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The role of predation in plankton models

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Abstract. Models of carbon and nitrogen cycles in the ocean are a major tool in elucidating short- and long-term patterns of chemical fluxes. Variability in space and time are usually attributed to changes in ocean physics at different scales. This paper stresses the significance of the upper (predatory) closure in these simple nutrient–plant–herbivore models. The mathematical form used to close the system and the values given to the parameters have very marked effects on the overall response. In particular the major differences between North Atlantic and Pacific patterns may depend on this aspect as much as on the physical cycles. It is shown that the selection of different closure forms in five recent modelling studies corresponds to differences in the nutrient dynamics and plankton cycles. Thus, in general, the character of the results from these models will depend on both the form of the mortality closure and the parameter values used. Our ignorance in both areas is considerable.

Introduction

Simple models of marine plankton have a relatively long history (e.g. Riley, 1946). There is a revival of interest in such models, through attempts to quantify the fluxes of elements such as nitrogen and carbon at regional, ocean basin or global scales (Steele, 1984). The ecological components are usually combined with numerical models of the physical circulation. This determines the need for compact biological equations and presupposes a generality across seasons and over large geographic areas. Also the testing of such models against chlorophyll measurements and satellite colour images requires bulk variables. The relatively good agreement between models and observations (e.g. Sarmiento *et al.*, 1989) is a measure of the validity of these simplifying assumptions.

Generally these models have three components: nutrients (N), phytoplankton (P) and herbivorous zooplankton (Z). They are driven by physical processes, mixing or upwelling, which introduce nutrients into the euphotic zone and are closed at the upper level by some 'mortality' of herbivores.

This review will examine some N–P–Z models which have been used to simulate different plankton systems in the open ocean and in coastal environments. Each model has specific individual features such as a bacterial loop or age-structured zooplankton. A major conclusion, however, is that the form of the mortality closure term plays a major role in determining the overall response of all the models (Steele, 1976). In particular there are comparisons of 'Atlantic' and 'Pacific' models. There are very different annual cycles of nitrate and chlorophyll in the sub-arctic Pacific and in the North Atlantic. These contrasting features provide a test of the possible generality of plankton models and, specifically, of the forms of closure.

Observed plankton cycles

There is great variability in the observed annual cycles of plankton in different regions of the oceans but the data in Figure 1 suggest two general or extreme patterns in chlorophyll; uniformly low annual values, or short periods with very high levels. These two patterns have different cycles of primary production but, especially, very different levels of major nutrients such as nitrate (Parsons and Lalli, 1988).

On this basis we can consider two simplified regimes (Figure 2) typified by the data sets from Bermuda (Menzel and Ryther, 1960) and from Station Papa in the sub-arctic Pacific (Frost, 1987). There are marked physical differences such as the North Pacific halocline, which confines winter mixing to 100–150 m compared with 250–400 m in the North Atlantic. At Station Papa the phytoplankton are predominantly <10 mm and are grazed mainly by microzooplankton. In the North Atlantic the spring outburst is due mainly to diatom growth and is grazed by copepods. Thus the superficial comparability in the three categories N–P–Z (Figure 2) conceals significant differences in species and in size structure (Parsons and Lalli, 1988) and this should be borne in mind in the following analysis. It has been assumed that these patterns (Figure 2) represent regimes in which the critical controlling factors are grazing pressure and nitrate limitation respectively. These assumptions underlie much of the ecological modelling and will provide the context for the analysis in this review. There are other hypotheses. In particular iron is proposed as the limiting nutrient in offshore areas of the North Pacific and Antarctic oceans (Martin *et al.*, 1988). However, some of the analytical problems described here would still apply.

General form of the models

A minimal set of interactions can be expressed as

$$dN/dt = \text{input} - \text{uptake} + \text{regeneration}$$

$$dP/dt = \text{uptake} - \text{grazing}$$

$$dZ/dt = \text{growth} - \text{mortality}$$

The forms used here will be derived as follows:

$$\text{input} = p\,(N_o - N), p = \text{mixing rate}$$

and this assumes a single 'box' with mixing from a deeper high nutrient source taken to be nitrate (N_o).

$$\text{uptake} = n(N).f(P), n(N) = N/(k + N)$$

where $n(N)$ is a Michaelis–Menten function and $f(P) \rightarrow 0$ at finite P (e.g. self-shading).

