelation function rapidly decays.
4. c/g is very large. In this case it takes a long time to reach the critical percent cover. Although with a high predation rate long-period cycles should in theory be observed, in real situations other stochastic processes would mask these long-period cycles.

In Appendix B we carry out a more thorough analysis of equation (4) to find an approximation for the decay rate of the autocorrelation function. The autocorrelation function decays faster when the predation rate is lower (fig. 2*A*). This agrees with our simple cases: If the predation rate is high then cycling in the autocorrelation function will be pronounced, with a period close to the time taken to reach the critical density, c/g. If the predation rate is very low the amplitude of the autocorrelation function cycles decays rapidly. The decay rate of the autocorrelation function decreases as the critical density increases (fig. 2*B*). For high

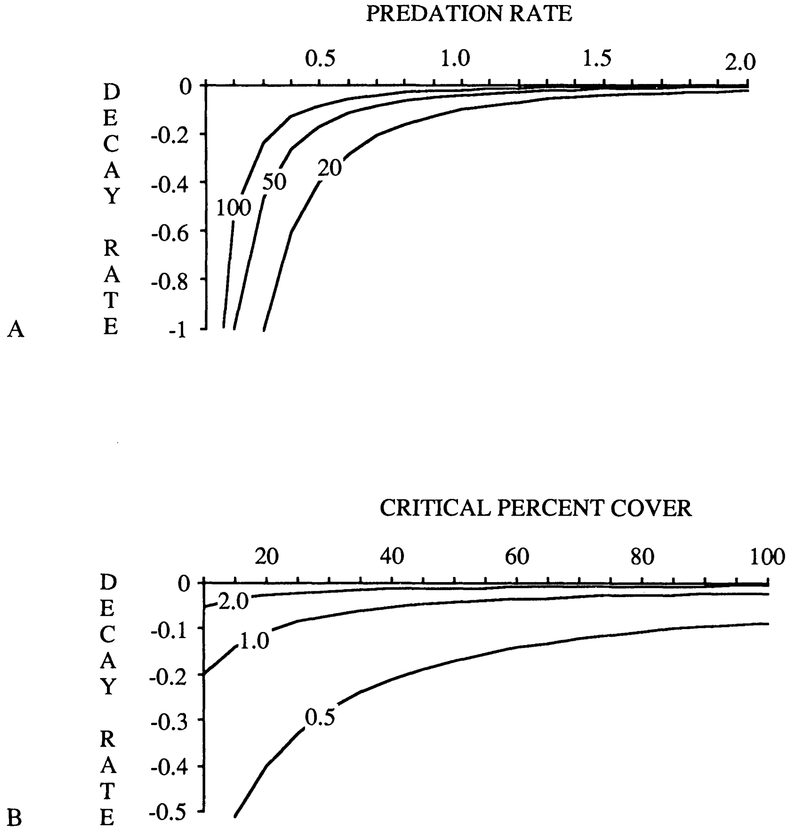

FIG. 2.—The rate at which the autocorrelation function approaches equilibrium. This sketch indicates the rate at which the amplitude of the population cycles is expected to decay. Large negative values indicate a rapid decay; small values indicate that cycling will persist for longer. *A*, The response of the decay rate to the predation rate; the number on each curve is the critical percent curve. *B*, The response of the decay rate to the critical percent cover; the number on each curve is the predation rate.

predation rates the decay rate is relatively independent of c. For low predation rates the critical density does have a significant effect on the decay rate of the autocorrelation function, implying that we are more likely to see cycling when the critical density is large.

So far we have assumed that the probability of entering the maximum state is negligible. If there is a maximum density that the population often reaches, a better approximation to the period is

$$T = \frac{c/g + 1/d - (m/g + 1/d)\exp[-d(m - c)/g]}{1 - \exp[-d(m - c)/g]} \tag{4}$$

(see App. C). The difference between equations (1) and (4) is illustrated in figure 3. As the value of $d(m - c)/g$ increases the difference between the approximations decreases. Equation (1) is a better approximation when the probability that a

