Modelling Phytoplankton Production at Shelf-Sea Fronts [and Discussion]

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Phil. Trans. R. Soc. Lond. A 1981 **302**, 605-615
doi: 10.1098/rsta.1981.0186

Phil. Trans. R. Soc. Lond. A **302**, 605–615 (1981)
Printed in Great Britain

Modelling phytoplankton production at shelf-sea fronts

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Large standing crops of phytoplankton are often found in the neighbourhood of shelf-sea fronts. How do these large biomasses come about? Special hypotheses have been proposed, but it seems preferable to treat frontal production in terms of a general theory. By assuming that phytoplankton behave as 'passive contaminants of water motion' and that vertical turbulent mixing is the dominant factor, it is possible to model the distribution of phytoplankton at fronts by means of simple expressions for photosynthesis, nutrient-controlled growth, and grazing. Because of their strong vertical and horizontal gradients, fronts are good places to test such simple models, which might also be applied to primary production in other regions of the ocean.

Introduction

Tidal fronts in shelf seas are boundaries between tidally mixed and thermohalinically stratified waters. The fronts often have a larger phytoplankton standing crop than the waters on either side (see, for example, Savidge 1976; Pingree *et al.* 1978; Simpson *et al.* 1979); for example, Pingree *et al.* (1975) found a surface chlorophyll concentration exceeding 20 mg m^{-3} at the Ushant Front in July 1975, when the surface concentration in surrounding waters was less than 1 mg m^{-3}. The enhanced standing crop need only grow at the same rate as that in the surrounding waters for there to be correspondingly enhanced production. Thus G. Savidge (personal communication) found incubator ^{14}C fixations implying primary production in excess of 1 g m^{-2} day^{-1} in frontal regions around the Scilly Isles in July 1979, compared with production of less than 0.3 g m^{-3} day^{-1} in thermally stratified waters to the south and west of the islands.

Several explanations have been proposed for the enhanced crops and productions. Each explanation involves interaction between the needs of phytoplanktonic algae for light and mineral nutrients and the advective or turbulent transports of water that can remove algae from illumination while bringing them nutrients they need. Pingree *et al.* (1975) put forward a hypothesis that explains enhanced standing crops at fronts solely in terms of régimes of vertical mixing. In the wind-mixed surface layer on the seaward side of a tidal front, shortage of nutrients depresses growth, whereas in the tidally mixed bottom layer, shortage of light prevents growth. In the pycnocline, however, is a region where phytoplankton are exposed to moderate illumination from above and to moderate rates of nutrient supply by diffusion from below, and yet are only slowly transported out of this beneficial régime by turbulent diffusion.

Inshore of a front, the water column is completely mixed, with the result that column algal respiration exceeds column gross photosynthesis because of low average illumination experienced by the algae. Offshore, the pycnocline dips below the compensation depth (at which gross photosynthesis equals algal respiration) and hence does not support phytoplankton growth. Thus the greatest standing crop and production occur in the frontal region, where there is a combination of adequate nutrient resupply and moderate vertical stability.

Vertical turbulent diffusion is, however, not the only transport process taking place at fronts. James (1978) has shown that a numerical model of a thermal front predicts a strong flow parallel to the front, a moderate upwelling on the mixed side of the front, and a convergence on the stratified side. Pingree (1978) discusses the role of cyclonic eddies in mixing water across fronts, and Pingree *et al.* (1975) suggest that movements of the entire front between spring and neap tides can stratify previously mixed water.

These processes, and their implication for nutrient resupply to phytoplankton in the frontal region, are discussed by Simpson & Pingree (1978), Pingree *et al.* (1978) and Simpson *et al.* (1979). Savidge (1976) discusses the stimulation of phytoplankton growth at a frontal upwelling and the accumulation of buoyant algae at a convergence (see also Bainbridge 1957; Okubo 1978). He also suggests that enhanced algal growth at fronts might result from the mixing of complementary water masses, each containing a nutrient lacked by the other.

Notwithstanding the existence of various processes for nutrient resupply, the success of vertical exchange models in the physical domain (Simpson *et al.* 1978), and the attractive simplicity of the light–nutrient-mixing hypothesis of Pingree *et al.* (1975), encourage an uncomplicated approach to modelling phytoplankton production at fronts. In this paper I present a simple model that has proven reasonably successful in predicting the distribution of phytoplankton in one frontal region, and which is applicable to any part of the sea in which vertical turbulent diffusion dominates transport processes.

THE MODEL

The most important feature of the model, which derives from that of Tett *et al.* (1981), is that it takes account only of vertical turbulent diffusion amongst all possible transport mechanisms. Like several one-dimensional models for phytoplankton growth (see, for example, Steele & Henderson 1976; Radach & Maier-Reimer 1975; Jamart *et al.* 1977; Jamart *et al.* 1979), it is of the general form

$$\begin{array}{c}\text{rate of change of}\\\text{phytoplankton biomass}\end{array} = \begin{array}{c}\text{biomass}\\\text{diffusion}\end{array} + \text{growth} - \begin{array}{c}\text{biological}\\\text{losses}\end{array}, \qquad (1)$$

$$\begin{array}{c}\text{rate of change of}\\\text{dissolved nutrient}\end{array} = \begin{array}{c}\text{nutrient}\\\text{diffusion}\end{array} - \text{uptake} + \begin{array}{c}\text{biological}\\\text{regeneration}\end{array}, \qquad (2)$$

and assumes that phytoplankton biomass, like dissolved nutrients, behaves as a passive tracer of water movements. It is further assumed that the kinematic eddy diffusivity for heat transport applies also to these tracers and thus that turbulent diffusivity K_z can be parametrized from the relation between vertical heat flux and temperature gradient.