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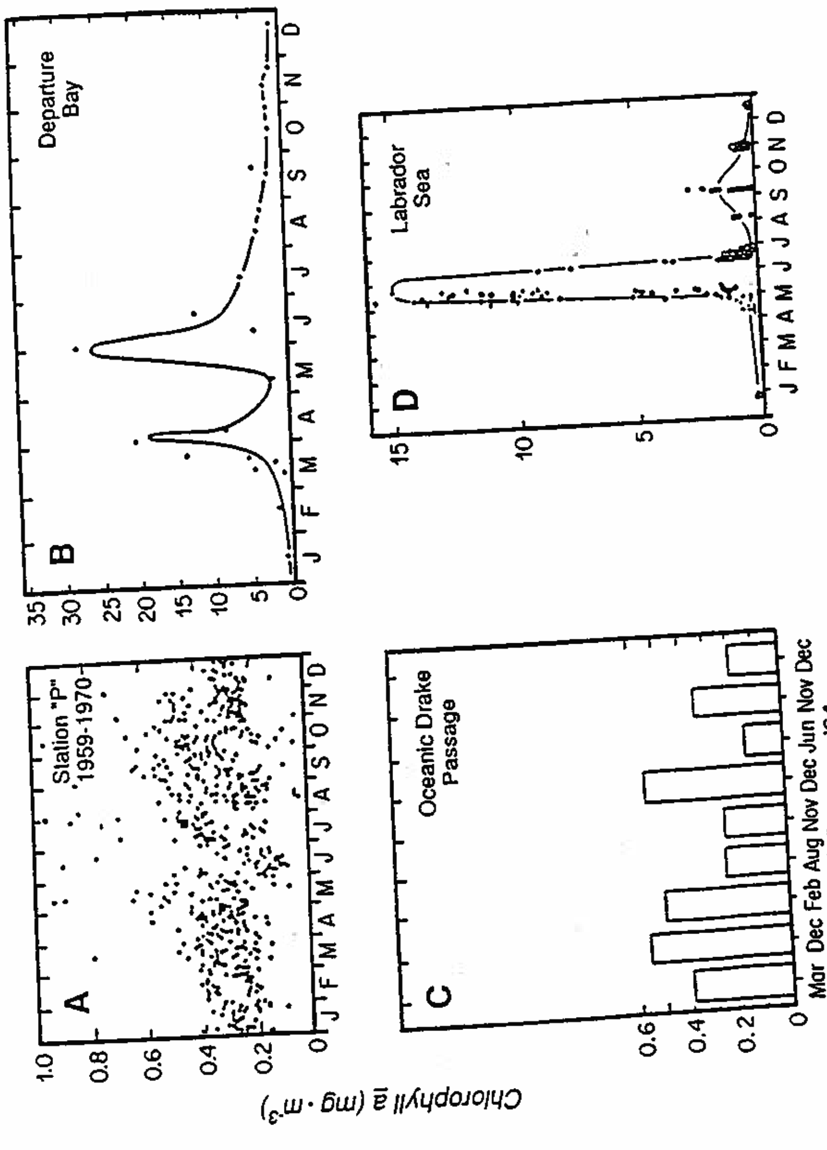

Fig. 1. Annual cycles of surface chlorophyll from (A) sub-Arctic Pacific (Station Papa); (B) Departure Bay, Vancouver Island; (C) Antarctic Ocean; (D) Labrador Sea, deep water (from Miller *et al.*, 1988).

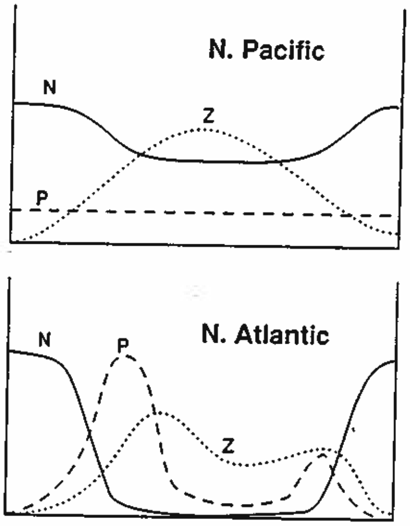

Fig. 2. Schematic presentation of the annual cycles associated with the North Pacific and Atlantic oceans.

$$\text{grazing} = g(P).\ Z$$

and $g(P)$ is bounded with various functional forms (see later).

$$\text{growth} = \alpha\ .g(P).\ Z, 0 < \alpha < 1$$

$$\text{regeneration} = (1 - \alpha).\ g(P).\ Z$$

Lastly, the mortality is given in a general form

$$\text{mortality} = \alpha.\ h(Z).\ Z$$

and a focus of the discussion will be on the various functions used for $h(Z)$ and their ecological interpretations.

Note that in this format

$$d(N + P + Z)/dt = 0$$

for

$$p.\ (N_o - N) = h(Z)$$

so that attention is focussed on the input and closure functions in terms of the overall fluxes through the system.

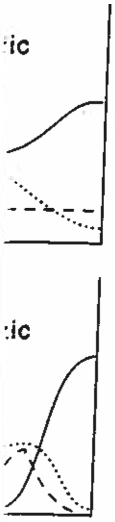

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Table I. Characteristics of five models (see text for details)

	Mortality $h(Z)$	Half-sat.[a] k	Grazing threshold	Other	Authors
I	a	0.5	Yes	Bacteria	Sarmiento *et al.* (1989)
II	a	0.2	No	Steady state	Wroblewski *et al.* (1988)
III	aZ	0.3	Yes		Steele and Henderson (1981)
IV	$aZ/(b + Z)$	1.0	Yes	Micro-zoop	Frost (1987)
V	$aZ/(b + Z)$	1.5 (0.05)	Yes	Age structure	Hofmann and Ambler (1988)

[a] Half-saturation values for ammonium, where different, are in parenthesis.

Five plankton models

Five models were selected for review as examples of the N–P–Z format because most of them have been developed in the context of flux studies, but, especially, they were selected to illustrate the range of closure terms, $h(Z)$ (Table I).

A second factor is the choice of the nutrient half-saturation constants, k. In several of the models the limiting nutrient, nitrogen, is separated into nitrate and ammonium corresponding to the input and regeneration terms respectively. This is done so that the uptake ratio

$$\text{(new/total) nitrogen}$$

can be tracked. However, in most models the values of k for nitrate and ammonium are the same or very close. The one exception is in Hofmann and Ambler (1988). In the later analysis of nutrient levels, their minimum (ammonium) value is used.

All these models use a hyperbolic grazing function of the form

$$\begin{aligned} g(P) &= \lambda\,(P - P_o)/(\mu + P - P_o) \\ &= 0 \text{ for } P \leq P_o \end{aligned}$$

Threshold grazing concentration $P_o > 0$ except for the steady state model (Wroblewski *et al.*, 1988) that considers only $P_o = 0$.

The Hofmann and Ambler model introduces five age classes for the herbivore population but the value for b in the mortality term (Table I) is the same for all classes. The Frost model considers microzooplankton as the main herbivores with the copepod populations taken to be mainly carnivorous.

