Incorporating the microbial loop in a simple plankton model

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The microbial loop, which recycles nutrients in the upper layers of the ocean, is an integral part of plankton dynamics. The usual method for modelling the complex patterns involved has been to consider the 'Z' in N/P/Z (nutrient/phytoplankton/zooplankton) models as containing all possible grazers on P and, implicitly, relegate the carnivorous metazoans to the loss term on Z. I propose the opposite approach—to define Z explicitly as the metazoans responsible for export fluxes—and to simulate the effects of the microbial loop implicitly in terms of grazing and excretion rates. The reasons for taking this alternative route are (i) the importance of copepods in the carbon/nitrogen flux from the euphotic zone to deeper water compared with (ii) the predominantly internal role of the microzooplankton in recycling nutrients; and (iii) the problems of sampling the microbial component, compared with sampling larger metazoans. Finally, there is the need to keep plankton models as simple as possible for later use in coupled physical/biological systems.

Keywords: microbial loop; plankton; model

1. INTRODUCTION

The microbial loop is an important component of planktonic systems, involving the recycling of nutrients through pico-phytoplankton, bacteria and microzooplankton (Azam *et al.* 1983; Gifford 1993). Microzooplankton are defined operationally as organisms that are smaller than 200 µm, and the group contains a diversity of protistan taxa including heterotrophic flagellates and ciliates, as well as metazoan nauplii (Gifford 1993). The dominant role of the protista in grazing the phytoplankton has been identified using elegant experimental methods (Landry *et al.* 1995). Again, these methods define microbial grazing operationally rather than in terms of rates per organism, as in traditional copepod experiments.

The general conclusion is that, on average in the open ocean, metazoan grazers larger than 200 µm consume only a small fraction of primary production by photosynthetic autotrophs. This fraction can be very variable, depending mainly on the size of the phytoplankton cells. The microbial loop provides a mechanism to retain nutrients in the highly stratified upper layers of oligotrophic regions of the ocean. The copepods act as predators on the microbial loop. They are the main pathway for export of carbon and nutrients from the euphotic zone, through faecal pellets, vertical migration and consumption by larger, long-lived predators. Thus the copepods determine the fluxes from the upper layers that must balance the input of nutrients from deeper water for new production (figure 1).

The usual method for modelling the complex patterns involving the microbial loop has been to consider the 'Z' in N/P/Z (nutrient/phytoplankton/zooplankton) models as containing all possible grazers on P and, implicitly, relegate the metazoans to the loss term on Z (Fasham *et al.* 1990). I propose to try out the opposite approach—to define Z explicitly as the metazoans responsible for export fluxes—and to simulate the effects of the microbial loop implicitly in terms of grazing and excretion rates.

2. MICROBIAL LOOPS

The original concept in Azam *et al.* (1983) referred back to work of Sheldon *et al.* (1972) on size-related food chains of flagellates → ciliates → zooplankton → fish. These food chains are dependent ultimately on phytoplankton and on bacteria consuming dissolved organic matter (DOM) excreted by the phytoplankton. It is likely that the system is a much more complicated food web, but the patterns of interaction are not known (Armstrong 1994). Therefore, as a simple starting point, the system schematized in figure 1 is used to illustrate the consequences of different numbers of loops.

Assume that, at steady-state,

1. There is a food chain, $X_0 \rightarrow X_1 \rightarrow X_2 \rightarrow \ldots \rightarrow X_L$, where X_0 are the primary producers and X_L are copepods.
2. As in figure 1, the mean size of the phytoplankton is determined by the rate of input to the mixed layer of nutrients that control new production (generally, but not always related to stratification). This cell size defines the number of links to copepods: 1, 2, 3 and 4, reading from the right in figure 1.
3. All the microbial 'species' have a growth efficiency of 30% with the remaining 70% recycling rapidly to the nutrient pool.
4. The copepods have 30% growth but 30% is faecal material that provides the export, leaving 40% for recycling.

