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### A SIMPLE PLANKTON MODEL

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Theoretical studies of an ecosystem tend to aim in two directions: either to capture the essence of some general feature such as predation or competition (May 1973), or to encompass a whole system such as a multispecies fishery (Andersen and Ursin 1977) or a forest (Jones 1977). The direction chosen will depend on the perception of the need to include details of the physical environment or to stress the internal relations between particular species and to close the system by breaking links with other communities. There are exactly comparable problems in experimental and observational work ranging from short-term laboratory studies of a particular behavioral aspect of one species to large-scale and long-term field programs.

In theory and experiment, the close study of some components can lead to predictable relations between parts of the systems that in turn may be expressed in a generally deterministic theory. These parts of the system, isolated by experimental technique or theoretical artifact, must be seen in the context of changes outside the system under study; and these changes often need to be regarded as unpredictable perturbations. Thus the translation of a controlled experiment, or of a theoretical model, back into the larger system can require the addition of unpredictable or random variations as boundary conditions.

These considerations are especially relevant to certain controlled experiments on marine ecosystems carried out in large plastic enclosures which capture 300– 1,300 m<sup>3</sup> of sea water containing at least three trophic levels, phytoplankton, herbivorous zooplankton, and invertebrate carnivores (Menzel and Steele 1978). The problem is to maintain mixed populations of plants and herbivores which in turn can depend on the size and nature of the carnivores. The thesis proposed here is that on capture the enclosure contains a particular level of predators which tends to force the other components to relatively high or low concentrations; whereas outside the enclosures, these lower trophic components are subject to highly variable levels of predation, thus keeping these parts of the system at intermediate concentration. A simple model combining deterministic and stochastic elements is used to illustrate this hypothesis. The mathematical relations have certain similarities with other models, in particular, that used by Ludwig

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et al. (1978) for forests subject to insect attack. This formal similarity raises questions concerning possible ecological comparisons and generalizations.

#### OBSERVATIONS

The patchiness of marine plankton has been studied extensively (see Steele [ed.] 1978) and occurs at all possible length scales. For the invertebrate zooplankton—herbivorous and carnivorous—diurnal vertical migration combined with vertical shear in water movement has the potential to alter the composition and the concentration of populations at all trophic levels (Hardy and Gunther 1935; Evans 1978). In the enclosure experiments the relative horizontal displacements are eliminated.

The enclosures are giant test tubes of translucent plastic, 5-10 m in diameter and 15-20 m deep. The methods and the results for 1976 are described in detail by Gibson and Grice (1977). Since the simple model will deal only with major categories of phytoplankton (P) and herbivores (H), the data are condensed to provide a comparison. We are concerned with relative concentration, and the appropriate method of display is the relation of P to H which can be given in a phase plot.

The first sets of data are derived from experiments carried out in Saanich Inlet on Vancouver Island, British Columbia (Gibson and Grice 1977; Grice et al. 1980). A comparison of P and H for 1976 and 1978 (fig. 1) shows that, after some initial variability, the two experiments took off toward two extreme conditions: low P/high H in 1976 and high P/low H in 1978. The two enclosures in 1978 underwent different physical and chemical treatments; one had no silicate added and no artificial mixing; the other had added silicate (as well as nitrate and phosphate), gentle mixing by occasional bubbling of air in the middle of the water column, and some shading. The gross trends in terms of P/H values are similar even though the trends in species composition of the phytoplankton in the two enclosures differed markedly (Grice et al. 1980). In both years initial conditions were moderate levels of P and H, and observations outside the enclosures in 1978 (fig. 1) showed that extreme conditions did not occur in the natural environment. In 1978 a large population of predatory ctenophores (Bolinopsis sp.) developed in the enclosures, causing the very low level of herbivores and producing large phytoplankton populations whose further growth was probably light limited (Grice et al. 1980). In 1976 predators were, effectively, absent within the enclosure and the low phytoplankton can be related to heavy grazing.