The model by Fasham *et al.* (1990) has seven components (Figure 3). [An earlier version of this model is coupled to a physical simulation of the North Atlantic (Sarmiento *et al.*, 1989) and this version is used for output data in the following discussion.] As discussed, nitrate and ammonium are kept separate for bookkeeping purposes but their uptake relations have the same half-saturation coefficient k. Similarly, grazing on bacteria by the zooplankton has the same 'half-saturation' rate as for phytoplankton. The cycle through dissolved organic nitrogen (DON) can introduce a delay term but this cycle is assumed to be rapid

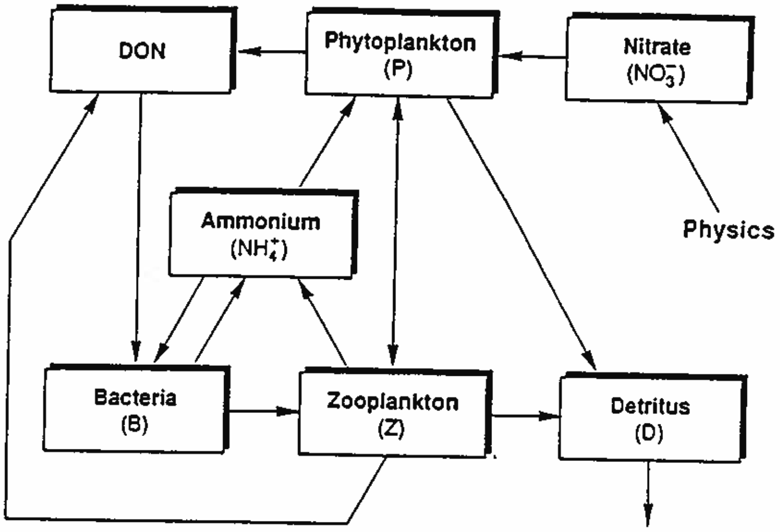


Fig. 3. Upper ocean ecosystem model used by Sarmiento *et al.* (1989) and Fasham *et al.* (1990). See text for explanation.

and so it is assumed here that this component can be combined with P. The detritus term for phytoplankton sinking in the following P/Z simplification, is equivalent to a decrease in phytoplankton growth rate.

Stability of simple P/Z models

A central question is whether grazing control, without explicit nutrient limitation, can reproduce the North Pacific pattern. Also such two-variable models (P/Z) are amenable to analytical study and there is a large literature on such systems (e.g. Nisbet and Gurney, 1982). This form will be used as a starting point before adding in nutrients with numerical illustrations.

The equations are

$$dP/dt = f(P) - Z.g(P) \qquad (1)$$

$$dZ/dt = \alpha.\ [g(P) - h(Z)].\ Z \qquad (2)$$

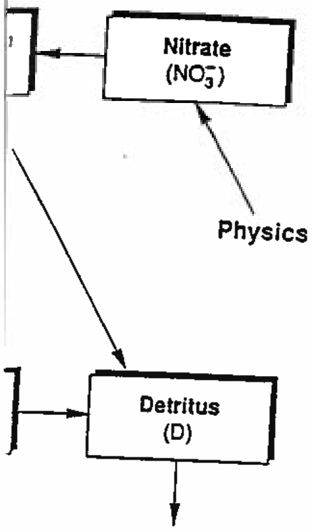
where

$$f(P) = \beta\ P.\ (1 - P/\gamma)$$

$$g(P) = \lambda\ P^n/(\mu + P^n) \qquad n = 1, 2$$

$$h(Z) = \delta\ Z^{m-1} \qquad m = 1, 2$$

The form for $f(P)$ is the standard logistic, assuming an upper bound to P. For



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$g(P)$ the form with $n = 1$ is the usual hyperbolic relation. With $n = 2$, we have the 's-shaped' curve (Holling, 1965) which corresponds to a threshold assumption.

These functions have been normalized by taking $\beta = \lambda = \mu = 1$

Then, at equilibrium

$$P(1 - P/c) = ZP^n/(1 + P^n) \tag{3}$$

$$aZ^{m-1} = P^n/(1 + P^n) \tag{4}$$

where $c = \gamma/\mu$ (carrying capacity)/(half-saturation grazing) and a depends on the original predation parameter, δ. Half-saturation grazing values are usually in the range 25–50 mg C/m^3 (Frost, 1987; Steele and Henderson, 1981) and this is about the same as the carbon/chlorophyll ratio. Thus normalized P can be considered as chlorophyll. Assuming an average doubling time for P of 2 days, then taking $\beta = 1$ gives unit time = 0(3) days (or 100 time units in the simulation is ~1 year). Lastly, one would expect the carrying capacity to be much larger than the half-saturation grazing so $c \gg 1$. From the peak chlorophyll values in Figure 1, $C \geq 10$ and the equality is used in the simulations.

The purpose of the normalizations in equations (3) and (4) is to focus on the significance of variations in a. The two forms for $h(Z)$ in Table I (a and aZ) are introduced by making $m = 1, 2$. The stability criteria for (3) and (4) with $m = 1$, 2 and $n = 1$, 2 are given by the isocline presentations of $dP/dt = dZ/dt = 0$ (Figure 4; see May, 1976 for explanation).

The form $m = 1$, $n = 1$ has had frequent use in freshwater ecology (Rosenzweig, 1971; McCauley et al., 1988) and is termed 'the paradox of enrichment' because increasing c, the carrying capacity, takes this system from stable equilibrium into limit cycles.