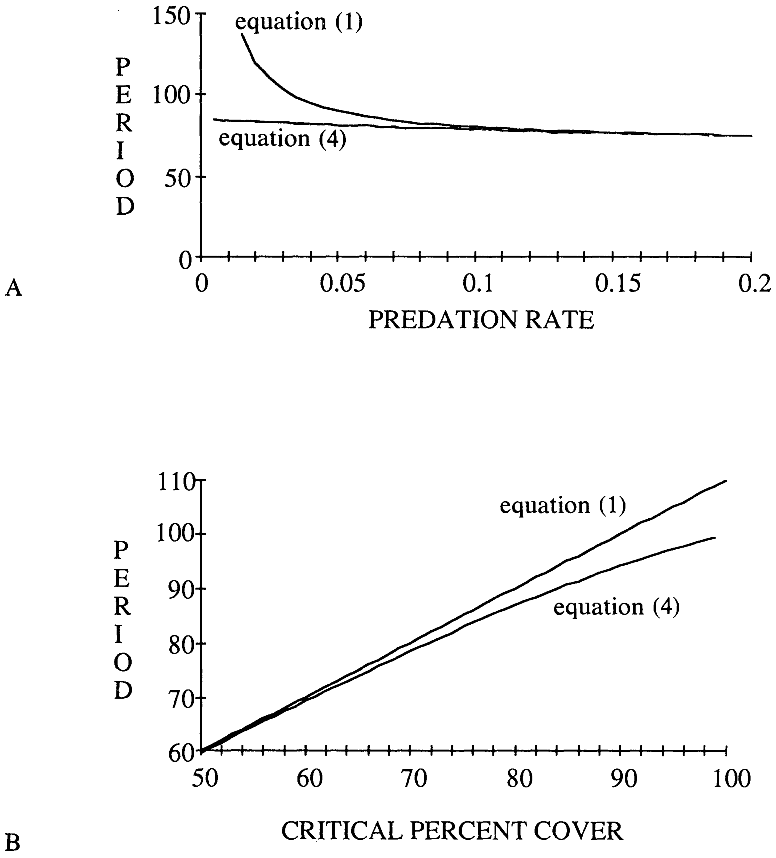

FIG. 3.—Comparison of the approximations of the period of the cycle calculated with equation (1), which ignores the possibility the percent cover reaches a maximum, and equation (4): *A*, the effect of varying the predation rate, d, for $c = 70$, $m = 100$, and $g = 1$; *B*, the effect of varying the critical density c, for $d = 0.1$, $m = 100$, and $g = 1$.

predation event occurs before the percent cover reaches m is low; however, even when $c = m$ the approximation can still be adequate.

DISCRETE STATE SPACE MODEL

The problem can be formulated and solved numerically for more general growth and predation processes if we assume that the state space for the process is finite. In this section we describe the problem in matrix notation and use this formulation to numerically generate autocorrelation functions for the process. Examination of the results yields insight into the nature of the cycling process and confirms the analytic approximations in the previous section.

Suppose the amount of cover in the quadrat increases from state 0 to state 100 in the absence of sea star predation. Time is scaled so that the process moves up one state each time step. When the random variable is at or above state c there is a constant probability μ that the patch is visited by a sea star and the percentage of space occupied by barnacles falls to zero. If $p_{j,t}$ is the probability the process is in state j at time t, then the probability of being in state j at time $t + 1$ is

$$
\begin{aligned}
p_{0,t+1} &= \mu \sum_{i=c}^{m} p_{j,t}\,, \\
p_{j,t+1} &= p_{j-1,t} && \text{for } j = 1, \ldots, c\,, \\
p_{j,t+1} &= (1-\mu)p_{j-1,t} && \text{for } j = c+1, \ldots, m-1\,,
\end{aligned}
$$

and (5)

$$p_{m,t+1} = (1-\mu)p_{m-1,t} + (1-\mu)p_{m,t}\,.$$

These transitions can be written in matrix form

$$\mathbf{p}_{t+1} = \mathbf{A}\mathbf{p}_t\,, \tag{6}$$

where $\mathbf{p}_t$ is the column vector $[p_{0,t}, p_{1,t}, \ldots, p_{m,t}]$ and $\mathbf{A}$ is the one-step transition matrix

$$
\begin{array}{ll}
\begin{array}{l}\text{Initial}\\ \text{State}\end{array} & \begin{array}{ccccccccccc} 0 & 1 & 2 & \cdots & c-1 & c & c+1 & \cdots & m-1 & m \end{array} \\
\mathbf{A} = & \left[\begin{array}{cccccccccc}
0 & 0 & 0 & \cdots & 0 & \mu & \mu & \cdots & \mu & \mu \\
1 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 \\
0 & 1 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 \\
\vdots & \vdots & \vdots & & \vdots & \vdots & \vdots & & \vdots & \vdots \\
0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & \cdots & 1 & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & \cdots & 0 & 1-\mu & 0 & \cdots & 0 & 0 \\
\vdots & \vdots & \vdots & & \vdots & \vdots & \vdots & & \vdots & \vdots \\
0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 1-\mu & 1-\mu
\end{array}\right].
\end{array}
$$

This transition matrix can be used to calculate the probability distribution at time t given initial condition $\mathbf{p}_0$ because

$$\mathbf{p}_t = \mathbf{A}^t\mathbf{p}_0\,. \tag{7}$$

Let l_i be the probability the percent cover in the quadrat rises to $i\%$ without a sea star visit—we will call this the survival probability to state i. In our model

$$l_i = 1 \qquad \text{for } i = 1, \ldots, c\,,$$

and (8)

$$l_i = (1-\mu)^{i-c} \quad \text{for } i = c+1, \ldots, m\,.$$

The equilibrium probabilities, $\boldsymbol{\pi}$, are described by the following:

$$\begin{aligned} \pi_0 &= 1/\left(c + \sum_{i=c+1}^{m-1} l_i + (l_m/\mu)\right) \\ \pi_i &= \pi_0 \qquad \text{for } i = 1, \ldots, c \\ \pi_i &= l_i \pi_0 \qquad \text{for } i = c+1, \ldots, m-1 \\ \pi_m &= l_m \pi_0/\mu . \end{aligned} \tag{9}$$

