

- Spurlock, B. O., V. C. Kattine, and J. A. Freeman, 1963. Technical modifications in maraglass embedding. *J. Cell Biol.* 17: 203.
- Strickland, J. D. H., and T. R. Parsons, 1968. *A Practical Handbook of Seawater Analysis*. Bull. Fish. Res. Board Can., Ottawa Canada, No. 167. 311 pp.

A Model of Annual Plankton Cycles

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Abstract A model is presented that exhibits a spring phytoplankton bloom as one feature of a steadily repeating annual cycle of plankton populations. Populations respond to seasonal changes in light (which are gradual) and in mixed layer depth (which may be rapid). The occurrence of a bloom does not require a shallowing of the mixed layer; it does require a low rate of primary production in winter. The lack of phytoplankton blooms in the subarctic Pacific can be explained in terms of this model.

Analysis of a simplified version of the model shows that a bloom is a deviation from quasi-equilibrium behavior and explains why this will occur when winter production rates are low.

Introduction

Observations of spring plankton blooms are of two sorts. There are detailed, deliberate programs which measure many variables for a relatively short time. There are also casual, anecdotal ob-

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servations that phytoplankton is abundant for a short period almost every spring; in other words, the phenomenon studied in the detailed programs is expected to recur every year. This second sort of observation is rather subtle, because it implies that the ecosystem not only produces a bloom in the spring but also recreates, over the fall and winter, the conditions necessary for a bloom. A spring bloom is not an isolated event, but one feature of a roughly repeating annual cycle.

Many mathematical models simulate programs of detailed observations of a bloom (e.g., Riley, 1946; Steele, 1974; Winter et al., 1975; Sjöberg and Wilmot, 1977). A model that represents the cyclic nature of blooms would have advantages. First, it would avoid the need to specify initial conditions. A differential equation model of population dynamics cannot by itself predict population densities; it can only predict how initially prescribed densities will change. Early behavior in a model is a consequence as much of the initial conditions as of the equations. However, we expect the limiting, long-time behavior of the model to be essentially independent of starting conditions: there is a steady cycle which is approached from almost all starting conditions. Secondly, a cyclic model would capture a common feature of ecosystems: they can recover from disturbances. Perturbations producing "initial" conditions well away from the steady cycle will often be forgotten, and the cycle will become reestablished after a short time. Thirdly, if we want not just to describe an ecosystem, but also to predict how it would react to permanent changes in its surroundings, we must remember that these changes will ultimately produce changes in the pre-bloom conditions. Observed initial conditions will not be appropriate for predicting the long-term effects of permanent changes; instead, we must examine the change in the steady cycle. Notice that the ability to make this sort of long-term prediction is a feature of mathematical models not shared by verbal descriptions. Kremer and Nixon (1978) calculate an annual cycle for Narragansett Bay, but they do not present it as an essential part of their work.

The cycle of plankton populations is driven by the annual cycle of physical conditions in the sea. These conditions include

surface light and water temperature, which undergo gradual seasonal changes, and the depth of the upper mixed layer, which can sometimes change rapidly due to the formation or breakdown of a seasonal thermocline. In the classical view, this sudden shallowing of the mixed layer causes the spring bloom. Phytoplankton cells that are trapped above the seasonal thermocline suddenly spend much more of their time in the light; they experience a sudden increase in their net growth rate, and a bloom follows (Gran and Braarud, 1935; Sverdrup, 1953). Sverdrup suggests that the bloom starts when the mixed layer depth becomes less than the critical depth, the depth down to which the average net growth rate is zero. Notice that his critical depth is determined in part by the density of herbivores, so that this depth depends on the plankton concentrations, which are part of the annual cycle.

We wish to investigate the features common to annual cycles (in particular, spring blooms) in different places, rather than simulate the physical and taxonomic detail of one place. We have therefore constructed a fairly simple, differential equation model of nutrients, phytoplankton, and herbivores in a mixed layer of varying depth, responding to physical changes that have exactly the same pattern year after year. The response of phytoplankton to light is modelled in some detail, other aspects in less detail. We examine the annual cycles of plankton concentrations produced by this model. Then, using techniques of qualitative analysis of differential equations, we explain the model's behavior. Finally, we discuss the relevance of the model to areas like the Subarctic Pacific, where spring blooms do not occur.

The Model

We modelled the exchanges of matter (expressed as nitrogen, although the choice of unit is not important) among various forms in the upper mixed layer of the sea. The forms were dissolved nutrients, phytoplankton, and herbivorous zooplankton. No horizontal effects were considered, so the model is appropriate for large, uniform areas of open ocean or possibly for gyres over coastal fishing banks. Because this is a model of annual

cycles, fluctuations with a period of a day or less were averaged. We assumed that photosynthesis, nutrient uptake, and herbivore grazing were immediately converted to population growth. This is a slight distortion for crustacean herbivores, whose population growth is limited by life-history patterns, as well as food availability. It more accurately represents continuously reproducing herbivores, such as ciliates and tunicates. Although they are underrepresented by older sampling methods, these herbivores are now being recognized as an important part of pelagic ecosystems (Heinbokel and Beers, 1979; Alldredge, 1981).