The introduction of a threshold or an 's-shaped' response $m = 1$, $n = 2$ is similar, in essence, to the model used by Evans and Parslow (1985) to provide an explanation of the different Pacific/Atlantic forms (Figure 2). They have

$$dP/dt = I(t).f(P) - Z.g(P) \tag{5}$$

$$dZ/dt = \alpha\,[g(P) - a].Z \tag{6}$$

which has equilibrium solutions of the form

$$P = \text{const},\ Z = \text{function}\ (P, t)$$

where $I(t)$ is a seasonal cycle. Evans and Parslow point out that if $I(t)$ is low amplitude the solutions of equations (5) and (6) track the equilibrium sufficiently closely to be comparable with the 'Pacific' pattern of observations. ? The problem is that this solution depends on the values being in the left-hand stable section of the isocline graph (Figure 4). If the value of a is changed the

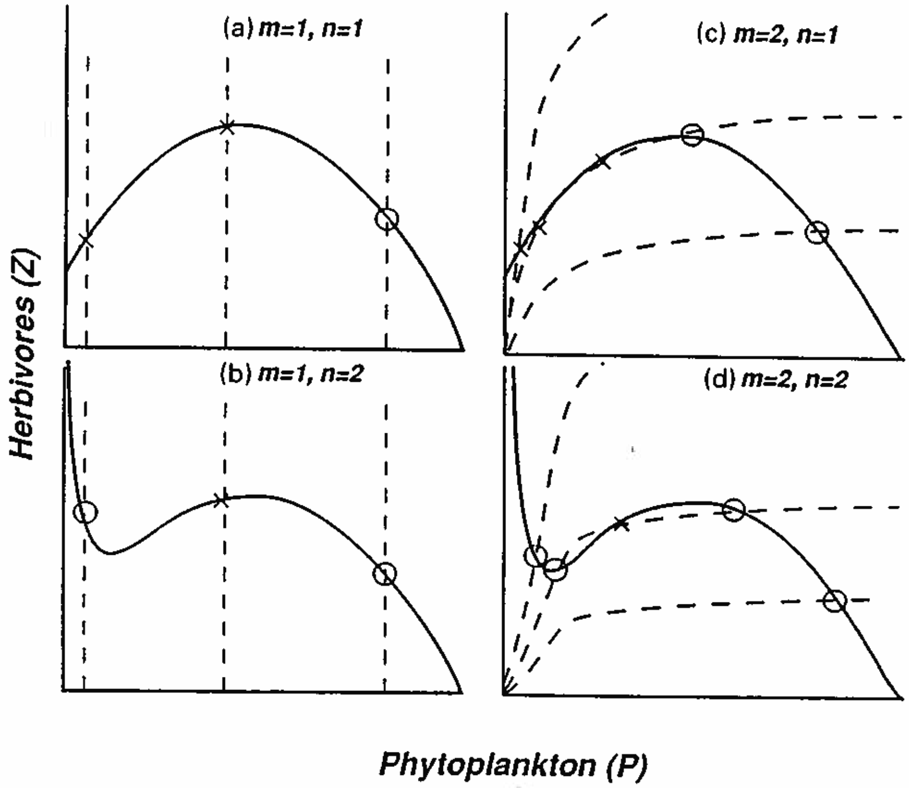


Fig. 4. Isoclines for $dP/dt = 0$ (——) and $dz/dt = 0$ (- - -) from Steele and Henderson (1981). See text for details.

solution can enter the unstable region giving large amplitude limit cycles even with low amplitude seasonal oscillations (Figure 5A). In the simulations by Evans and Parslow a 40% change produces this result. Thus, this intriguing explanation of the patterns in Figure 2 is insufficiently general, unless there can be an ecological reason for small a, i.e. for low predation ($0 < a < 0.5$).

If nutrient, N, is added, then

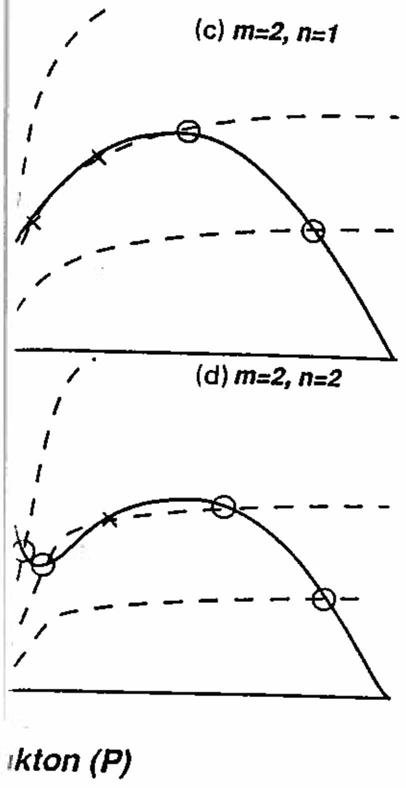
$$dN/dt = p.(N_0 - N) - n(N).f(P) + (1 - \alpha).g(P).Z \qquad (7)$$

$$dP/dt = n(N).f(P) - Z.g(P) \qquad (8)$$

$$dZ/dt = \alpha\,[g(P) - h(Z)].Z \qquad (9)$$

where equations (8) and (9) are normalized following equations (3) and (4).

Taking $h(Z) = a = 0.7$, ($\alpha = 0.5$) then simulations can be run with a low amplitude 'seasonal' cycle. Figure 5(A) shows the typical limit cycle behaviour



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without nutrients (or with $k = 0$). Figure 5(B), with a low rate of mixing of nutrients ($p = 0.1$ and $N_0 = 4$) gives low P values but little cycle in Z. However, a larger mixing rate $p = 0.3$ (or an increased N_0) results in a return to the limit cycle behaviour (Figure 5C). Equally relevant, the 'summer' nutrient levels in Figure 5B are very low, less than the half-saturation value of $k = 0.5$. Thus for $0.5 < a < 0.96$ [the right-hand stable regime in Figure 4(b) is confined to $0.96 < a < 1.0$] limited nutrient input can stabilize the system but does not simulate the Station Papa observations.

This leads to a consideration of the alternative form, $h(Z) = aZ$. For the case $m = n = 2$ (Figure 4) it can be seen that varying a takes the P/Z system through a bifurcation between two stable solutions with low P/large Z and large P/low Z. [This is the two-variable analogue of a frequently used population equation (Ludwig *et al.*, 1978; May, 1977; Steele and Henderson, 1981)]. For a relatively low value of a (Figure 6) with a low amplitude cycle, the response gives low P and cyclic Z and values of N that are large compared with the half-saturation $k = 0.5$. This corresponds to the 'Pacific' case. With intermediate a, in the bifurcation region, P has large amplitude seasonal cycles and N has minima close to the half-saturation value similar to the 'Atlantic'. Finally, with very large mortality of the herbivores, P remains large and near the carrying capacity ($P = 10$), while Z is low and constant. This can be regarded as a more realistic 'breakdown' of the system than a limit cycle.