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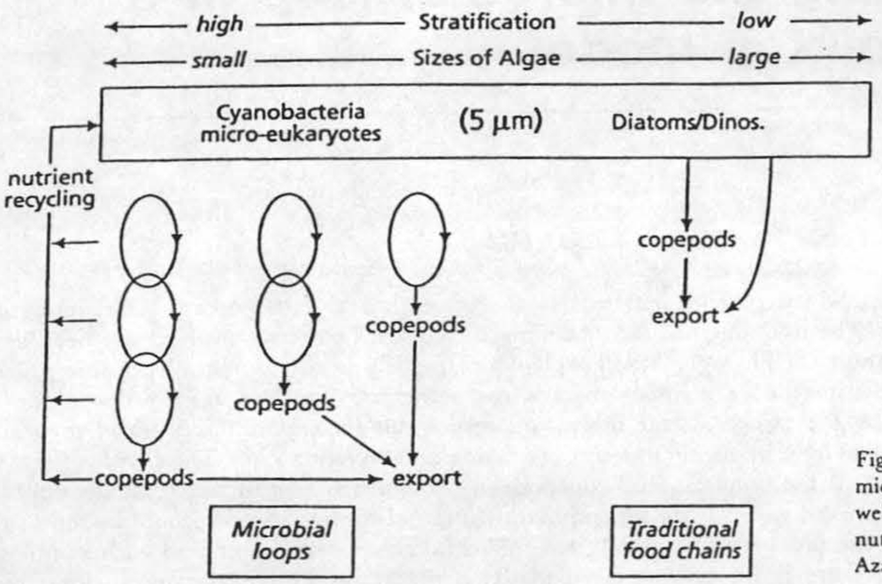

Figure 1. A simple representation of microbial loops and the changes in food web structure with decreasing rates of nutrient input from right to left (from Azam *et al.* 1983; Cushing 1989).

Table 1. *Growth, grazing and recycling of essential nutrients at steady state in the euphotic zone*

(Values expressed as percentages of primary production for different numbers of microbial loops.)

loops	meso-grazing	meso-growth	total recycling	total export	*f*-ratio
1	100	30	50	50	0.50
2	30	9	85	15	0.15
3	10	3	95	5	0.05
4	3	1	98	2	0.02

5. To close the system, predation on the copepods results in a further 70% export, so that a fraction $F=0.3$ (30%) of this predation goes to recycling.

In table 1, increasing the number of loops causes the system to switch rapidly from export to recycling. This is associated with a decreasing role of the copepods in overall consumption while retaining their function as exporters. The consequence is a major shift from export to recycling of nutrients; a feature captured by the *f*-ratio, defined here as

(rate of new nutrient input)/(rate of total nutrient uptake).

The major consequence, derived from this illustration, is the shift in *f*-ratio, which depends on the decrease in the ratio of meso- to micrograzers. If the usual N/P/Z model was simulating the system then, typically, the Z has fixed fractions (or functional relations) for growth, recycling and export of its consumption of phytoplankton and bacteria (Fasham *et al.* 1990; Steele & Henderson 1993). The ratio of growth of Z to grazing on P, in particular, can be high (0.75 in Fasham *et al.* (1990)) as might be expected in high-nutrient environments, or low for oligotrophic situations (0.2 in Steele & Henderson (1993)). The concepts underlying the calculations in table 1 suggest that this ratio should vary significantly with the amount of internal recycling that occurs within a heterogeneous Z. Furthermore, it should vary with the rate of input of new nutrient. Because the input of new N balances the losses by export at steady-state, the latter is a critical number that would also vary with total Z but would remain a constant fraction of mesoplankton grazing (table 1).

All of the evidence suggests that fixed percentages for growth and regeneration are less satisfactory than some relation for these percentages that varies with nutrient status. A fixed percentage could apply only to one area or season. A variable factor would capture the seasonal or latitudinal changes.