We did not attempt to model upper-layer dynamics. Instead, we assumed that the ocean is divided into two completely mixed layers: an upper, biologically active layer containing nutrients and plankton whose concentrations do not change with depth; and a lower, inactive layer containing nutrients but no plankton. The rate of change of mixed layer thickness was prescribed by a function $\zeta(t)$ chosen to represent observations or alternatives we wished to investigate. Changes in mixed layer depth affect the model asymmetrically. As the mixed layer deepens ($\zeta > 0$), water from the inactive zone is mixed with surface water, producing a mixing of surface and deep nutrients and a dilution of phytoplankton within the upper mixed layer. As the mixed layer shallows, no new water is mixed into the surface; so, nutrient and phytoplankton concentrations do not change. Thus, a deepening mixed layer preserves the amount of phytoplankton under a square meter; a shallowing mixed layer preserves the concentration of phytoplankton in a cubic meter. We assume that herbivores can maintain their position feeding in the upper mixed layer, and therefore a shallowing mixed layer will concentrate them. To capture this asymmetry, it is convenient to define $\zeta^+(t) = \max(\zeta(t), 0)$. Nutrients and phytoplankton are also subject to diffusion across the bottom of the mixed layer.

The photosynthetic rate of phytoplankton is a function $\alpha(t, M, P)$ of time of year t , mixed layer depth M , and phytoplankton concentration P (because of shading). (The details of calculating α , including seasonal changes in light, are described in the appendix.) Growth is reduced by nutrient limitation, according to a Michaelis-Menten hyperbola, and by a constant representing

soluble metabolic loss. Grazing of phytoplankton by herbivores is modelled by a Michaelis-Menten hyperbola above a threshold concentration. Carnivores are not modelled explicitly; their effects are simulated by constant mortality of the herbivores.

In summary, the model equations for mixed layer depth, M , dissolved nutrient concentration, N , phytoplankton concentration, P , and herbivore concentration, H , are:

$$\begin{aligned}\frac{dM}{dt} &= \zeta(t) \\ \frac{dN}{dt} &= -\left[\frac{\alpha(t, M, P) N}{j + N} - r\right]P + \frac{m + \zeta^+(t)}{M} (N_o - N) \\ \frac{dP}{dt} &= \left[\frac{\alpha(t, M, P) N}{j + N} - r\right]P - \frac{c(P - P_o) H}{K + P - P_o} - \frac{m + \zeta^+(t)}{M} P \\ \frac{dH}{dt} &= \frac{fc(P - P_o) H}{K + P - P_o} - gH - \frac{\zeta(t)}{M} H\end{aligned}\quad (1)$$

Table 1 gives meanings and typical values of the parameters. Although these values are believed to be correct, or at least well within the observed range, the conclusions we shall draw do not depend on obtaining exact values. The physical parameters in Table 1 are appropriate to Flemish Cap, an offshore bank east of Newfoundland; we shall later use parameters suitable for other regions. Some rates taken to be constant will, in fact, vary over the course of the year; they include maximum photosynthesis, maximum herbivore grazing, and vertical mixing. We have no reason to think that a more detailed treatment would alter the points we wish to make. In particular, experimenting with different values of the mixing rate, m , the least certain parameter, does not lead to any important changes in our conclusions. Note the use of $\zeta(t)$ rather than $\zeta^+(t)$ in the H equation: The shallowing of a mixed layer concentrates herbivores.

Figure 1 shows the long-term, steady, cyclic behavior of the model for the parameters of Table 1. Data on the mixed layer were from Station 27, near St. John's, Newfoundland. This area is not in a gyre, but limited data from the gyre on Flemish Cap

Table 1
The model parameters

Parameter	Symbol	Unit	Value	Source
Deep nutrients	N_o	mM m^{-3}	10	(1)
Uptake half saturation	j	mM m^{-3}	0.5	(2)
Plant metabolic loss	r	d^{-1}	0.07	(3)
Grazing threshold	P_o	mM m^{-3}	0.1	(4)
Grazing half saturation	K	mM m^{-3}	1.0	(4)
Maximum grazing rate	c	d^{-1}	1.0	(5)
Grazing efficiency	f	—	0.5	(6)
Loss to carnivores	g	d^{-1}	0.07	(6)
Maximum photosynthetic rate	Q	d^{-1}	2	(7)
Low light photosynthetic slope	α	$(\text{ly})^{-1}$	0.04	(8)
Light attenuation by water	k	m^{-1}	0.10	(9)
Light attenuation by phytoplankton	l	$(\text{mM m}^{-1})^1$	0.12	(10)
Latitude	ϕ	degrees	47	(11)
Diffusion rate	m	m d^{-1}	3	(12)
Cloud cover	b	—	0.9	(13)