The point is not the degree of correspondence with the ocean data; but that the gross similarities in a simple model are achieved by varying the rate of predation (or herbivore mortality) rather than changing the seasonal cycle or the rate of vertical mixing.

The last formulation to be considered (Table I) is

$$h(Z) = a\,Z/(b + Z)$$

Figure 7(A) shows the three forms for $h(Z)$ and illustrates how this last formula combines characteristics of the two preceding relations. The isoclines for $Z = 0$ with varying a and b (Figure 7B) display the fact that, by choice of a and b, essentially the same isoclines as for $h(Z) = a$ or $h(Z) = aZ$ can be obtained. Thus, the free choice of a and b permits any of the responses in Figure 4 to be produced.

For this reason the method of selecting values for these parameters a, b, is critical since, as shown, the form of $h(Z)$ and the values for the parameters are dominant factors in determining the general response of the N–P–Z system. The following quotations from papers using this form are relevant.

> 'No data are available for predation rates . . . Therefore (a and b) were determined by a series of numerical experiments' (Hofmann and Ambler, 1988).
>
> 'There is no observational basis for selecting values of (a and b); values were chosen to give reasonable estimates of annual primary production' (Frost, 1987). (In a later formulation values from the grazing by copepods on large phytoplankton are used.)

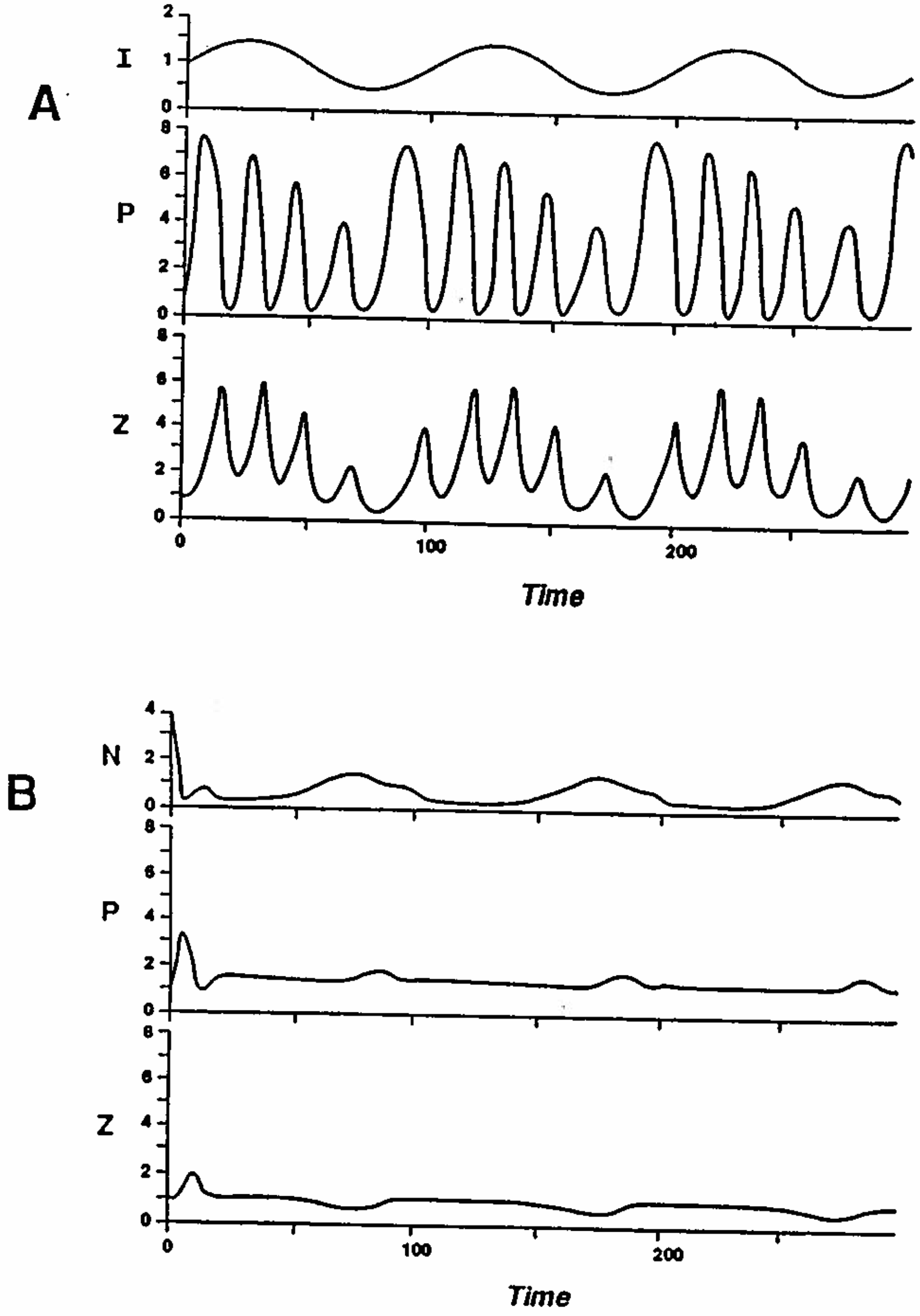
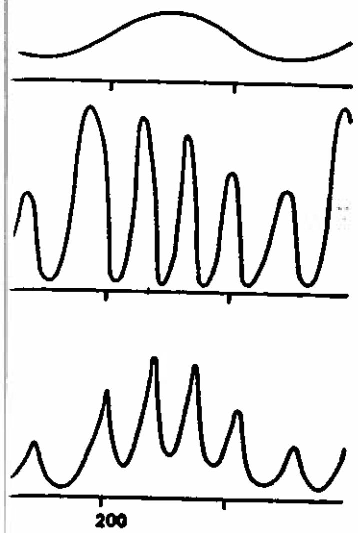
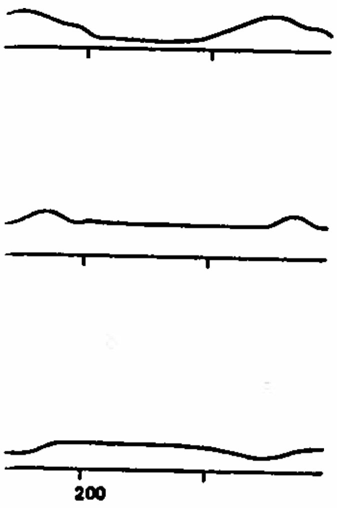