The simplifying assumption in figure 1 and table 1 is that the shift from eutrophic to oligotrophic occurs as a change in cell size of P and in the number of trophic links. In practice, one would expect the changes to be in the relative abundances of different cell sizes and of the number of loops, i.e. in the relative proportions of the rows in table 1. This would translate into trends in the fraction of the total grazing on P that was attributable to the mesoplankton.

My proposal is to take Z to represent the mesoplankton (essentially copepods) which will have a fixed export function. It is then assumed that the total grazing by the microzooplankton is some multiple of the mesograzing. This factor depends on the size structure of the phytoplankton which, in turn, is related to nutrient concentrations or, possibly flux rates. If Z represents mesozooplankton, then

$$\text{mesozooplankton growth rate} = E\cdot g(\mathrm{P}),$$

where $E = \text{growth/grazing}$ for mesozooplankton. Then

$$(\text{mesograzing})/(\text{total grazing}) = G(\mathrm{N}),$$

so that

$$\text{total grazing} = g(\mathrm{P})/G(\mathrm{N}), \tag{1}$$

and

$$\text{recycled nutrients} = (1/G(\mathrm{N}) - E\cdot(1-F)). \tag{2}$$

The general assumption about $G(\mathrm{N})$ is that it increases monotonically with some aspect of nutrient concentration. In the terms of figure 1 and table 1, as L increases, N and $G(\mathrm{N})$ decrease. The quantitative nature of this relation is unknown at present. However, all the evidence indicates that injections of nutrients into an oligotrophic system do not produce merely an increase in the magnitude of flow in one of the vertical food chains in figure 1, but instead produce a shift to the right that will change significantly the proportions of micro- and mesoplankton. From the illustration in table 1, this will change the relative fractions going to recycling and export. This formulation removes the fixed percentages for growth and regeneration but requires some functional form for $G(\mathrm{N})$.

The limiting nutrients and the method of introduction can vary over ocean regions. The IRONEX results demonstrate the changes in quality as well as quantity of production with addition of a limiting nutrient (Cullen 1995). For the North Atlantic there is some basis to assume that nitrogen is the limiting nutrient, particularly in the form of nitrate for 'new' production. There is also some basis for the assumption that significant injections of nitrate, Ni—at the start of the spring outburst, or from a storm event—will trigger growth of large diatoms (Goldman 1993) that are grazed on by copepods. Thus, as an initial test of this approach, I shall assume that

$$G(\mathrm{N}) = G(\mathrm{Ni}) = \mathrm{Ni}/(\mathrm{Kn}+\mathrm{Ni}), \qquad (3)$$

when Kn is the half-saturation concentration for nitrate uptake.

It would be possible to use other variables such as silicate, which is specific for diatoms. The implicit assumption here is that the Si/Ni ratio is the same in deep water and in diatoms. The advantage of this formulation for $G(\mathrm{Ni})$ is that no new variables or parameters are added.

It is necessary to separate the two main forms of inorganic nitrogen, nitrate (Ni) and ammonium (Na). We assume that all external input by mixing is Ni and all recycling is Na. Furthermore, it is usually assumed that, at low concentrations, the smaller cells take up Na preferentially and faster than the large cells (Haney & Jackson 1996). In addition, it is assumed that high concentrations of ammonium inhibit nitrate uptake. This can be expressed by having the total uptake of N by all phytoplankton, the Michaelis–Menten term, of the form

$$(\exp(-\phi\cdot\mathrm{Na})\cdot\mathrm{Ni}+\mathrm{Al}\cdot\mathrm{Na})/(\mathrm{Kn}+\mathrm{Ni}+\mathrm{Al}\cdot\mathrm{Na}),$$

where $\phi=2$ is the inhibition factor, $\mathrm{Al}=2$ indicates preference for ammonium and $\mathrm{Kn}=0.2\ \mathrm{mmol\ N\ m^{-3}}$.