In most instances, a wide range of parameter values is reported in the literature; we have used an apparently reasonable value from within the range. Sources noted are: (1) Parsons et al., 1977; (2) Eppley et al., 1969; (3) Harris and Piccinin, 1977; (4) Frost, 1975; (5) Paffenhöfer and Harris, 1976; (6) Steele, 1974; (7) intermediate between Eppley, 1972; and Cote and Platt, 1983; (8) Cote and Platt, 1983; (9) Ivanoff, 1977; (10) a linear approximation of Riley, 1956; (11) Dietrich, 1969; (12) Kullenberg, 1974 (this is a particularly uncertain parameter, depending on the vagaries of the weather and the artificial assumption of a perfectly mixed upper layer with a sharp lower boundary); (13) J. T. Anderson, pers. comm.

are consistent with this picture. In April, the thermocline rises quickly from 80 m to 25 m, and a phytoplankton bloom follows. (In order to represent high and low concentrations at different times of year on the same graph, we use a square-root transformation of phytoplankton and herbivores. The peak amplitudes therefore appear compressed.)

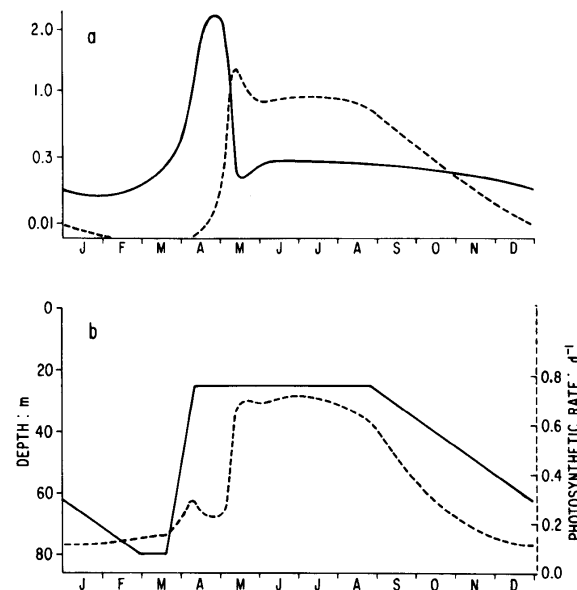


FIGURE 1. (a) The annual cycle of Model 1 phytoplankton (—) and herbivores (---), expressed in millimoles of nitrogen per cubic meter, for the parameters of Table 1. (b) The annual cycle of mixed layer depth (—; m) and photosynthetic rate α (---; d^{-1}).

Intermezzo

As a description of the annual cycle, this model (any model, any description) is incomplete. By extending it in various ways, one could ask interesting questions about vertical distributions of phytoplankton and herbivores, phytoplankton species succession, life-history patterns of herbivores, carnivore population dynamics, and so on. For all such questions, studying steady annual cycles, which regenerate their own initial conditions, will provide valuable insights.

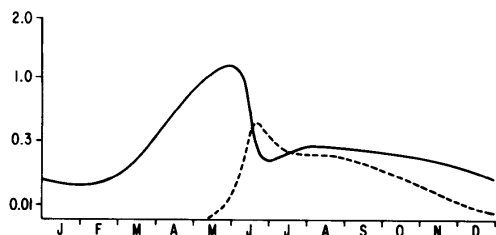


FIGURE 2. The annual cycle for a mixed layer depth of 80 m.

Our interest, however, is in the model as an explanation, rather than a description of blooms. The question here is not whether we have put enough into the model, but whether we have put too much. Before claiming that rapid shallowing of the mixed layer is the cause of the spring bloom, we must see what happens if such shallowing is absent. Therefore, we examined the steady cycles of Model (1) corresponding to mixed-layer depths fixed at the extreme values. With the mixed layer fixed at 80 m (Figure 2), there is still a bloom. It occurs later in the year and is somewhat smaller (21 instead of 27 times its minimum level), but it is a bloom nonetheless. In fact, if we plot total phytoplankton under a square meter rather than in a cubic meter, the constant 80 m mixed layer could be considered to produce a larger bloom (Figure 3). On the other hand, if the mixed layer is fixed at 25 m, there is no spring bloom (Figure 4). Do blooms depend on deep, rather than shallow, mixed layers?

The Reduced Model

To explore this question, we can look at simpler models, removing as much of the model structure as possible while retaining the phenomenon of interest. The explanation of the phenomenon must then lie in the structure that is left, and will be easier to find once distractions have been removed.

If we are interested simply in whether blooms can occur, and not in their detailed development, we can eliminate the nutrient

equation: nutrients are abundant in winter, and could become limiting only after a bloom had occurred in the spring. On similar grounds, we eliminate the shading effect of phytoplankton on their growth rate. We have already demonstrated that changes in mixed layer depth are not essential. The growth rate α then depends only on the time t , and can be modified to include losses to metabolism and mixing. As it turns out, $\alpha(t)$ is well approximated by a sinusoidal function with a period of one year, varying between its calculated midwinter and midsummer values. We thus have Model (2):

$$\begin{aligned} \frac{dP}{dt} &= \alpha(t) \cdot P - \frac{c(P - P_0)}{k + P - P_0} H \\ \frac{dH}{dt} &= \frac{fc(P - P_0)}{k + P - P_0} H - gH \end{aligned} \quad (2)$$

Running Model (2) with $\alpha(t)$ corresponding to an 80 m mixed layer produces Figure 5 (cf. Figure 2); with a 25 m mixed layer we get Figure 6 (cf. Figure 4). Although there are differences in timing and magnitude, the general pattern has not been changed by this simplification. (Figure 5 actually represents a parameter set in which the phytoplankton metabolic rate $r = 0.064$. If $r = 0.07$ as usual, the bloom is larger but qualitatively similar.)