Fig. 5. Model outputs for $m = 1$, $n = 2$ (Figure 4): (**A**) without nutrient limitation and with a cyclic growth rate of P (1 ± 0.5); (**B**) with nutrient limitation and a low mixing rate; (**C**) as (**B**) but with higher mixing showing the return to a limit cycle.





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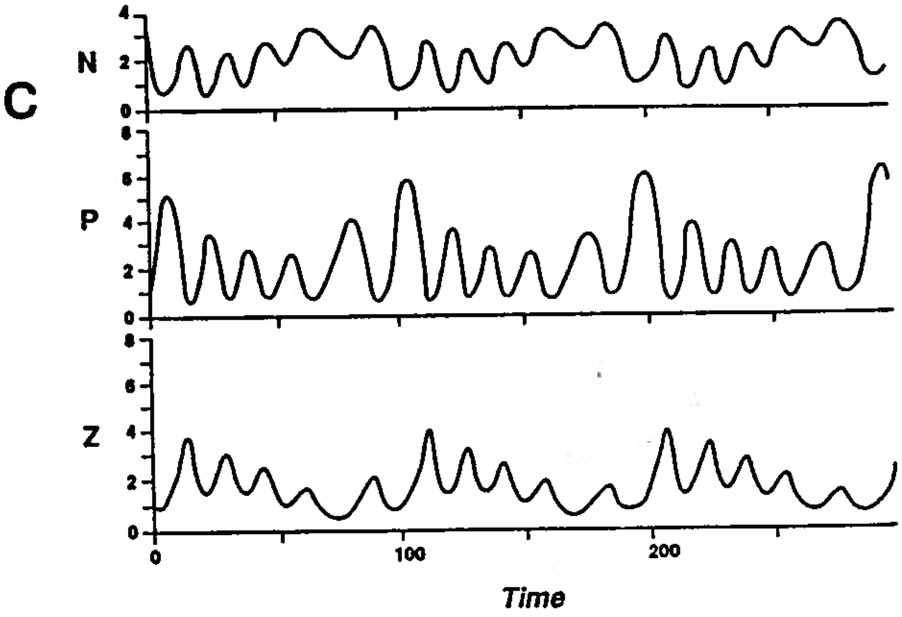


Fig. 5. Continued.

Consequences of the mortality formulations

Each of the models in Table I has many individual features which preclude detailed comparisons with each other or with the simplified forms in the preceding analysis. There is, however, one major conclusion from this analysis. Even with s-shaped grazing ($n = 2$) limit cycle response occurs with certain values. For systems with $h(Z) = a$, nutrient limitation may be necessary to prevent limit cycle behaviour. For $h(Z) = aZ$, or for $h(Z) = aZ/(b + z)$ with appropriate choice of coefficients, large values of nutrient concentration relative to the half-saturation value can be obtained.

To test this conclusion, the equilibrium values $N = N^*$, in the five models were derived from the graphical results. The ratio N^*/k was calculated using the minimum value of k (nitrate or ammonium) (Table II). The results are also shown in relation to the normalized Michaelis–Menten curve (Figure 8). It is apparent that the primary conclusion holds.

$$\text{For } h(Z) = a,\ N^*/k < 1$$

$$\text{for } h(Z) = aZ,\ N^*/k > 1$$

$$\text{and for } h(Z) = aZ/(b + Z)$$

the values of N^*/k are largest.

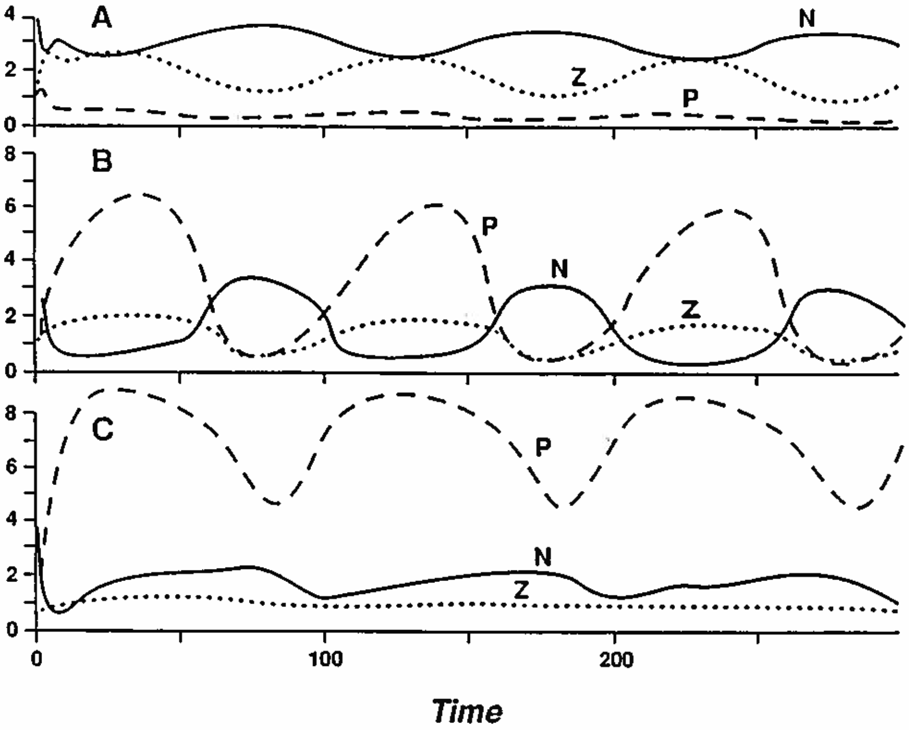


Fig. 6. Model outputs for $m = 2$, $n = 2$ (Figure 4) with three values of the predation/mortality parameter (A) $a = 0.10$; (B) $a = 0.50$; (C) $a = 1.00$.