This formulation is similar to that of Fasham *et al.* (1990), but the model differs from Fasham *et al.* (1990) in not having any variables for detritus, bacteria or dissolved organic nitrogen. Recycling through these compartments is implicit in the representation of microbial activity by $G(\mathrm{N})$.

3. SIMULATIONS

The model used here is a simple N/P/Z version developed for studies of multi-year variability at Bermuda (Steele & Henderson 1993). It incorporates the quadratic predation term (Steele & Henderson 1992). The main change in the model is the incorporation of equations (1) and (2) in the equations for $\mathrm{d}P/\mathrm{d}t$ and $\mathrm{dNa}/\mathrm{d}t$ respectively, with the values of E and F used for table 1. Ni and Na are tracked separately as new and recycled N, so that the f-ratio of new to total production can be calculated as

$$f=\mathrm{Ni}/(\mathrm{Ni}+\exp(\phi\cdot\mathrm{Na})\cdot\mathrm{Al}\cdot\mathrm{Na}).$$

For the illustrations here, a fixed 'spring-to-summer' condition with a mixed layer on 50 m is used. The initial condition is $\mathrm{Ni}=0.9\ \mathrm{mmol\ m^{-3}}$, $\mathrm{Na}=0.1\ \mathrm{mmol\ m^{-3}}$ with low P and Z, corresponding to conditions at Bermuda when the thermocline has just shallowed in the spring.

A major impetus for this model is to simulate the consequences of sporadic nutrient enrichment in the euphotic zone. As a very simple illustration, after 100 days and for a period of 15 days, the nitrate concentration at the base of the mixed layer is increased from 2 to $20\ \mathrm{mmol\ m^{-3}}$. The latter figure corresponds to the maximum in the thermocline (McGillicuddy & Robinson 1997) and gives a tenfold increase in nitrate flux, comparable to more physically realistic simulations (D. J. McGillicuddy, personal communication).

The traditional N/P/Z simulation is obtained by setting $G(\mathrm{Ni})=1$ (figure 2). This is used as the control for comparison with the $G(\mathrm{Ni})$ variable (figure 3). In figures 2 and 3, the different values for $G(\mathrm{Ni})$ have relatively little effect on the output of the normally observed variables: P, Z and Ni. There is a generally good correspondence of the steady-state minima in the simulations with summertime observations at the Bermuda Atlantic Time-series Study (BATS) site off Bermuda (Michaels *et al.* 1994). Nitrate observations are $<0.1\ \mathrm{mmol\ m^{-3}}$; the P-values compare well with observations of particulate organic carbon of 0.02–$0.03\ \mathrm{mg\ C\ m^{-3}}$; and mesozooplankton ($>200\ \mu\mathrm{m}$) are in the range 0.17–$0.45\ \mathrm{g\ C\ m^{-3}}$ (Roman *et al.* 1993).

The differences between constant and variable $G(\mathrm{Ni})$ become apparent in the primary production, in the f-ratio and especially in Na. Observations of ammonium from the North Atlantic Bloom Experiment (G. Evans, personal communication) are in the range of 0.05–$0.5\ \mathrm{mmol\ m^{-3}}$, comparable to the output in figure 3. Primary production is higher because there is much more recycling of nutrient, and it is in line with observations that show these rates are not greatly depressed in oligotrophic waters (Michaels *et al.* 1994). The f-ratio in the control (figure 2) shows a dip after 20 days with a return to higher values. This is a consequence of the fixed fractional conversion of phytoplankton to export by the grazers. The same feature is found in the Fasham *et al.* (1990) model, and is even more marked there. When the $G(\mathrm{N})$ factor is introduced and the fraction going to recycling varies (figure 3), then the f-ratio follows a more acceptable pattern for oligotrophic waters (Eppley & Peterson 1979).