In the earlier study (Gaines and Roughgarden 1985) the cyclical behavior of the percent cover is represented by an autocorrelation function. The autocovariance function, $\rho(\tau)$, of a time series $X(t)$ is (Grimmett and Stirzaker 1983) described by the following equation:

$$\rho(\tau) = \mathrm{E}[(X(t) - \mathrm{E}(X))(X(t+\tau) - \mathrm{E}(X))],$$

and the autocorrelation function is $\rho(\tau)/\rho(0)$. For a sufficiently long time series we can obtain an expression for the autocovariance function in terms of the matrix elements

$$\rho(\tau) = \sum_{i=0}^{m} \left[\pi_i(i - \mathrm{E}(X)) \sum_{j=0}^{m} a_{j,i}^{\tau}(j - \mathrm{E}(X))\right], \tag{10}$$

where $a_{j,i}^{\tau}$ is the element of $\mathbf{A}^{\tau}$ in the jth row and ith column, and

$$\rho(0) = \sum_{i=0}^{m} [\pi_i(i - \mathrm{E}(X)]^2,$$

which is merely the variance of the equilibrium distribution. The autocorrelation function for any μ, c, and m can be calculated by calculating the matrix $\mathbf{A}^{\tau}$ and evaluating equation (10) for all τ.

Results and Discussion

In figure 4 the autocorrelation function for the process is graphed for $m = 100$, $c = 70$, and $\mu = 0.1$. The autocorrelation function suggests a cycle in the process, and the period of this cycle approximates the period predicted by the analytical continuous state space model, $c + 1/\mu$. We will use this discrete state space model to consider the influence of the parameters.

As we showed in the previous section, a high rate of sea star predation produces a more pronounced cycle and also shortens the period of the oscillation. Figure 5 displays the influence of μ on the autocorrelation function. In figure 6 we vary the percent cover at which sea star predation begins. Increasing c increases the amplitude of the oscillation at a decreasing rate and lengthens the period of the oscillation in an approximately linear fashion. The way in which the decay rate of the cycling decreases as c increases is seen most clearly when the rate of sea star predation is high. As expected, when $c = 0$, the memoryless nature of

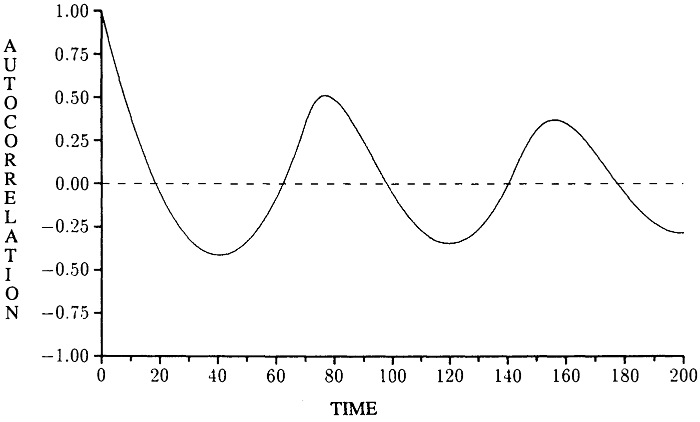

FIG. 4.—The autocorrelation function of the discrete state space process described by equation (6) and calculated with equation (11) for $\mu = 0.1$, $c = 70$, and $m = 100$.

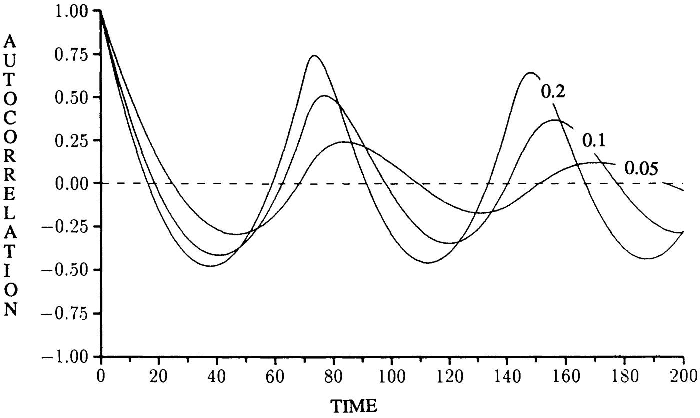

FIG. 5.—The effect of changes in the rate at which sea stars visit the patch, μ, on the autocorrelation function of the discrete state space process described by equation (5) and calculated with equation (10), $m = 100$, $c = 70$.

the predator arrival process means the autocorrelation function approaches zero monotonically at a rate that depends on the sea star visitation rate (fig. 6). The percent cover at which the growth process stops, *m,* has very little influence on the period and amplitude of the population cycles; however, if $c > m$ then the patch is never subjected to predation and there will be no cycles. These conclusions are consistent with the analytic analysis of the previous section.