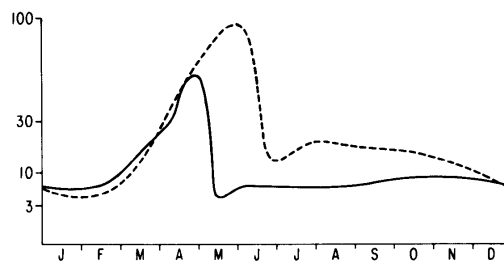


FIGURE 3. Vertically integrated phytoplankton (millimoles under a square meter) from Figure 1 (—) and Figure 2 (-----).

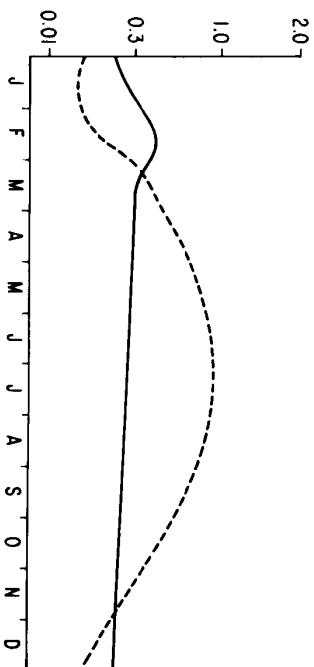


FIGURE 4. The annual cycle for a mixed layer depth of 25 m.

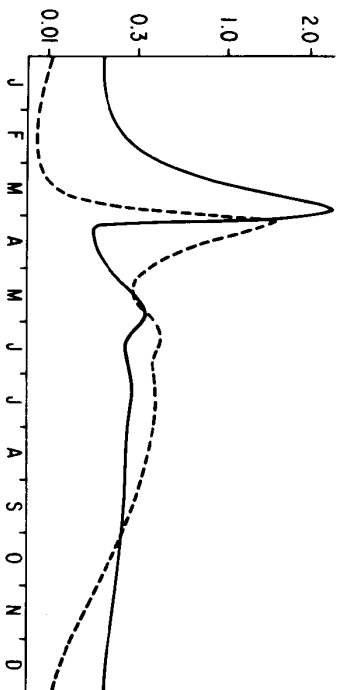


FIGURE 5. The annual cycle of Model 2 corresponding to a mixed layer depth of 80 m.

Analysis

In simplifying the model, we have preserved the feature of interest: there is a spring bloom when the mixed layer is deep but not when it is shallow. Comparing Figures 5 and 6, we see that high winter production maintains herbivore densities large enough to graze down incipient blooms and a low winter rate does not. However, in a repeating cycle, every event comes both before and after every other, including itself; and so, any explanation of the form, "One event in the cycle causes another," is ultimately circular.

The advantage of simplifying is that more tools of mathe-

matical analysis become available to help us understand why the model behaves as it does. One of the most useful methods of analysis is to look at the cycle of equilibrium points. Let us suppose that $\alpha(t)$ is held constant at some value. If Model (2) were run for long enough, it would tend toward a stable equilibrium point. This point is the solution (P^* , H^*) of the equations $dP/dt = 0$, $dH/dt = 0$; namely

$$\begin{aligned} P^* &= P_o + gk/(fc - g) \\ H^* &= \alpha(t)P^*f/g \end{aligned} \quad (3)$$

If to each time of year we assign the equilibrium point corresponding to the value of α at that time, we get an annual cycle called the quasi-equilibrium cycle (Parslow, 1981). It is the annual cycle that the model would track if the ecological responses were so fast that the system was always in equilibrium with the prevailing physical conditions. The quasi-equilibrium cycle corresponding to Figure 6 is shown in Figure 7, and indeed there is good agreement between the two. Moreover, P^* is the same for 80 m or 25 m mixed-layer depth. We therefore have another way to express the question, "Why is there a spring bloom?"; namely, "Why (in what circumstances) is there a large deviation from the quasi-equilibrium cycle?"

This new manner of expression is useful because each point on the quasi-equilibrium cycle is calculated using only data for

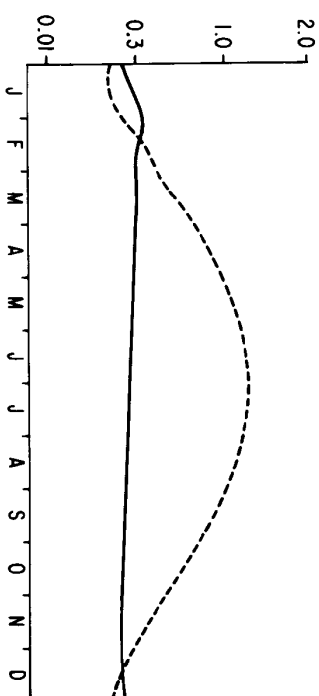


FIGURE 6. The annual cycle of Model 2 corresponding to a mixed layer depth of 25 m.