One consequence, observable in data from Bermuda, is the major effect on the rate of primary production per square metre. In figure 2 the steady-state values for the control are less than $100\ \mathrm{mg\ C\ m^{-2}}$, whereas with variable

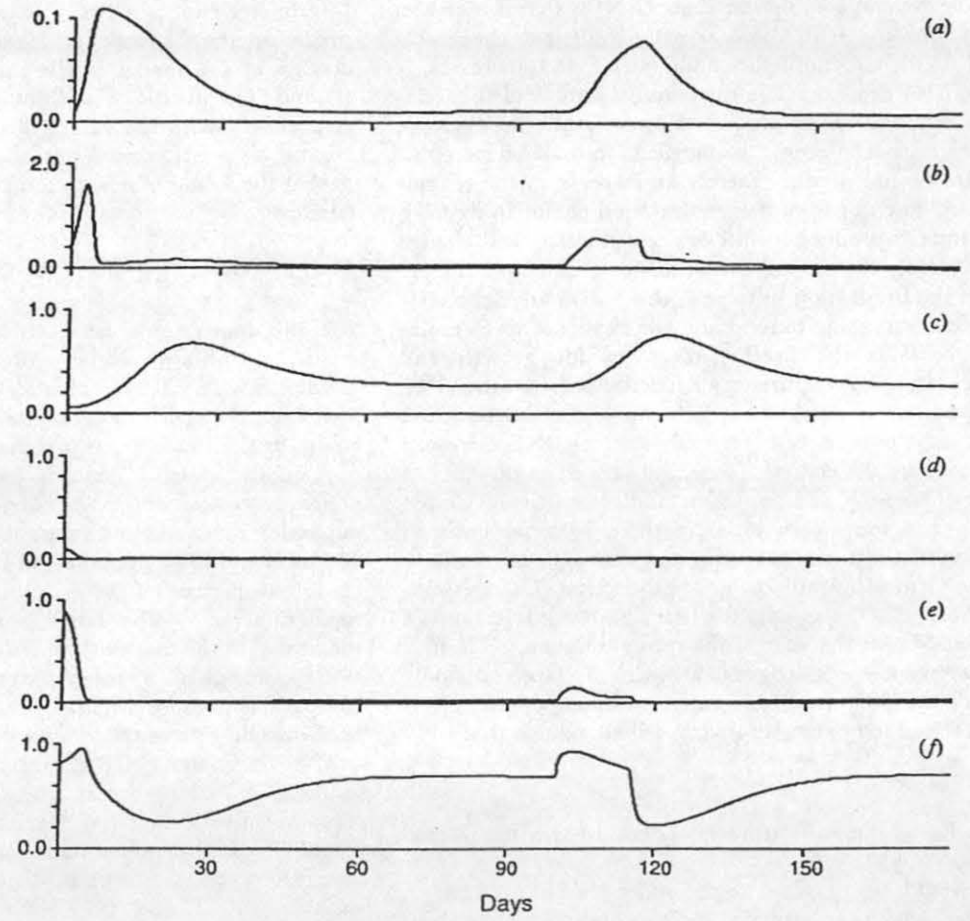

Figure 2. Output from the control simulation described in the text with $G(\mathrm{N})=1$. (*a*) P ($\mathrm{g\,C\,m^{-3}}$); (*b*) production ($\mathrm{g\,C\,m^{-2}\,day^{-1}}$); (*c*) Z ($\mathrm{g\,C\,m^{-2}}$); (*d*) Na ($\mathrm{mmol\,m^{-3}}$); (*e*) Ni ($\mathrm{mmol\,m^{-3}}$); (*f*) *f*-ratio.

$G(\mathrm{N})$ the values are $400\,\mathrm{mg\,C\,m^{-2}\,day^{-1}}$ (figure 3). The observations from BATS (figure 4) agree reasonably well with the '$G(\mathrm{N})$' value. Finally, as a check on the model, the export of excreted particulate organic carbon from the mixed layer at Bermuda (figure 4) implies an *f*-ratio of about 0.1. This is in good agreement with the model output at steady-state (figure 3).