In all these examples (figs. 4, 5, and 6) equation (1) overestimates the period of the cycle. This is because equation (1) assumes that the process never reaches the maximum state. Using the approximation in equation (4) corrects for this assumption and the match between the numerical and analytic results becomes

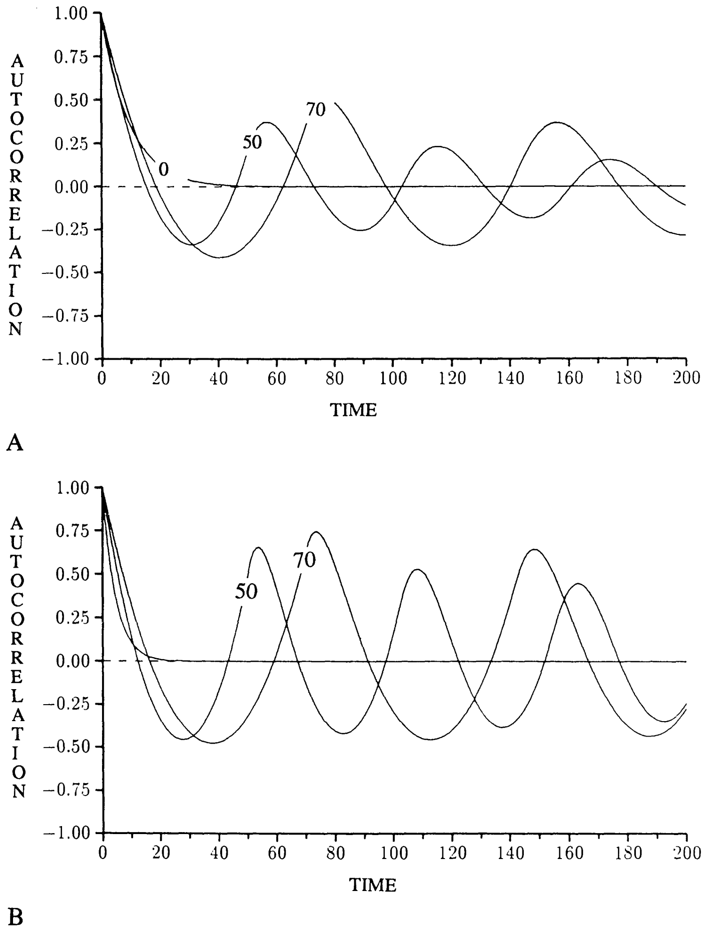

FIG. 6.—The effect of changes in the critical density below which sea stars do not consume barnacles in the patch, c, when covered space increases linearly, $m = 100$, and (*A*) $\mu = 0.1$, (*B*) $\mu = 0.2$. The autocorrelations are calculated with equation (10).

closer. The relationship between equation (1) and equation (4) is sketched in figure 3 for parameter values that correspond to figures 4, 5, and 6. As the predation rate falls, equation (1) becomes a worse estimate of the period. Similarly, as the distance between the critical density and the maximum density decreases, equation (1) becomes a worse approximation to the true period.

In summary, the likelihood of observing cycles in percent cover in field data is primarily determined by the rate of predation. If the sea star predation rate is too low the amplitude of the cycles will be too small to notice in real data. For high predation rates the time it takes the population to reach the critical percent cover dominates the period of the oscillations. If the critical density is too small, for example, if $c = 0$, there will be no cycle. As a rule of thumb, cycling may be observed in the autocorrelation function if $c/g > 2/d$, that is, the time it takes to reach the critical density is at least twice the mean time between predation events. When the chance of reaching a maximum state becomes large enough equation (4) will become a significantly more accurate estimate of the period than equation (1).

A key observation presented in the earlier study (Gaines and Roughgarden 1985) is that statistically significant oscillations were only observed on the sites that received persistently high settlement rates. In low-settlement sites no oscillations were observed, and the oscillations in the high-settlement sites ceased when the settlement rate decreased. Our models suggest that there are two elements necessary for statistically significant cycles: (i) a critical density of barnacle cover below which there is very little sea star predation, but above which the rate of sea star predation increases rapidly; (ii) a consistent rise in percent cover, in the absence of sea stars. If the rate at which the percent cover increases varies a lot, any peak in the autocorrelation data will be blurred. In the simple linear model described above, an increase in the rate at which barnacles cover the quadrat can be interpreted as an increase in settlement rates. The increase in settlement rate decreases the period of the cycle. According to our simple model this results in cycles that decay more rapidly. At this point it would appear that the low-settlement sites should show clearer cycles than the high-settlement sites from autocorrelation data. Although the model provides a qualitative fit to the data (Gaines and Roughgarden 1985), two observations remain to be explained. Why do we only see statistically significant oscillations in the high-settlement sites, and why is the period of the cycle between 25 and 32 wk? To answer these questions we extended our discrete state space model to include more details of the particular biological processes involved.