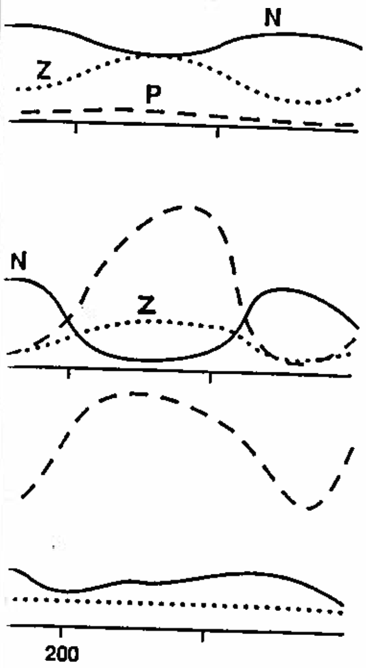
This is taken to be empirical evidence of the primary conclusion; that the form of $h(Z)$ is critical to the general nature of the ecological consequences used in these larger regional models. Probably the closure terms are more important than some of the 'internal' details.

The regional modelling approach of Sarmiento *et al.* (1989) has been extended to the equatorial Pacific. The initial runs (J.R.Toggweiler, personal communication) show that the output goes into a limit cycle (~10 cycles/year) at the eastern margin where physical circulation is reduced and nitrate is high. These results would be in accord with the analytical conclusions.

Discussion

Model formulations

The analysis of the simple N–P–Z models, combined with a review of the output from more complicated formulations, has focused on the closure of these models at the upper level. Generally very little explanation is provided for the choice of the form of $h(Z)$ or for the value of the coefficients. Yet, these choices can determine the overall patterns in all variables and are particularly relevant to the question of nutrient limitation versus grazing control. Even if the iron hypothesis



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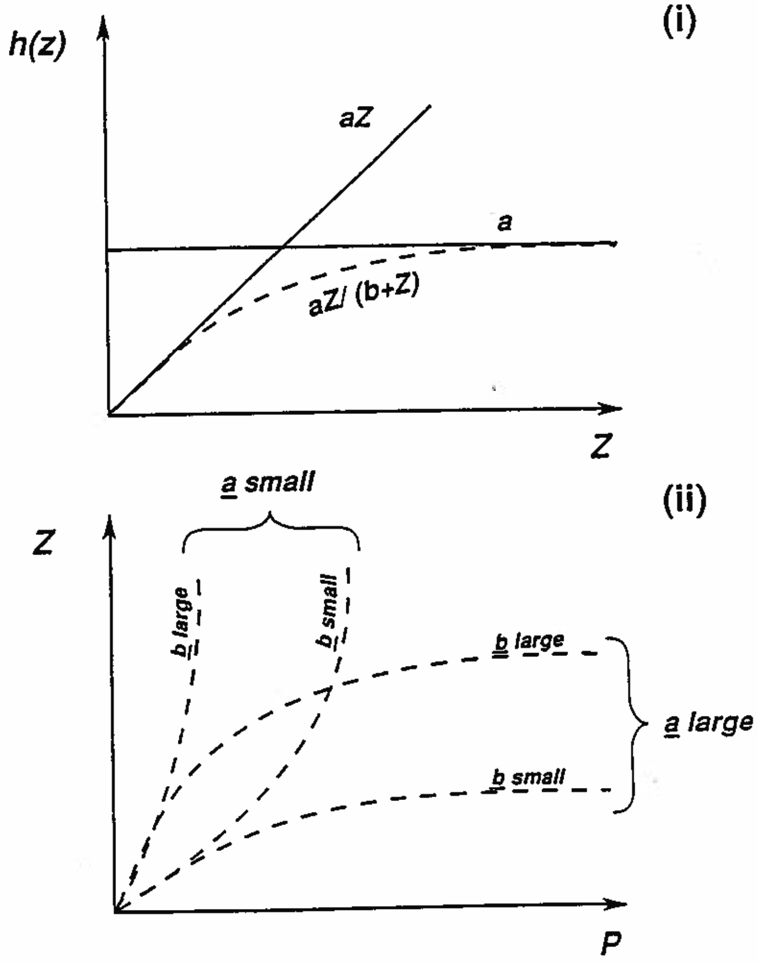


Fig. 7. (i) The three forms for $h(Z)$. (ii) The isoclines for $h(Z) = aZ/(b + Z)$ for different values of a and b.

(Martin, 1989) were established the problem of deriving the observed seasonal cycles would still remain.

The ecological basis for the choice of $h(Z)$ is important not only for model response but also because it determines a major component of the organic flux out of the system—a factor of prime concern for the overall physical–biological programmes using these models.

(i) The form $h(Z) = a$ can be justified as the simplest and most economical way to close the system. The choice of a can be made to fit the output to a particular data set (e.g. the seasonal cycle at Bermuda) and then tested on the scale of an ocean basin (Sarmiento *et al.*, 1989). There can be a strong empirical basis for this approach if nothing is known (or can be known) about the actual ecological context.