The perturbation at 100 days indicates the kind of results that might be obtained with this approach. The output (figure 3) shows the resulting bloom in P and Z with a threefold increase in primary production. Note that there is little increase in nitrate but there is a marked rise in the *f*-ratio, unlike the control (figure 2). The largest changes, however, occur in the downward particulate fluxes (figure 5) shown for three individual components: the copepods, their predators, and the sinking plus mixing of the phytoplankton. At the peak, there is a sevenfold increase in this flux due mainly to copepod faecal material. This peak is explained by the fourfold increase in the *f*-ratio combined with the twofold increase in Z. The former could not have occurred without the more realistic formulation of the *f*-ratio derived by this simulation of the variable microbial component. In addition, the general correspondence between the increase in total production, *f*-ratio and downward flux implies that essentially all the increased production is going to the copepods that switch from a microbial to a phytoplankton diet, which is in line with recent evidence. This illustrates the pronounced effect that a nutrient pulse, nitrate or iron, could have on the flux of organic matter to deeper water.

4. CONCLUSIONS

The purpose of this exercise has been to demonstrate how the main consequences of the microbial loop can be incorporated in an N/P/Z model without any increase in variables or parameters. The relations used to do this, in equations (1), (2) and (3), are all qualitatively reasonable. The major requirement is a formal definition of $G(\mathrm{N})$ based on experimental data.

The approach taken here is to use the Michaelis–Menten relation

$$G(\mathrm{Ni}) = \mathrm{Ni}/(\mathrm{Kn} + G \cdot \mathrm{Ni}).$$

The null case of no 'microbial' effect (figure 2) is given with $G=0$, and $G=1$ gives the simulations in figures 3–5. To illustrate the robustness of the simulations, figure 6 shows the values of the *f*-ratio at steady-state for a range of G. It is apparent that the main consequences of this formulation hold for a wide range of $G>0$. Thus the