DISCRETE STATE SPACE MODEL WITH NONLINEAR GROWTH AND PREDATION THAT VARIES AS A CONTINUOUS FUNCTION OF PERCENT COVER

In this section we use further information to try to fit the data collected in the earlier study (Gaines and Roughgarden 1985) more precisely. The assumption that the percentage of occupied space in a quadrat increases linearly in the absence of sea star predation is not accurate. Instead, let us use information about the settlement process, density-independent death, and the rate at which individual barnacles grow to construct a better deterministic model of increase in occupied space. Suppose that s larvae settle per cm^2 per week. Assume that an individual barnacle, i wk after settling, occupies $a_0 i^2$ cm^2 of space, where a_0 is chosen so that a barnacle 103 wk old occupies an area of 7.07 cm^2 (Roughgarden et al. 1985). Assume there is density-independent mortality such that the proportion of barnacles that move into the next age class is q. Hence the total area occupied by the barnacles i wk after a quadrat is cleared to free space is, in the absence of sea star predation,

$$w_i = \min\left[sQa_0 \sum_{j=0}^{i} j^2 q^j,\ Q \right], \tag{11}$$

where Q is the total area of the quadrat. Each element of the discrete state space is now weighted by a value w_i, which is the space occupied by barnacles in a quadrat that was depleted to zero occupied space i wk ago. The new autocovariance function is

$$\rho(\tau) = \sum_{i=0}^{m} \left[\pi_i (w_i - \mathrm{E}(X)) \sum_{j=0}^{i} a^{\tau}_{j,i} (w_j - \mathrm{E}(X)) \right], \tag{12}$$

where now the equilibrium probabilities are

$$\begin{aligned} \pi_0 &= 1 \Big/ \left(c + \sum_{i=c+1}^{m-1} l_i + (l_m/\mu) \right) \\ \pi_i &= \pi_0 \qquad \text{for } i \text{ such that } w_i < c \\ \pi_i &= l_i \pi_0 \qquad \text{for } i \text{ such that } w_i \geq c \\ \pi_m &= l_m \pi_0 / \mu\,. \end{aligned} \tag{13}$$

To date we have assumed that the probability a sea star visits a quadrat is μ above a critical density. In reality the probability of sea star visitation each week varies as a continuous function of occupied space. Data on the survival rate of barnacles (Gaines and Roughgarden 1985) indicate that (i) there is a density-independent probability of surviving a week of about 0.98 and (ii) the probability of attracting sea star predation begins to increase rapidly at around 60% occupied space. Assume that the probability a sea star visits a quadrat with $x\%$ occupied space in a particular week is given by the single parameter expression

$$\mu(x) = \exp[-(100 - x)/100a], \tag{14}$$

that is, a quadrat with no free space will always be visited, and the probability of being visited declines exponentially as occupied space decreases. We chose a so that at 40% free space the probability of being visited each week is 0.1 (see Gaines and Roughgarden 1985, fig. 2).

Results and Discussion

In figure 7 we present autocorrelation curves for seven different choices of the settlement rate, s. The density-dependent predation rate is plotted in figure 8*A*, and the way in which percent free space decreases with time, in the absence of sea star predation, is plotted in figure 8*B*. When the settlement rate is four cyprids per cm^2 per week the period of the oscillation is almost precisely 30 wk. This is quantitatively consistent with the data collected at the high-settlement sites in the earlier study (Gaines and Roughgarden 1985). When the settlement rate falls below $s = 0.2$ there are no clear cycles, which is again consistent with the data collected previously (Gaines and Roughgarden 1985). For the low-settlement sites our model suggests two reasons for the lack of statistically significant oscillations. (i) For very low-settlement sites, the barnacles never reach a density that is high enough to attract sea star predation (see figs. 7, 8*B*). (ii) We have assumed that