These results were obtained in different seasons of different years. In the intervening year, 1977, large physical perturbations caused by pumping nutrients and particulate matter from the bottom of the enclosure to the top appeared to produce correspondingly large fluctuations between the extremes of 1976 and 1978, indicating that physical variability and corresponding changes in nutrient status cannot be ignored.

The second set of data respond to the question of whether the two trends in P/H can be observed within the same experiments. At Loch Ewe in western Scotland similar experiments (Gamble et al. 1979) were conducted in 1977 except that extra



FIG. 1.—Phase plots of chlorophyll (P) and no. of calanoid copepods (H) from enclosure experiments at Saanich Inlet, British Columbia; 1978 (1) and (2) are data from enclosures; 1978 (3) is from samples outside the enclosures.

predators (herring larvae) were introduced, leading to high concentrations of larvae in one enclosure B and very low levels in the other A. The P and H plots for these enclosures (fig. 2) show the same general divergence. Further, the variations are again of greater amplitude than the changes outside (fig. 2c).

The measurements outside the enclosures reveal a significant amount of variation (Takahashi et al. 1977). Thus in Loch Ewe the chlorophyll varies by an order of magnitude  $(0.5-5.0 \text{ mg/m}^3)$ . These observations are comparable to others in this area (Steele and Baird 1968, 1972) and to observations in the North Sea (e.g., Steele 1978). The range of values within the enclosures is much greater than that usually observed in the open sea and tends to extremes  $(0.1-15.0 \text{ mg/m}^3)$  beyond the normal range.

These results from two very different locations form the basis for the theoretical development. The underlying hypotheses are in two parts. First, that the populations captured on enclosure (including herring larvae added) determine the



FIG. 2.—Phase plots of P and H (see fig. 1) from experiments at Loch Ewe, Scotland. A, enclosure with very small no. of herring larvae; B, enclosure with large no. of larvae; C, water column outside the enclosure.

subsequent time series of biomass changes. Thus the enclosures are considered as "deterministic" systems. The second assumption is that, in the natural environment from which the enclosures were abstracted, predation on the herbivore population is very variable and, as a first approximation, can be regarded as a sequence of random encounters with predator populations varying daily between very high and very low densities. There are very few quantitative data on predator patchiness at scales of 1-100 m (Wiebe 1970) and none for ctenophores, but divers in Loch Ewe observe patchy distribution of ctenophores with clumps on the scale of a few meters (J. C. Gamble, personal communication).

In the enclosures a more regular sequence of predator populations is found. Figure 3 portrays the sequences in 1978 for herbivores and for ctenophore predation rate determined from experimental studies (M. R. Reeve, unpublished). These observations show that there is a time lag between the development of the herbivores and their predators. Initially this lag will be ignored, but its consequences will be explored after the simple model has been developed.

### THEORETICAL DEVELOPMENT

In the context of the problem defined by the observations it appears inappropriate to attempt to portray the full details of the plankton ecosystem by one elaborate model. Instead, a simple caricature will be developed in the hope of providing insight into the possible factors which may cause those divergent trends in the enclosures and relate these to events outside.

For nutrients N, phytoplankton P, and herbivores H, three equations are used and detailed in Appendix A.



FIG. 3.—A, calanoid copepod numbers in the two enclosures at Saanich Inlet in 1978; B, estimates of clearance rate by the ctenophore predators in the two enclosures in 1978.

$$\frac{dN}{dt} = -\text{uptake} + \text{excretion} + \text{added } N, \tag{1}$$

$$\frac{dP}{dt} = [\text{growth } (P) - \text{grazing}] - \text{sinking} - \text{mixing}, \qquad (2)$$

$$\frac{dH}{dt} = [\text{growth } (H) - \text{predation}]. \tag{3}$$

A qualitative understanding of the P-H components of the system can be obtained by examining the bracketed relations of equations (2) and (3), expressed in the simplified form

$$\frac{dP}{dt} = (a - P)P - \frac{P^n}{1 + bP^n}H,$$
(4)

$$\frac{dH}{dt} = \frac{cP^n}{1+bP^n}H - dH^m.$$
(5)