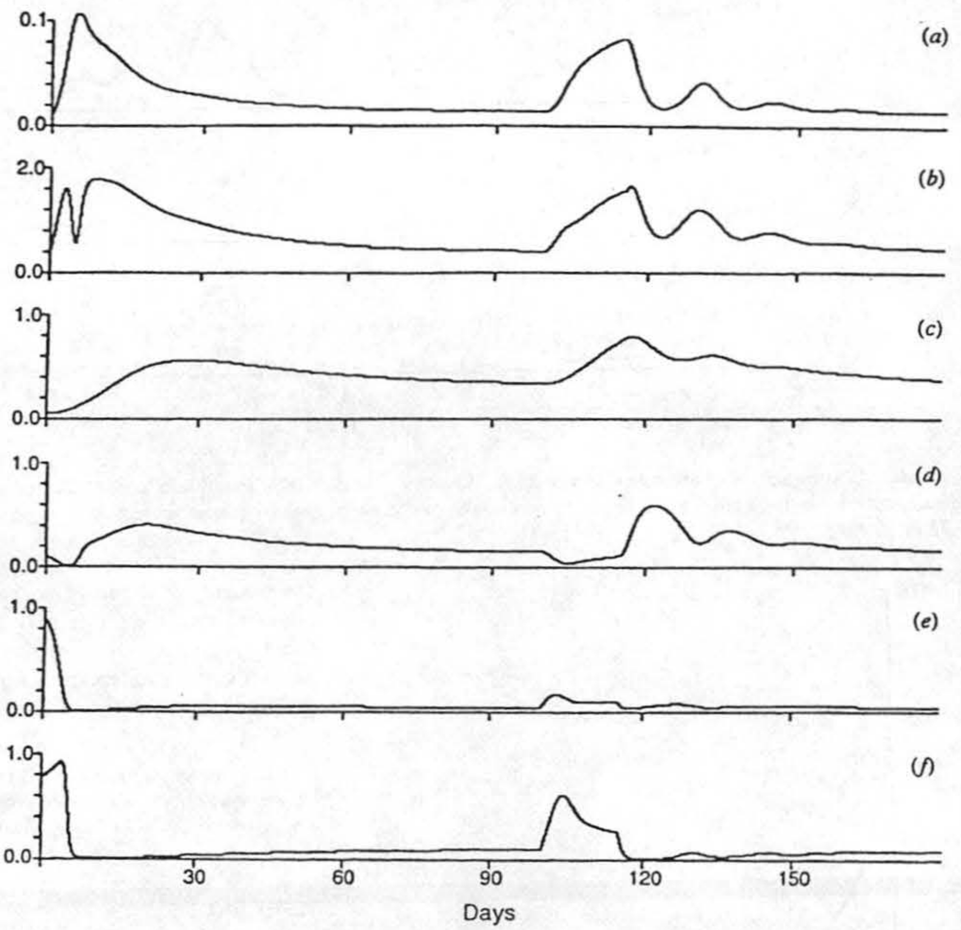

Figure 3. (*a–f*) As figure 2, but with $G(N)$ variable.

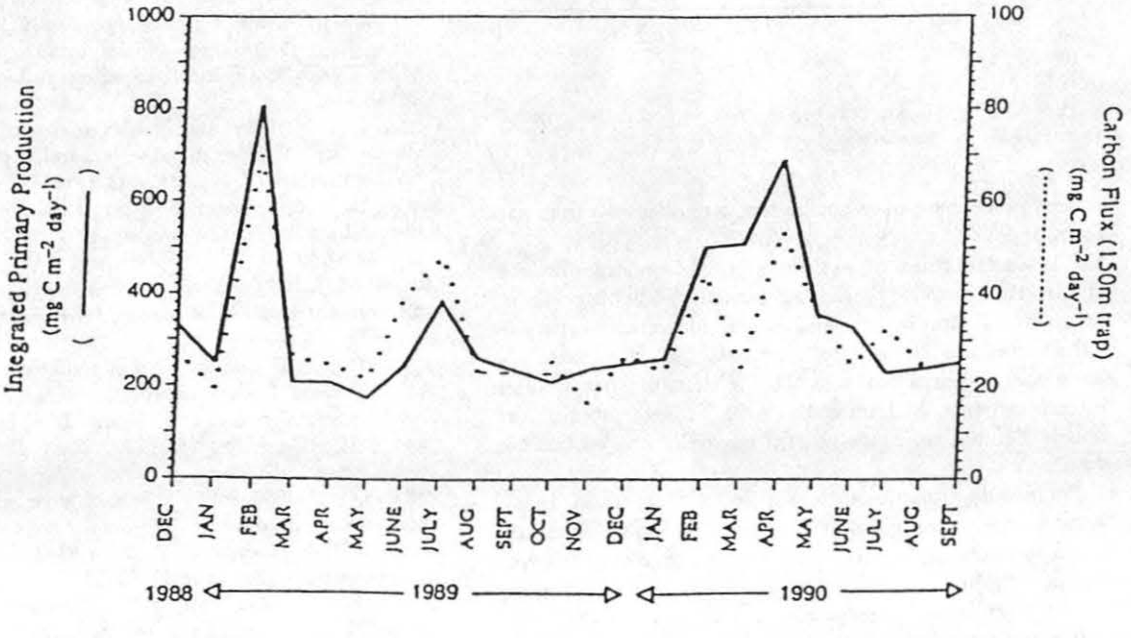

Figure 4. The integrated primary production (0–150 m) and export of particulate organic carbon to a sediment trap at 150 m at the BATS site off Bermuda (from Michaels *et al.* 1994).