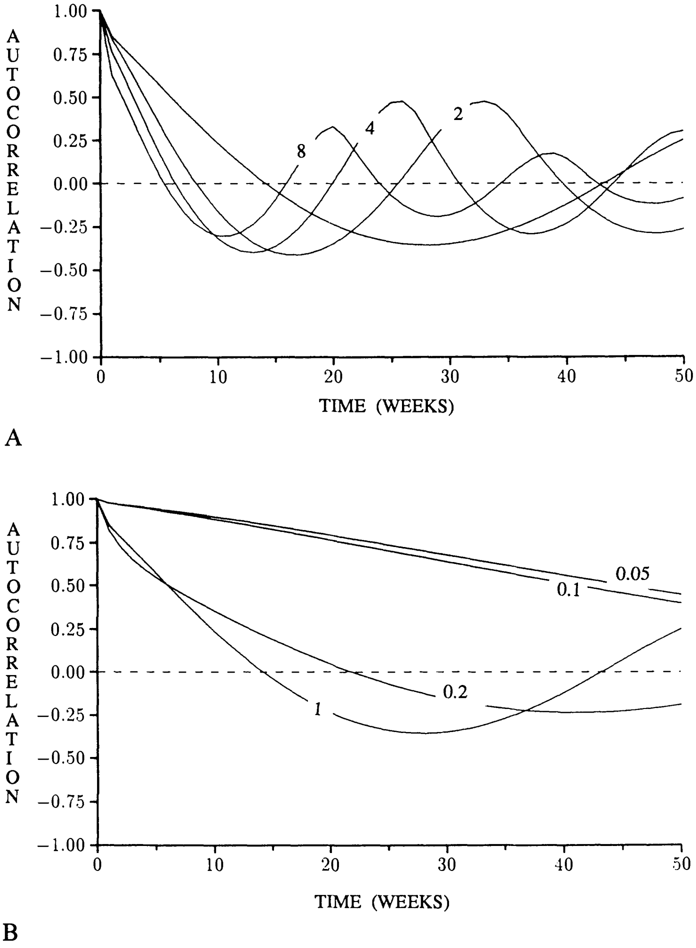

FIG. 7.—The autocorrelation functions calculated with equations (12) and (13) using parameters that fit the data collected in an earlier study (Gaines and Roughgarden 1985): *A*, high settlement rates; *B*, low settlement rates. When the settlement rate is less than one the long period cycles have low amplitude and are unlikely to be observed given background noise.

the only stochastic element is sea star predation. Other stochastic elements, such as demographic stochasticity and larval settlement, will tend to obscure cycles as time passes. Consequently, the greater the period of the oscillation, the less likely we are to discern it in real data. With low-settlement sites we are unlikely to find a peak in the autocorrelation function because of a background of aperiodic noise.

Of these explanations, (i) is most plausible for sites with very low settlement. However, explanation (ii) may indicate why the high-settlement sites failed to show a significant period when the settlement rate dropped below two larvae per cm^2 per week (Gaines and Roughgarden 1985).

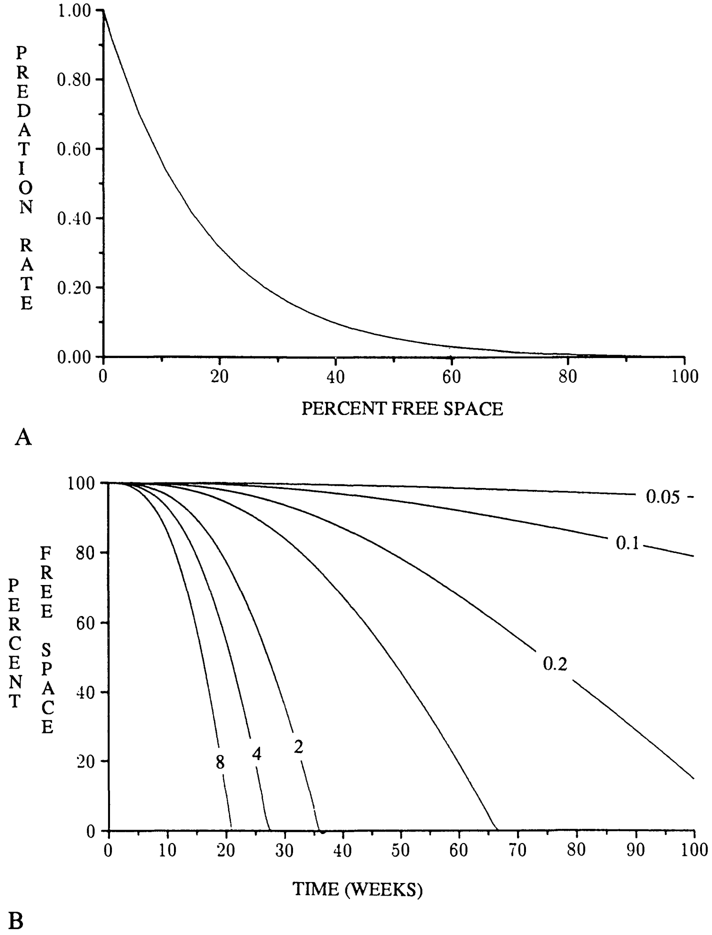

FIG. 8.—Submodels used to fit data collected in an earlier study (Gaines and Roughgarden 1985). Part *A*, the rate at which sea stars visit a patch as a function of the percent free space in a quadrat, equation (14), with *a* chosen so that at 60% cover the probability of sea star predation is 0.1 per week. Part *B*, the rate at which covered space increases with time in the absence of sea star predation for seven different settlement rates (see eq. [14]).