Table II. The estimated values of the equilibrium nutrient concentration (nitrate or ammonium) and the ratio with the minimum half-saturation value from Table I for the five models

	Minimum half-sat.	Equilibrium nutrient	N^*/K
I	0.5	0.1	0.2
II	0.2	≤0.1	≤0.5
III	0.3	1.0	3.3
IV	1.0	6.0	6.0
V	0.05	0.4	8.0

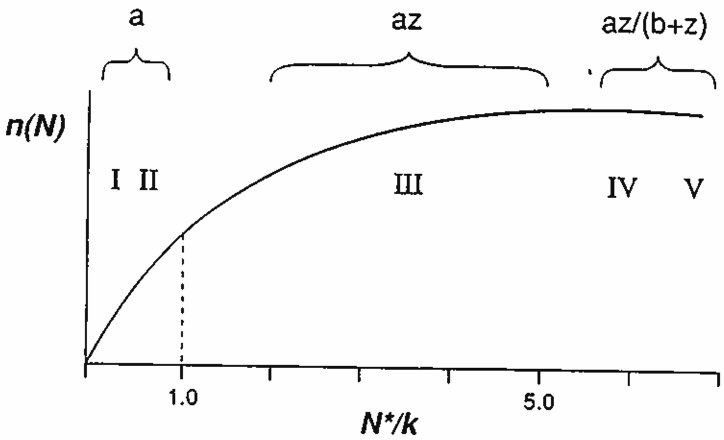


Fig. 8. The derived values of N^*/k in relation to a Michaelis–Menten curve for the five models listed in Table I.

(ii) The form $h(Z) = aZ$ can be explained as cannibalism (Taylor and Joint, 1990). Alternatively it must be assumed that some undefined predator population has a biomass proportional to its prey (Steele and Henderson, 1981). This may be more reasonable intuitively than assuming predators are always constant.

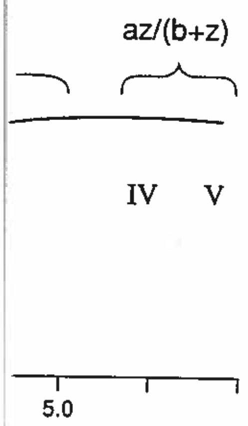
(iii) In considering the third form for $h(Z)$ it is necessary to look at the whole term in the Z equation

$$h(Z).\ Z = [aZ/(b + Z)].Z$$

The obvious interpretation of $h(Z)$ is as a hyperbolic rate for a satiable predator. In turn this implies that the Z term represents the predator biomass and so presupposes, as in the previous form, that the predators vary proportionately with their prey. More explicitly this would require one to (i) define predator species; (ii) estimate seasonal cycles; and (iii) measure functional response. These requirements indicate the need for fairly detailed observational and experimental programmes. They imply a limitation on simple generality across, say, the North Atlantic and Pacific. The review by Parsons and Lalli (1988) suggests that such differences are important. Thus the North Pacific Calanoids

entration (nitrate or ammonium) and
for the five models

m nutrient	N^*/K
	0.2
	≤ 0.5
	3.3
	6.0
	8.0



nten curve for the five models listed

nibalism (Taylor and Joint,
some undefined predator
rey (Steele and Henderson,
than assuming predators are

cessary to look at the whole

Z

rate for a satiable predator.
e predator biomass and so
dators vary proportionately
one to (i) define predator
easure functional response.
detailed observational and
on simple generality across,
y Parsons and Lalli (1988)
the North Pacific Calanoids

which Frost considers as significant predators, have a very different life style (larger, annual) compared with their herbivorous Atlantic counterparts (smaller, opportunistic).

Other factors

This analysis has focused on ecological processes and used the simplest N–P–Z format. It did not include phytoplankton sinking, bacterial loops, zooplankton age structure or, more generally, species diversity within a trophic level. The reasons were analytical convenience, and the empirical result that the more complicated ecological models had outputs which could be deduced from the simpler forms. The computer simulations (Figures.5 and 6) had a seasonal cycle.

There are several important biochemical processes not considered explicitly. The modes of input and uptake of other elements such as iron is one example. The longer-term cycles in dissolved organic carbon and nitrogen are topics of present interest (Brewer *et al.*, 1986). It is not yet clear how these would interact with the particulate exchange processes.

But the most important factors are the effects of physical processes, horizontal and vertical, at a wide range of scales. It is well known (Okubo, 1980) that addition of horizontal diffusion terms to prey–predator equations can alter the stability criteria. Evans and Parslow (1985) pointed out the importance of the seasonal cycle in mixed layer depth. The introduction of vertical shear and zooplankton migration can transform temporal limit cycles into horizontal patchiness which appears to be chaotic (Evans, 1978).

As an example, Hofmann and Ambler (1988) point out that the threshold condition $P_o > 0$ is necessary in their ecological model, but can be removed in the combined physical–biological model, presumably because of the effects of horizontal mixing. The grid scale in their comprehensive model is 5 km. This spatial scale is in the range appropriate for phytoplankton–herbivore interactions proposed theoretically and observed in coherence studies (Steele, 1978; Denman and Freeland, 1985).

Such effects would not be expected in basin scale models with grid scales of 0 (100 km). This raises the question of whether sub-grid processes need to be parameterized in such larger-scale models. There is a direct analogy with similar problems in the physical modelling where 'diffusion' is introduced to ensure numerical stability.

Similarly, variable vertical distributions of phytoplankton and vertical migration of zooplankton may alter the overall grazing patterns transforming the grazing relationship from a hyperbolic to an 's-shaped' response (Steele and Mullin, 1977). Also with a 12-layer vertical simulation model the threshold condition could be removed. Thus the apparent 'functional response' may be determined as much by the physics as by the inherent biological behaviour.

For these reasons, separate construction of biological and physical models and their later combination is unlikely to be adequate. We need further analytical studies of the ways in which the physics and biology interact at different spatial scales.

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