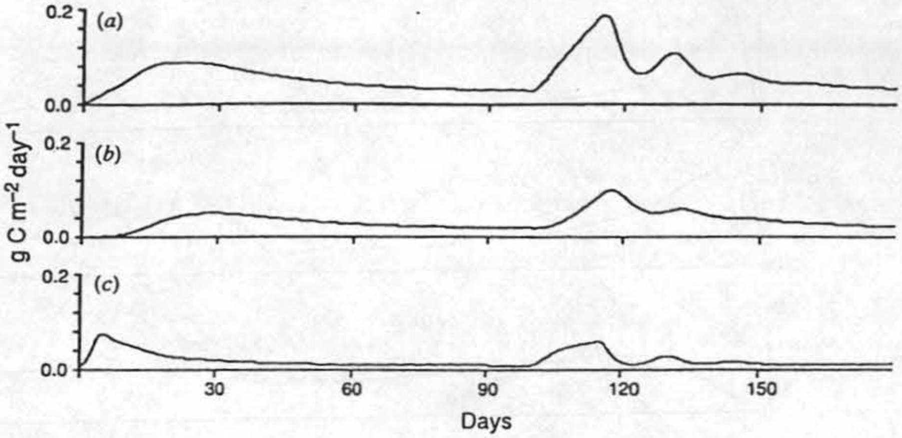

Figure 5. Consequences of an influx of nitrate for 15 days after day 100. The fluxes are calculated assuming that (*a*) copepod faecal material is 30% of intake; (*b*) predator growth and excreta goes to deeper water; and (*c*) phytoplankton sink at 0.25 m day^{-1}.

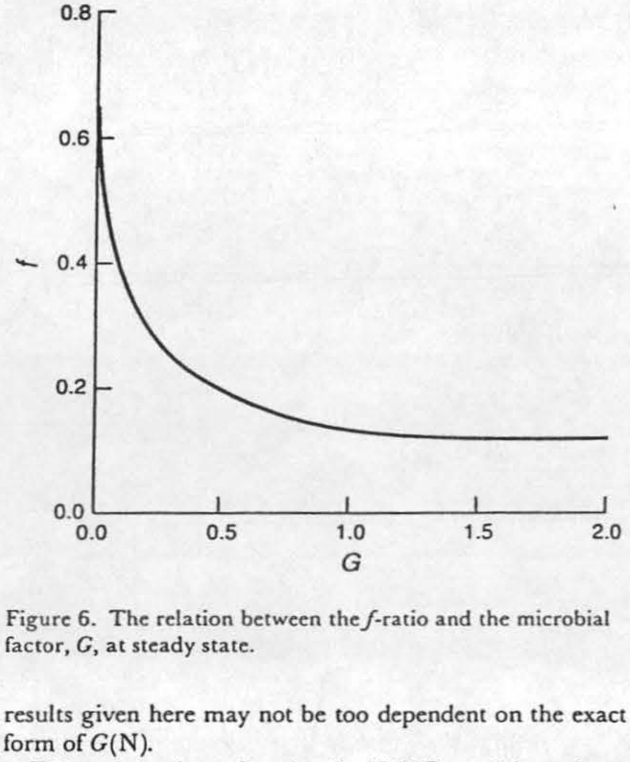

Figure 6. The relation between the *f*-ratio and the microbial factor, *G*, at steady state.

results given here may not be too dependent on the exact form of $G(\mathrm{N})$.

This adaptation of a simple N/P/Z model produces results that provide better agreement with observations of primary production and more intuitively satisfying values for the *f*-ratio. In particular, it eliminates the need for an extra variable, *D*, for detritus that is often introduced (e.g. Fasham *et al.* 1990). This variable is very poorly defined ecologically, and normally has no basis in data.

Potentially, functional forms for $G(\mathrm{N})$ could incorporate other limiting nutrients such as iron. Generally, this approach might permit a broader range of eutrophic-to-oligotrophic environments to be simulated with the same variables and parameters.

It is not intended that this simple formulation be an end in itself. Rather, it might help in making more realistic models of systems involving other physical or biological components of the larger ocean system. It would be interesting to introduce this procedure to vertically and horizontally structured models that can reproduce more explicitly the sudden incursions of nutrient-rich water to the lower layers of the euphotic zone.

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