DISCUSSION

We have considered the influence of density-dependent predation on a space-limited prey. We found that, if predation intensity is low at low prey density and increases rapidly at some critical prey density, then the abundance of prey will cycle when observed at the same spatial scale as the predation mechanism. The period of the cycle will be approximately equal to the time it takes the space-limited prey to increase from zero percent cover to the density at which predation becomes attractive, plus the mean time between predation events. The cycles will be most pronounced when the predation rate is high. If there is a maximum prey density, and the prey often reach that density under natural circumstances, then equation (4) provides a more accurate approximation to the period of the cycling. Our conclusions are supported by a detailed model that was tested on data on barnacles collected previously (Gaines and Roughgarden 1985).

Despite the specific nature of the test, the simple models presented here are believed to be relevant to a much wider class of space-limited organism. Indeed, cycles analogous to the ones presented here have been observed in plant communities in which the community-dependent agent of disturbance is fire (White 1979; Horn 1981; Minnich 1983) or wind (Sprugel 1976; Reiners and Lang 1979).

Many authors have noted that space-limited communities can be regarded as a mosaic of patches, with different patches in the mosaic reflecting different types and times of past disturbances (Sousa 1984). As a whole, the composition of the community remains fairly constant, but on smaller spatial scales the composition of the community appears to be constantly changing. The modeling framework we have introduced here fits into this mosaic concept. At the level of an individual, sea star predation appears to be independent of age. At the level of the quadrats in the earlier study (Gaines and Roughgarden 1985), sea star predation depends on the density of individuals in the quadrat. At a larger spatial scale, for example, 100 m of coastline, sea star predation could be simply combined with other density-independent mortality factors. The cycles we have modeled are scale-dependent. The scale at which the cycles are observed depends on the scale of the predation event. By focusing on a dependent variable that reflects the scale of the disturbance we have unraveled the cause of the cycles.

Recently, there has been an increase in interest in stochastic models of population dynamics, especially for sessile organisms (Chesson and Warner 1981). The stochastic approach is particularly relevant where time series data, and other sorts of statistical data, exist about sessile populations and communities. In essence, these stochastic models have the great advantage of predicting not only the average behavior of a system, but also the variability about that average behavior. The model presented in this article is stochastic. The model illustrates the ability of stochastic models to be solved analytically for simple cases, and numerically for more complicated assumptions without recourse to Monte Carlo type simulation. We hope that our efforts here will help to stimulate further modeling in this vein, particularly with regard to building a more comprehensive stochastic picture of the community structure of sessile organisms that incorporates ideas of scale in both space and time.

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APPENDIX A

DERIVATION OF THE DYNAMICS OF THE PROBABILITY DENSITY FUNCTION OF THE PROCESS

From our assumptions about the random process, the transitions in $X(t)$ between t and $t + \Delta$ may be summarized by considering a small time interval t to $t + \Delta$ and a small interval of width h in the percent cover, to get the equation

$$\mathrm{Prob}[X(t + \Delta) \in (x + g\Delta, x + g\Delta + h)] = \mathrm{Prob}[X(t) \in (x, x + h)](1 - d\Delta I_c[X(t)]] .$$

Here we use the indicator function defined as $I_c(x) = 0$ if $x < c$ and $I_c(x) = 1$ if $x \geq c$ to account for the critical value below which predation does not occur. The infinitesimal probability that a predator visits the patch in the time small time interval is $d\Delta$.

Using this equation and considering the ranges $0 \leq x < c$ and $c \leq x < m$, we take the limits $\Delta, h \rightarrow 0$ to find equations (2a) and (2b). The net probability flux at x is $(\partial/\partial x)(gp(x,t))$. Taking the limit of this at $x = m$ and adding in the predation rate yields equation (2c). The part of the probability density function between 0 and $g\Delta$ comes from predation in any patch over the period Δ. Following a similar process this yields equation (2d).

APPENDIX B

ESTIMATING THE DECAY RATE AND THE PERIOD OF THE AUTOCORRELATION FUNCTION

Rescaling with respect to time by dividing equations (3) through by g and defining $t_g = gt$ and $d_g = d/g$ yields

$$\begin{aligned} &\partial p(x, t_g)/\partial t_g + \partial p(x, t_g)/\partial x = 0 && \text{for } 0 \leq x < c \\ &\partial p(x, t_g)/\partial t_g + \partial p(x, t_g)/\partial x = -d_g p && \text{for } x \geq c \\ &p(0, t_g) = d_g \int_c^\infty p(x, t_g)\, dx . \end{aligned} \tag{B1}$$