The phytoplankton growth is given in a logistic form with *a* containing effects of varying incident light or nutrient concentration. The "carrying capacity" component will arise from self-shading that, with increasing populations, reduces average light in a mixed layer until photosynthesis balances respiration. The rate of grazing by H on P may be expressed as a hyperbolic relation, with n = 1, or as an S-shaped curve with n = 2 (Holling 1959). Predation on H is given as  $d \cdot H^{m-1}$  per unit of H. If m = 1, then predation rate is a fixed fraction of the herbivore population; if m = 2, then it is assumed that the predator population changes in proportion with the herbivores.



FHITOFLANKTON (F)

FIG. 4.—Phase plots of the equilibrium conditions for P and H from eqq. (4) and (5) with m = 1, 2; n = 1, 2. Solid line gives solutions with dP/dt = 0; dashed line gives solutions of dH/dt = 0 with a range of values of d. Intercepts marked by circles are stable equilibria; crosses indicate unstable equilibria.

There are four cases that can be considered by taking m = 1, 2; n = 1, 2 and examining the equilibrium solutions of (4) and (5). These are illustrated in figure 4 to show the effects of different values of d on the intercepts and so on solutions for P and H at steady state. There is a large literature on such graphical expressions of prey-predator systems (e.g., Noy-Meir 1975) which points out the existence of multiple solutions that permit the system to bifurcate as the value of some coefficient, such as d, changes in a continuous manner. This bifurcation occurs in figure 4d and, in essence, is the same as the system proposed for the spruce budworm in which a slowly changing parameter takes the system abruptly from one state to another (Ludwig et al. 1978).

We are concerned here with the applicability of any part of figure 4 to the planktonic system and, in particular, to the subsystems studied in enclosures. There is argument about the appropriateness of n = 1 or n = 2 to herbivore grazing (see Steele and Mullin 1977) with conflicting evidence for n = 1 in the laboratory but n = 2 in experiments with natural populations (Parsons et al. 1969; Adams and Steele 1966). In choosing a value for m, changes in the enclosures in 1978 suggest m = 2 since the invertebrate predators followed the herbivore density, although there was a time lag. Further, the theoretical results in figure 4d for low and high predation most nearly approach the observations of low P/high H. For these reasons (and because the results are more interesting) m = 2, n = 2 will be used here.

The consequences of added variability can be investigated. For this simple example, stochastic changes in d are imposed by adding a term  $d = do + d^*$ , where  $d^*$  is derived at each daily time step in a simple simulation of (4) and (5)



PHYTOPLANKTON (P)

FIG. 5.—Equations (4) and (5), with equilibrium conditions comparable to fig. 4d, were run for 100 time intervals (days). Values for d, fixed for each run, were chosen within a range  $d_{\text{max}}$ ,  $d_{\text{min}}$  where  $d_{\text{max}} = 10.d_{\text{min}}$ . Ninety percent of all the values of P and H at each time step lie close to the solid lines. When d was varied randomly at each time interval between the limits used for the deterministic runs, 90% of the values lay within the dotted line and 70% within the dashed line.

using a random number generator that gives a statistically uniform distribution of d between  $d_{\text{max}}$  and  $d_{\text{min}}$ . The values of  $d_{\text{max}}$  and  $d_{\text{min}}$  are chosen to give single-valued solutions on the upper and lower limbs of the cubic in figure 4d. The average of  $d_{\text{min}}$  and  $d_{\text{max}}$  lies in the region of triple-valued solutions.