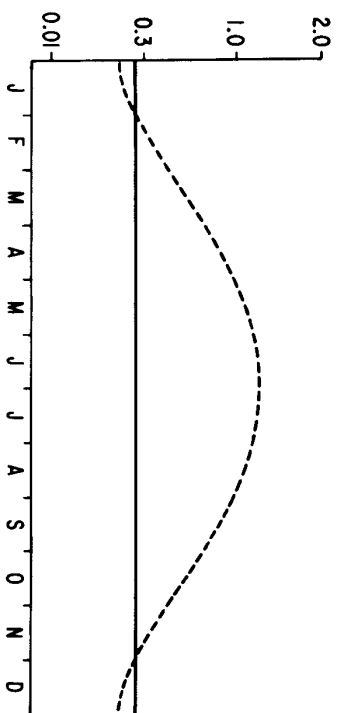


FIGURE 7. The quasi-equilibrium cycle corresponding to Figure 6.

that time of year, without involving infinite causal regress. We can then explain the difference between Figures 5 and 6 as follows: if the model is to stay close to quasi-equilibrium (i.e., if P is to track the fixed P^* and H the moving H^*), then we must have $P \approx P^*$ and $1/H \cdot dH/dt \approx 1/H^* \cdot dH^*/dt$. The latter becomes, substituting for the left side from (2) and the right side from (3):

$$\frac{fc(P - P_0)}{K + P - P_0} - g \approx \frac{1}{\alpha} \frac{d\alpha}{dt}$$

For the cycle of Figure 5, the specific rate of change $1/\alpha \cdot d\alpha/dt$ reaches a minimum value of -0.1 day^{-1} , and $1/H \cdot dH/dt$ cannot attain this value even when $P = 0$. The quasi-equilibrium value is moving too fast to be tracked. By contrast, for the cycle of Figure 6, the minimum value of $1/\alpha \cdot d\alpha/dt$ is -0.019 , and $1/H \cdot dH/dt$ attains this value when $P = 0.21 \approx P^* = 0.26$. Therefore, both variables can be near quasi-equilibrium at the same time.

According to this analysis, spring blooms are caused not by rapid changes in the phytoplankton growth rate α , but rather by rapid specific changes. The classical view of spring blooms invokes a rapid change in α due to sudden stratification. Certainly if $d\alpha/dt$ is large enough, the specific rate of change $1/\alpha \cdot d\alpha/dt$ will be large enough to trigger a bloom even if α itself is large. However, Figures 2 and 5 show that a spring bloom can occur even when $d\alpha/dt$ is small, if winter values of α are small enough

to make $1/\alpha \cdot d\alpha/dt$ large. In an extreme case α , the net growth rate, taking account of metabolism and sinking, might become negative in midwinter. There would then be no positive equilibrium to be tracked, and the system would be far from equilibrium when α became positive, resulting in a spring bloom. (This would have been the case in Figure 5 if the metabolic rate had been left at 0.07. The reason for reducing it slightly was to point out that a bloom can occur even when there is a positive, stable equilibrium all year round.)

The Subarctic Pacific

The cycle of Figure 6 is reminiscent of the Subarctic Pacific Ocean, where the phytoplankton concentration remains more or less constant, while the zooplankton concentration varies with phytoplankton production (McAllister, 1961; Parsons, 1965). In the open ocean the attenuation of light is much less (approximately 0.04 m^{-1} instead of 0.10), and there is a permanent halocline at around 100–150 m in the Subarctic Pacific, compared to 1000 m or more in the North Atlantic. We ran Model (1) with the following parameters: attenuation due to water, 0.04; due to phytoplankton, 0.06 (because much of the light at depth will be of a less attenuated color); latitude, 50; phytoplankton metabolic rate, 0.06; and mixed layer depth 100 m. This resulted in a near

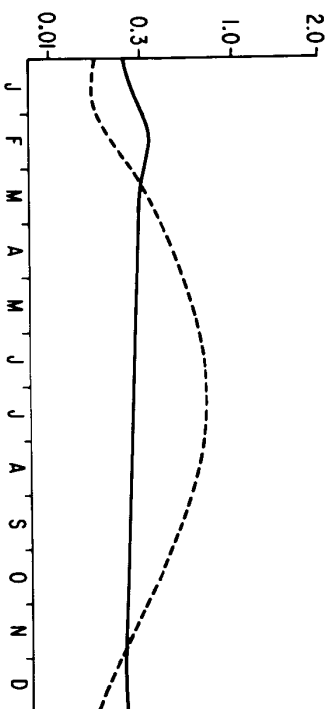


FIGURE 8. The annual cycle of Model 1 for parameters appropriate to the Subarctic Pacific.

quasi-equilibrium cycle (Figure 8). We did not take account of the changes in mixed layer depth which do occur, but in the Subarctic Pacific a shallow seasonal thermocline is established gradually rather than suddenly in the spring (Denman, 1972). A detailed simulation based on observations from the weather ship at Ocean Station "P" (50°N, 145°W) showed that the resulting change in α could trigger a large bloom only if the values assigned to physiological parameters led to low midwinter values of α . Despite uncertainties about midwinter growth rates, it is at least possible that phytoplankton growth rates are high enough to prevent a spring bloom in the Subarctic Pacific but not in the more deeply mixed North Atlantic (Parslow, 1981).