Now define

$$\begin{aligned} l(x) &= \exp[-d_g(x - c)] && \text{for } x \geq c \\ &= 0 && \text{for } x < 0 , \end{aligned} \tag{B2}$$

which is the probability of a patch being visited before it reaches state x. Putting $p(0, t_g) = \exp[rt_g]$ in equation (B1) and using (B2) yields

$$d_g \int_c^\infty \exp[-rx]\, l(x)\, dx = 1 , \tag{B3}$$

which is the equation we need to solve, for r, to determine the behavior of the autocorrelation function. In general r is a complex number, let $r = u + iy$, with a real part, u, that determines the rate at which the autocorrelation function approaches equilibrium and an imaginary part, y, that determines cycling behavior. Equation (B3) can be rewritten as

$$\begin{aligned} &d_g \int_c^\infty \exp[-ux] \cos(yx)\, l(x)\, dx = 1 \\ &d_g \int_c^\infty \exp[-ux] \sin(yx)\, l(x)\, dx = 0 . \end{aligned} \tag{B4}$$

Coale (1972) does a geometrical analysis of the second equation in (B4), showing that the longest period sine wave that works must have $y \approx \pi/(\text{average of } l(x))$. Thus we estimate that $y \approx \pi/(c + 1/d_g)$ and the period of the process is $T = c + 1/d_g$, which is the same as equation (1).

As the purpose of this section is to find the decay rate of the cycles, u, and the correction to the period approximated by equation (1), w, let

$$r = u + iw + i\pi/T = s + i\pi/T. \tag{B5}$$

Equation (B3) can be rewritten

$$\begin{aligned} 1 &= d_g \exp[d_g c] \int_c^\infty \exp[-sx] \exp[-x(i\pi/(T + d_g))]\, dx \\ 1 &= d_g \exp[d_g c] \int_c^\infty \exp[-\alpha x]\, dx - s d_g \exp[d_g c] \int_c^\infty x \exp[-\alpha x]\, dx + 0(s^2) \end{aligned} \tag{B6}$$

with the expansion

$$\exp[-sx] = 1 - sx + 0(s^2),$$

where

$$\alpha = (i\pi/T + d_g).$$

Solving the integrals in equation (B6) to find s yields

$$s = (c + 1/\alpha)^{-1} \log(K_0), \tag{B7}$$

where

$$K_0 = d_g \exp[d_g c] \exp[-\alpha c]/\alpha \tag{B8}$$

and

$$(c + 1/\alpha) = c + (d_g - (i\pi/T))/((d_g^2 + (\pi/T)^2). \tag{B9}$$

It still remains to reduce s into its real and imaginary parts. Rewriting equation (B8)

$$K_0 = d_g \exp[-i\pi c/T]/(i\pi/T + d_g), \tag{B10}$$

so

$$|K_0| = d_g/(d_g^2 + (\pi/T)^2)^{1/2}. \tag{B11}$$

Also

$$(i\pi/T + d_g) = (d_g^2 + (\pi/T)^2)^{1/2} \exp[i\phi], \tag{B12}$$

where

$$\phi = \tan^{-1}(\pi/d_g T). \tag{B13}$$

Using equations (B10), (B11), and (B12) we find that

$$K_0 = |K_0| \exp[-i(\phi + (\pi c/T))]. \tag{B14}$$

Using equations (B9) and (B14) in equation (B7)

$$s = [c + d_g/(d_g^2 + (\pi/T)^2) - i\pi T/(d_g^2 + (\pi/T)^2)] \times [\log|K_0| - i(\phi + \pi c/T)]. \tag{B15}$$

Multiplying out equation (B15) yields expressions for the real and imaginary parts of s:

$$u = c \log|K_0| + d_g \log|K_0|/(d_g^2 + (\pi/T)^2) - (\pi/T)(\phi + \pi c/T)/(d_g^2 + (\pi/T)^2), \tag{B16}$$

$$w = -(\pi/T) \log|K_0|/(d_g^2 + (\pi/T)^2) - (\phi + \pi c/T)[c + d_g/(d_g^2 + (\pi/T)^2)]. \tag{B17}$$

By calculating equations (B16) and (B17) numerically it is possible to find the decay rate of the cycling, u, and the correction to the period. It can be shown that unless d_g is very small or c is very small w is a very large negative number and T accurately approximates the period of the cycling. Equation (B16) was calculated for a range of values of c and d_g and the following rules emerged: the amplitude of the period decays at a rate roughly proportional to $1/d_g$, and the amplitude of the period decays fastest for small values of c (see fig. 2).

APPENDIX C

ESTIMATING THE PERIOD OF THE CONTINUOUS STATE SPACE PROCESS WITH A FINITE MAXIMUM PERCENT COVER

If there exists a maximum state, m, and the probability of reaching that maximum state is not negligible, then a better approximation to the period is found by referring back to Coale's (1972) original equation and equation (1) (see App. B). The more accurate approximation to the period is

$$T = \frac{c/g + 1/d - (m/g + 1/d)\exp[-d(m - c)/g]}{1 - \exp[-d(m - c)/g]}. \tag{4}$$

The presence of a maximum state reduces the period of the population fluctuations. The magnitude of the error depends on the values of the critical percent cover and the predation rate (see fig. 3).

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