By making a number (10) of runs with different random sequences but the same initial values of P and H, it is possible to generate distributions of the frequency of occurrence of values of (P, H) within certain regions of the phase plane. An example (figure 5) shows that the distributions from stochastic runs are very different from those which would be found with the deterministic model using values between  $d_{\text{max}}$  and  $d_{\min}$ . There is, however, one limitation. To achieve the results in figure 5, the rate of growth a must be comparable to the rate at which d varies. If d changes rapidly with the growth rate, then the system can average out the fluctuations in d. If d changes very slowly compared with a, then the system goes through a small sequence of "deterministic" runs. The latter situation, with d changing monotonically, is comparable to the budworm, with periods of very low density followed by "outbreak" population levels. For phytoplankton, on the other hand, daily doubling rates are possible, and this is comparable to the frequency of changes in predators if these changes are assumed to result from diurnal vertical migrations combined with vertical shear.

### The Effects of Nutrient Limitation

The simple system used so far has considered only the phytoplankton-herbivore interactions with a variable coefficient, d, representing changes in predator population. We can also expect changes in the growth rate of the phytoplankton



FIG. 6.—Equilibrium conditions of P and H from eq. (4) with a range of values of a.



PHYTOPLANKTON GROWTH FACTOR (a)

FIG. 7.—The relations between a and d which define the regions where single- and triple-valued solutions of eqq. (4) and (5) exist. Changes in a and d which transfer the system across the triple-valued region cause very large changes in P and H.

population. Some of these changes may be relatively rapid as a result of variations in daily total of incident light. (We are ignoring the diurnal components in this initial analysis.) Other changes will depend on rates of uptake of nutrients which will affect growth rates. Again we are ignoring the complexities of the uptake/ growth relation (Droop 1974).

For this simple initial analysis we can assume that decrease in nutrients will result in decrease in the value of a. The consequence (figure 6) of such changes on the form dP/dt from equation (4) is to eliminate the triple intersections for sufficiently small a. Also, with changing a, the values of d where there is an unstable solution will change. This bifurcation can be represented in the a/d plane (figure 7) by the (a, d) values where the two isoclines are tangent (see Ludwig et al. 1978). In the discussion of the natural environment, d was considered as a fast,

random variable. Changes in a due to nutrients are likely to be slower and, typically, a will decrease monotonically to near zero over a 10–30 day period. This will tend to take the system out of the three-valued region toward a regime of relatively low variance.

In the enclosures, however, it is necessary to add nutrients to the upper layer so that primary production does not run down completely. This addition is sometimes done by pumping the high nutrient concentrations from the bottom to the top of the enclosures. For systems with low predator populations (low d), this could cause the sytem to "jump" across the bifurcation barrier into a different regime and so produce a quite different sequence after the enrichment. In a very general sense, this may explain some of the large and erratic variations observed in the 1977 enclosures when such "upwelling" was used.

The qualitative behavior of the simplest model provides insight into the responses of the system that may occur under different natural or experimental conditions. The remaining questions concern the quantitative response when realistic values are chosen for the various coefficients.

# Numerical Solutions

Even with such a simple model as that outlined in equations (1)-(3) and detailed in Appendix A, there is still the need to specify 14 coefficients. Appendix B lists the values and summarizes the sources used. Most of these coefficients can have a relatively large range, so the output is certainly not specified unambiguously. However, the choice of a range of d can be made to produce effects similar to that of the simple two-level model, and the predation rates derived from this range can be compared with those deduced from the enclosure experiments. In the stochastic runs a was also varied randomly on a daily basis by a factor of three to simulate fluctuations in incident radiation.

The results of numerical simulations are presented as phase plots in figure 8 for two different initial conditions. With the overall condition, N + P + H = 1 (g C/m<sup>3</sup>). It can be seen that the complete system including nutrients still "bifurcates." The critical value of d is about 1.0, and the change produces large changes in P but only small fluctuations in N (fig. 9) between the two runs around the bifurcation value. (For small values of d, there is a later increase in N which is not observed in the enclosure experiments because nutrient addition was stopped when N reached a value of 1 mg at/m<sup>2</sup>.) Thus the introduction of a nutrient equation does not change the qualitative nature of the results derived for the P/H system.