There is a long-standing alternative explanation of the difference between the annual cycles in the two regions. The life cycles of the large herbivores (*Neocalanus* spp.) in the Subarctic Pacific are peculiar; they involve overwintering as CV copepodids below the halocline, maturation and reproduction at depth, and recruitment of the nauplii to the surface layers during the spring. This may be important for two reasons. First, it avoids a delay in the numerical response of crustacean herbivores in the spring, as occurs with *Calanus finmarchicus* in the North Atlantic (Heinrich, 1962). Secondly, by overwintering below the halocline with negligible metabolic rates (Fulton, 1973) and possibly low predation rates, the *Neocalanus* avoid a decline in midwinter herbivore biomass, regardless of phytoplankton production.

Thus there are two differences between the North Atlantic and Subarctic Pacific, one physical and one biological, either of which may account for the difference in plankton cycles. This apparent redundancy tempts one to wonder if the different life-history strategies might have evolved in response to the physical differences. A (speculative) argument for such a process follows. The large copepods in both oceans exist against a background of other herbivores which reproduce more or less continuously. It may be that these other herbivores could by themselves prevent a spring bloom in the Subarctic Pacific but not in the North Atlantic, due to the differences in the physical conditions. The different life-history strategies of the large

copepods could then have evolved in response to these differing phytoplankton cycles.

Discussion

The textbook by Levinton (1982, p. 183) expresses a commonly held view: "The stabilization of the water column causes . . . the birth . . . of the spring diatom bloom." Although it seems intuitively reasonable that a sudden effect should have a sudden cause, ecological systems need not behave intuitively. Our analysis shows that spring blooms can occur without any sudden changes in driving variables. Mixed-layer shallowing certainly occurs in the spring and influences the local timing of spring blooms in, for example, the Norwegian Deep (Rey, 1981) or the Scotian shelf (Fournier et al., 1979). However, this may not be the fundamental controlling variable that the textbook view suggests.

Note that, whether or not there is a spring bloom, the model returns close to quasi-equilibrium in the summer. This explains why the occurrence of the spring bloom is not affected by details like mixing parameters, the vertical structure of phytoplankton at the seasonal thermocline, or the omission of nutrient limitation in Model (2). These all influence the summer equilibrium biomass but do not change the qualitative stability properties.

The classical explanation for the unusual cycle in the Subarctic Pacific ecosystem depends on the unusual organisms that happen to be there (Heinrich, 1962; Miller et al., 1984). This explanation of one event in terms of another is unsatisfactory for an annual cycle. We offer a more fundamental explanation: the Subarctic Pacific can be explained by the same model that explains other areas, with one unusual parameter value due to its shallow permanent halocline.

In exploring the behavior of the model, we found that the form of the annual cycle is very sensitive to the midwinter phytoplankton growth rate. It is difficult to estimate this rate, because it represents the difference between two nearly equal quantities, gross photosynthesis and losses due to metabolism and sinking. Phytoplankton respiration rates in dark, cool water are of critical

importance and cannot be simply extrapolated from observations in brighter, warmer water (Smayda and Mitchell-Innes, 1974). (One awkward conclusion of this work is the importance of measurements in winter, which are more difficult and less pleasant.)

It is worth emphasizing the advantages of analyzing simple models, and simplifying models until they can be analyzed. Model (2) does not present the full story; more complicated descriptions can and should be built (bearing in mind that as their complexity grows, they can behave as mysteriously as the real world). But the behavior of more complicated models, if they are intended as explanations, must be studied in terms of deviations from some background behavior. Model (2) provides this background: it is the formal working out of our simplest ideas, and it shows that these ideas contain more of the patterns of interest than one might have expected.

Appendix. Modeling Phytoplankton Growth Rate

In this appendix, we determine the growth rate of phytoplankton as a function of surface light and the depth of the mixed layer. We are interested in the growth rate averaged over the course of a day, and therefore assume that growth is in balance with uptake of nutrient and carbon; i.e., formulas for uptake or photosynthetic rate will be taken as formulas for growth rate. Our basic formula for growth rate as a function of light is the curve of Smith (1936), recommended by Jassby and Platt (1976) when (as now) analytic integration is desired:

$$G = Q\alpha I / (Q^2 + \alpha^2 I^2)^{1/2}$$

where I is the local light level, Q is the growth rate as $I \rightarrow \infty$, and αI is the growth rate as $I \rightarrow 0$. The local light level varies with time of day and depth in the water column. The variation with time of day is taken to be triangular, as in Steele (1962), to permit analytic integration. The shape is not quite correct, but as long as the total area and the length of the base are correct, we do not believe the difference to be important. The variation with depth

is a constant rate of attenuation. We then have

$$I = I(z, t) = J e^{-kz} t/\tau$$

between sunrise and noon, where J is the light level at the surface at noon, k is the light attenuation coefficient (which might depend on phytoplankton concentration), and t , measured in days, is 0 at sunrise and τ at noon. The extension of the formula to other times of day is obvious.