When the stochastic elements are introduced, then marked differences appear compared with the deterministic runs. The results of two sets of 10 runs (fig. 8) show the same general features as the simpler model, but the detailed response appears to depend on the initial distribution of nutrients between the three components; soluble inorganic, plant, and herbivore.

This somewhat more complex model, which introduces nutrients, exhibits the same general features as the simpler plant-herbivore system. The inclusion of some extra detail can permit a quantitative comparison with observation. This is best done through the choice of the range of values of d necessary to produce the



FIG. 8.—Solid lines describe the trajectories of (P, H) in the phase plane resulting from two initial conditions (a) N = 0.77, P = .08, H = 0.15; (b) N = 0.96, P = 0.02, H = 0.02, and from values of d between 0.25 and 1.75. The shaded areas depict the distribution of values in runs where d varied randomly, daily, between 0.25 and 1.75: (a) 90% within the shaded area; (b) 75% within the shaded area.

qualitatively different responses shown by observations in figures 1 and 2 and by theory in figure 7. From the observations, the rates of predation required to produce a high P/low H system have a maximum (fig. 3) of 0.10. From the theory, the corresponding value is  $d \cdot H$  which, according to figure 7, must exceed 0.10 to produce the required effect. It should be noted that other predators, such as *Sagitta* spp. and carnivorous copepods, occur in the enclosures, increasing the predation rate over that deduced from the *Bolinopsis* experiments. Therefore the numerical comparison is, at least, of the right order. Thus a more quantitative analysis supports the general explanation in terms of differing predation rates derived by the simpler qualitative model.

### Time Lags

There is, however, a further artificiality in the theoretical system. For large d the values of H show no peaks in the development of the populations with time. In consequence, there is no corresponding peak in predation rate dH, such as that observed in 1978 (fig. 3).



FIG. 9.—Time sequence of (a) N and (b) P for two values of d; 0.75, 1.25.

If, however, time lags are introduced into the predation term so that the predation rate at time t is  $d \cdot H_{t-\delta}$  then we can simulate the consequences of the observed delay in the peak of predation rate compared with the herbivore peak.

Using the critical value of d = 1.0 and the initial conditions of figure 7*a*, three time delays have been used,  $\delta = 5$ , 10, and 15 days, which span the probable delay observed in figure 3. As would be expected, time delays introduce greater variability in the response, (fig. 10) and produce the requisite peaks at intermediate times in each of the runs.

It is also of interest to note that with d = 1.0 the cycle of P, H from  $\delta = 5$  to  $\delta = 15$  days (fig. 10) is similar to that of d = 1.25 to d = 0.25. Thus, in principle, increasing the time lags has the same effect as lowering the predation rate, since both decrease the control on the growth of the herbivore populations.

### DISCUSSION

Natural planktonic ecosystems display great variability in space and time. As a rough method of separation, the variability between samples can be divided first into differences of biomass of each trophic level, and then to relative changes in species composition within a trophic level. The samples can be taken as a series in space, a sequence in time, or, for most sampling programs, a combination of the two. The enclosed plankton ecosystems provide the opportunity to sample from a time sequence, and the results have been very useful in studying the ef-



FIG. 10.—Effects on the (P, H) relations of time lags of a, 5, b, 10 and c, 15 days.

fects of pollutant additions on the species structure of populations (Menzel 1977; Davies and Gamble 1979). At the same time there are differences in biomass between or within experiments and, especially, between the enclosures and the outside environment. Some of these differences appear to be the consequence of enclosure; others can help to elucidate processes which can occur in the normal environment.

The very simple theory developed here concentrates on the biomass aspect and ignores the internal structure of each trophic level, particularly the size composition (Steele and Frost 1977). This theory permits emphasis upon the external factors, light and nutrients (represented by a) and predation (d). Regular diurnal changes in light have not been included explicitly. Light cycles may influence spatial patterns through a combination of vertical migration and vertical shear (Evans 1978). With present physical and biological sampling methods, it is not possible to test this directly in the open sea. One factor, the shear, is removed in the enclosures, and it is this component which may be responsible for random variations of the predators in relation to the herbivore population outside the enclosure. Thus the addition of a day-to-day random element to the predation rate is used to simulate the potentially significant effects of diurnal changes. (The

effects of variable weather in changing the total daily insolation are included in the final stochastic runs.)

In general, alterations in growth rate as a result of nutrient changes can be expected to have a time scale of weeks rather than days. The general pattern in nutrient concentration is a monotonic decrease in the spring and increase in the fall. Superimposed on this are "spikes" of nutrient addition caused by rapid vertical mixing usually induced by high winds (or by upwelling in the enclosures). Ignoring the seasonal cycle, which has, of course, very marked effects on biomass, we have considered different starting concentrations of nutrients, with the condition that initial total nutrient in the three components N, P, H is constant. When the deterministic and random runs are compared with those using only a P/H system, we still have the general conclusion that the fast fluctuating parameter d removes the bifurcation observed with fixed d. The slower changes in a due to nutrients do result in significant differences (in the models) for the statistical distributions of (P, H) values but do not alter the generally unimodal patterns.

This simple theory attempts to provide an explanation for the differences between enclosures and the open sea. It has two essential postulates: (1) the existence of interactions which, in a deterministic theory, lead to the possibility of multiple stable states for the ecosystem, and (2) the existence of spatial variations which lead to large amplitude fluctuations in the predation rate on the herbivores, fluctuations which are removed by enclosure. There is evidence for the postulated functional response of the herbivores and for variability of the predators, but the evidence is not unambiguous. Thus it is of interest to look at a comparable theory for a quite different ecosystem.

The spruce budworm in Canadian forests can increase its density several hundredfold and defoliate mature trees. The outburst and defoliation take about 7 yr and occur every 30-50 yr (Ludwig et al. 1978). The budworms are preyed on by birds whose functional response is assumed to be the same as that used here for the plankton predators. A logistic form was used in a simple model for budworm growth. Thus the basic budworm equation is the same as the herbivore equation (4). (In fact, the choice of the plankton equations was influenced by discussions with the late Dixon Jones comparing the two ecosystems.)

The difference between the two systems is that the natural state in one system corresponds to the manipulated state in the other, and vice versa. Normally, the budworm is in one or other of two extreme conditions, very low or "outbreak" levels. Manipulation by spraying with insecticide when budworm concentrations or foliage condition approach the threshold for outbreak can keep the system between these extremes. The implication is that the normal system is dominated by the slowly changing parameter forest growth and there are no spatially variable factors, such as budworm or bird migrations, capable of sufficiently fast change to override the slow variables (Clark 1979). Thus the tree growth rate defines the periodicity of potentially fast-growing insect populations.

Apart from the annual seasonal cycles, there are no readily observable periodicities in natural plankton populations, although these could occur in association with the life cycle of herbivorous copepods which is approximately 50 days (Steele 1974). The variability in data prevents any observation of such periodicities and the analysis here would suggest that spatial heterogeneity provides mechanisms to prevent trends to extreme conditions which can be found in the manipulated ecosystems of the enclosures.

Thus in the spruce budworm and plankton ecosystems similar processes, formalized by the same basic equations, may be present; but the observed systems are very different. This difference depends on the similarity, in plankton, between rates of growth and of fluctuation; and in the budworm, on the very great difference in the rates of change of forest and budworm.