We assume that the time a phytoplankton cell spends at a particular depth is long compared to the photosynthetic reaction time (so that it is appropriate to use the light at that level), but short compared to the cell division time (so that total phytoplankton can be considered constant over the averaging period). A more refined treatment must await better knowledge of the path of a single plant cell through the mixed layer, as in Falkowski (1983) and Denman and Gargett (1983). The growth rate of a phytoplankton cell, totalled over a day, averaged over a mixed layer of depth M , is

$$\bar{G} = 2 \int_0^\tau \frac{1}{M} \int_0^M G(z, t) \cdot dz \cdot dt$$

where

$$G(z, t) = \frac{Q\alpha J}{\tau} \frac{e^{-kz} t}{\left(Q^2 + \frac{(\alpha J)^2}{\tau^2} e^{-2kz} t^2\right)^{1/2}}$$

We now change the vertical coordinate from depth to reciprocal light, by setting

$$\beta = \frac{Q\tau}{\alpha J} \quad \text{and} \quad y = \beta \cdot e^{kz}$$

Then $G = Qt/(y^2 + t^2)^{1/2}$, $dz = dy/ky$; $y = \beta$ at $z = 0$; $y = \beta \cdot e^{kM}$ at $z = M$, the mixed layer depth, and

$$G = \frac{2Q}{kM} \int_0^\tau \int_\beta^{\beta e^{kM}} \frac{t \, dy \, dt}{y (y^2 + t^2)^{1/2}}$$

Integrating, we get

$$G = \frac{2Q}{Mk} [F(\beta \cdot e^{kM}, \tau) - F(\beta, \tau) - F(\beta \cdot e^{kM}, 0) + F(\beta, 0)]$$

where

$$F(y, t) = (y^2 + t^2)^{1/2} - t \cdot \ln \frac{t + (y^2 + t^2)^{1/2}}{y}$$

The attenuation kM at the bottom of the mixed layer can be adjusted for phytoplankton density by changing it to $(k + cP)M$, where P is the density of phytoplankton and c is the attenuation per unit density of phytoplankton (linear, instead of Riley's [1956] more accurate formula). Riley (1956) would suggest $c \approx 0.12$. However, for deep layers, where most of the light is necessarily of the less attenuated colors, a smaller value (≈ 0.06) might be more appropriate.

We find τ and J by standard trigonometric/astronomical formulae (e.g., Brock, 1981). Daylength 2τ is given by

$$2\tau = \arccos(-\tan \delta \tan \phi)$$

where the declination $\delta = -0.406 \cos(2\pi T)$, where T is years and ϕ is the latitude. Total solar radiation, at the top of the atmosphere, normal to the earth's surface, during a day is $J\tau = (\sin \delta \sin \phi \tau + \cos \delta \cos \phi \sin \tau)R/\pi$, where R is the solar constant.

Transmission losses from the top of the atmosphere through the surface of the ocean, in the absence of the clouds, are taken to be constant. We assume that $\frac{3}{8}$ of the light at the top of the atmosphere is available, at photosynthetically active wavelengths, just below the ocean surface. Transmission losses due to clouds are taken to be 70% of the cloud cover.

References

- Allredge, A. L., 1981. The impact of appendicularian grazing on natural food concentrations in situ. *Limnol. Oceanogr.* 26: 247-257.
- Brock, T. D., 1981. Calculating solar radiation for ecological studies. *Ecol. Model.* 14: 1-19.
- Cote, B., and T. Platt, 1983. Day-to-day variations in the spring-summer photosynthetic parameters of coastal marine phytoplankton. *Limnol. Oceanogr.* 28: 320-344.
- Denman, K. L., 1972. The response of the upper ocean to meteorological forcing. Ph.D. thesis. University of British Columbia, Vancouver, Canada. 117 pp.
- Denman, K. L., and A. E. Gargett, 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnol. Oceanogr.* 28: 801-815.
- Dietrich, G., 1969. Atlas of the Hydrography of the Northern North Atlantic Ocean. ICES Hydrographic Service, Charlottenlund, Denmark. 140 pp.
- Eppley, R. W., 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull. U.S.* 70: 1063-1085.
- Eppley, R. W., J. N. Rogers, and J. J. McCarthy, 1969. Half saturation constants for uptake of nitrogen and ammonium by marine phytoplankton. *Limnol. Oceanogr.* 14: 912-920.
- Falkowski, P. G., 1983. Light-shade adaptation and vertical mixing of marine phytoplankton: A comparative field study. *J. Mar. Res.* 41: 215-237.
- Fournier, R. O., M. van Det, J. S. Wilson, and N. B. Hargreaves, 1979. Influence of the shelf-break front off Nova Scotia on phytoplankton standing stock in winter. *J. Fish. Res. Board Can.* 32: 1228-1237.
- Frost, B. W., 1975. A threshold behavior in *Calanus pacificus*. *Limnol. Oceanogr.* 20: 263-266.
- Fulton, J. D., 1973. Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. *J. Fish. Res. Board Can.* 30: 811-815.
- Gran, H. H., and T. Braarud, 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. *J. Biol. Board Can.* 1: 279-467.
- Harris, G. P., and B. B. Piccinin, 1977. Photosynthesis by natural populations. *Arch. Hydrobiol.* 80: 405-457.
- Heinbokel, J. F., and J. R. Beers, 1979. Studies on the functional role of tintinnids in the Southern California bight. III Grazing impact of natural assemblages. *Mar. Biol.* 52: 23-32.
- Heinrich, A. K., 1962. The life histories of plankton animals and seasonal cycles of plankton communities in the oceans. *J. Cons. Int. Explor. Mer* 27: 15-24.
- Ivanoff, A., 1977. Oceanic absorption of solar energy. In: E. B. Kraus (ed.) *Modelling and Prediction of the Upper Layers of the Ocean*. Pergamon Press, Oxford: 47-71.
- Jassby, A., and T. Platt, 1976. Mathematical formulation of the relationship

- between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.* 21: 540-547.
- Kremer, J. N., and S. W. Nixon, 1978. *A Coastal Marine Ecosystem*. Springer, Berlin. 217 pp.
- Kullenberg, G., 1974. An experimental and theoretical investigation of the turbulent diffusion in the upper layer of the sea. University of Copenhagen, Institute for Physical Oceanography. Report No. 25. 212 pp.
- Levinton, J. S., 1982. *Marine Ecology*. Prentice-Hall, Englewood Cliffs, New Jersey. 526 pp.
- McAllister, C. D., 1961. Zooplankton studies at Ocean Weather Station "P" in the Northwest Pacific Ocean. *J. Fish. Res. Board Can.* 18: 1-29.
- Miller, C. B., B. W. Frost, H. P. Batchelder, M. J. Clemons, and R. E. Conway, 1984. Life histories of large grazing copepods in a subarctic oceanic gyre: *Neocalanus plumchrus*, *Neocalanus cristatus* and *Eucalanus bungii* in the northeast Pacific. *Prog. Oceanog.* 13: 201-243.
- Paffenhöfer, G.-A., and R. P. Harris, 1976. Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus*. *J. Mar. Biol. Assoc. U. K.* 56: 327-344.
- Parslow, J. S., 1981. Phytoplankton-zooplankton interactions: Data analysis and modelling (with particular reference to Ocean Station P and controlled ecosystem experiments). Ph.D. thesis, Mathematics Dept., University of British Columbia, Vancouver, Canada. 400pp.
- Parsons, T. R., 1965. A general description of some factors governing primary production in the Strait of Georgia, Hecate Strait and Queen Charlotte Sound, and the N.E. Pacific Ocean. *Fish. Res. Board Can. Ms. Rept. Ser. (Oceanogr. Limnol.)*: 198.
- Parsons, T. R., M. Takahashi, and B. Hargrave, 1977. *Biological Oceanographic Processes*. Pergamon, Oxford. 332 pp.
- Rey, F., 1981. The development of the spring phytoplankton outburst at selected sites of the Norwegian coast. In: R. Sætre & M. Mork (eds.) *The Norwegian Coastal Current*, vol. 2. University of Bergen: 649-680.
- Riley, G. A., 1946. Factors controlling phytoplankton populations on Georges Bank. *J. Mar. Res.* 6: 54-73.
- Riley, G. A., 1956. *Oceanography of Long Island Sound*, 1952-54. II. Physical oceanography. *Bull. Bingham Oceanogr. Coll.*, Yale Univ. 15: 15-46.
- Sjöberg, S., and W. Wilmot, 1977. System analysis of a spring phytoplankton bloom in the Baltic. Askö Laboratory, University of Stockholm. *Contrib. No.* 20. 99 pp.
- Smayda, T. J., and B. Mitchell-Jones, 1974. Dark survival of autotrophic, planktonic marine diatoms. *Mar. Biol.* 25: 195-202.
- Smith, E. L., 1936. Photosynthesis in relation to light and carbon dioxide. *Proc. Nat. Acad. Sci. U.S.A.* 22: 504-511.
- Steele, J. H., 1962. Environmental control of photosynthesis in the sea. *Limnol. Oceanogr.* 7: 137-150.

- Steele, J. H., 1974. *The Structure of Marine Ecosystems*. Harvard University Press, Cambridge, Massachusetts. 128 pp.
- Sverdrup, H. U., 1953. On conditions for the vernal blooming of phytoplankton. *J. Cons. Int. Explor. Mer* 18: 287-295.
- Winter, D. F., K. Banse, and G. C. Anderson, 1975. The dynamics of phytoplankton blooms in Puget Sound, a fjord in the northwestern United States. *Mar. Biol.* 29: 139-176.