#### SUMMARY

Data on plankton ecosystems in large enclosures are used as a basis for consideration of the role of deterministic and random processes in these systems. Using a simple model, it is proposed that the exclusion of random variations in predators can lead to greater extremes in the phytoplankton/herbivore populations in enclosures compared with those outside. These results depend on the relative rates of internal and exogenous changes, and comparisons are made with results for a forest ecosystem.

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### APPENDIX A

EQUATIONS USED FOR NUTRIENTS (N), PLANTS (P) AND HERBIVORES (H)  

$$\frac{dN}{dt} = -F1(P,N)*P + F2(P)*H + F2A(H)*H + F3(N)$$

$$\frac{dP}{dt}F1(P,N)*P - F4(P)*H - F5(P)$$

$$\frac{dH}{dt} = F6(P)*H - F7(H)*H$$

where

$$F1(P,N) = \frac{N}{R2 + N} * \frac{A3}{A4 + A5*P} - A6$$

$$F2(P) = \frac{C2*P^{n}}{1 + B2*P^{n}} F2A(H) = C3*D3*H^{m-1}$$

$$F3(N) = K1* (NO - k2*N), F5(P) = K3*P$$

$$F4(P) = \frac{B1*P^{n}}{1 + B2*P^{n}}, F6(P) = \frac{C1*P^{n}}{1 + B2*P^{n}}$$

$$F7(H) = D3*H^{m-1}$$

A3 = A1 + A2\*RAND(Z1,Z2) D3 = D1 + D2\*RAND(Z1,Z2)

Z1 = minimum of range Z2 = maximum of range

# APPENDIX B

#### NUMERICAL VALUES USED FOR THE MODEL

Units used are gC/m<sup>3</sup> with the equivalences 1 g C/m<sup>3</sup> = 20 mg Chl/m<sup>3</sup> = 10 mg at N/m<sup>3</sup>. The term  $A3/(A4 + A5^*P)$  is equated to the phytoplankton growth term  $2.5/(kZ_e)$  in Steele and Frost (1977) where  $Z_e$  is the mixed layer depth taken here for convenience as 12.5 m, half the maximum bag depth of 25 m. The attenuation coefficient k depends on chlorophyll, and this factor is taken from Steele and Frost using the conversion to carbon. The respiration rate, A6, is taken from Steele and Frost's value for a 10  $\mu$ m diameter cell at 10° C. The sinking rate, K3, is chosen to lie within the range of values for a 10  $\mu$ m cell used in Steele and Frost.

The nutrient coefficients were selected in discussion with Curt Davis. The zooplankton terms were derived on the assumption of a "Pseudocalanus" type herbivore growing from an initial carbon content of about 0.1  $\mu$ g to a final content of 10  $\mu$ g over a 30-day period.

In summary, the values used for the "deterministic" runs were:

- A3 = 0.2, to give a maximum growth coefficient of 1.0;
- A4 = 0.2, to give 1% light at 20 m maximum;
- A5 = 0.4, from Steele and Frost (1977);
- A6 = 0.15, to give a 15% respiration rate;
- K3 = 0.04, equivalent to 0.5 m/day sinking rate;
- R2 = 0.03, corresponding to  $k_s = 0.3$  mg at N/m<sup>3</sup>
- K1\*N0 = 0.03, K2 = 0, defining a daily rate of addition of 0.3 mg at N/m<sup>3</sup>;
  - B1 = 480, (4\*C1) gives growth efficiency of 25%;
    - B2 = 800, gives half maximum grazing at P = .035 g C/m<sup>3</sup>;
    - C1 = 120, lets "Pseudocalanus" grow from egg to adult in 30 days;
    - C2 = 160, from the ratio C2/B1, nutrient excretion is 33% of intake;
    - C3 = 0.5, half the predation is returned as nutrient;
    - D3 = 1.0, see text.

For the stochastic runs, A1, A2, D1, D2, 21, and 22 were chosen so that  $0.1 \le A3 \le 0.3$  and  $0.25 \le D3 \le 1.75$ .

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