The model differs in the following main respects from Radach & Maier-Raimer (1975), Steele & Henderson (1976) and Jamart *et al.* (1977).

(i) It is generally simpler. This is achieved by ignoring all biological effects other than diel averages of algal growth and nutrient uptake, and grazing and nutrient excretion by zooplankton. Thus sinking (cf. Steele & Yentsch 1960), and diurnal changes in photosynthesis and grazing (cf. Radach & Maier-Raimer 1975), are ignored. The simplest effective statements of each relation are used; thus, after Sverdrup (1953) gross photosynthesis P^B is related to average illumination I by

$$P^B = \alpha I, \qquad (3)$$

and illumination is treated as a simple inverse exponential function of depth:

$$I = I_0 e^{-\lambda z}. \qquad (4)$$

Grazing is parametrized as a constant phytoplankton-specific rate (g), after the argument in Tett *et al.* (1981).

(ii) Nutrient-control of growth (μ) is described in terms of a variable phytoplankton content (Q) of nutrient, by using the model of Droop (1968):

$$\mu = \mu'_{\mathrm{m}}(1-k_Q/Q). \tag{5}$$

This description results in the separation of nutrient uptake (u) from growth, the former being described by a hyperbolic relation with the concentration (s) of dissolved nutrient:

$$u = u_{\mathrm{m}}s/(k_s+s). \tag{6}$$

It becomes necessary to add an equation for rate of change of particulate nutrient to those for phytoplankton biomass and dissolved nutrient in (1) and (2).

(iii) During 24 hours algal cells experience a variable illumination, not only because of changes in surface light, but also because of turbulence. The average thickness of the layer through which algae at depth z are moved by turbulence is denoted by H. Because of the simple form of equation (3) its integration after substitution of equation (4) is simple, and gives

$$P^{\mathrm{B}} = \alpha I_0\,\mathrm{e}^{-\lambda z}(\mathrm{e}^{\frac{1}{2}\lambda H}-\mathrm{e}^{-\frac{1}{2}\lambda H})/\lambda H. \tag{7}$$

The average thickness H can be determined from K_z (see Appendix).

(iv) The control of growth by nutrients and light is considered to be alternative (see Tett *et al.* 1981), not multiplicative as is generally supposed. Thus

$$\mu = P^{\mathrm{B}} - R^{\mathrm{B}} \quad \text{or} \quad f(Q) \tag{8}$$

whichever is the smaller, where R^{B} is the phytoplankton respiration rate. The function $f(Q)$ is given by equation (5) and P^{B} by equation (7).

The model consists of a set of three nonlinearly coupled second-order partial differential equations in which the state variables biomass (x), phytoplankton nutrient (N), and dissolved nutrient (s), depend on time and depth:

$$\left.\underbrace{\frac{\mathrm{d}x}{\mathrm{d}t}}_{\substack{\text{rate of change}\\ \text{of biomass}}} = \underbrace{\frac{\partial}{\partial z}\left[K_z\left(\frac{\partial x}{\partial z}\right)\right]}_{\substack{\text{biomass}\\ \text{diffusion}}} \underbrace{+\mu x}_{\text{growth}} \underbrace{-gx}_{\text{grazing}},\right\} \tag{9}$$

$$\left.\underbrace{\frac{\mathrm{d}N}{\mathrm{d}t}}_{\substack{\text{rate of change of}\\ \text{phytoplankton}\\ \text{nutrient}}} = \underbrace{\frac{\partial}{\partial z}\left[K_z\left(\frac{\partial N}{\partial z}\right)\right]}_{\substack{\text{phytoplankton}\\ \text{nutrient}\\ \text{diffusion}}} \underbrace{+ux}_{\text{uptake}} \underbrace{-gN}_{\text{grazing}},\right\} \tag{10}$$

$$\left.\underbrace{\frac{\mathrm{d}s}{\mathrm{d}t}}_{\substack{\text{rate of change}\\ \text{of dissolved}\\ \text{nutrient}}} = \underbrace{\frac{\partial}{\partial z}\left[K_z\left(\frac{\partial s}{\partial z}\right)\right]}_{\substack{\text{dissolved}\\ \text{nutrient}\\ \text{diffusion}}} \underbrace{-ux}_{\text{uptake}} \underbrace{+egN}_{\text{grazing-excretion}},\right\} \tag{11}$$

In these equations μ is given by equation (8) expanded by the substitution of equation (5) for $f(Q)$, and equation (7) for P^{B}, and u is given by equation (6); $Q = N/x$. Other symbols are defined in table 2.

Finally, production is defined as the product of biomass and specific growth rate, thus allowing for the alternation of growth control between nutrients and light. Column production is given by

$$P^{\square} = \int_0^{z_{\max}} \mu x\,\mathrm{d}z. \tag{12}$$

RESULTS

The model was used to predict the distribution of phytoplankton standing crop and production in the complex frontal region around the Scilly Isles. Observations were made in this region from R.R.S. *Challenger* in July 1979, and I am grateful to J. Simpson, A. Edwards and K. Jones for permission to use some of their results. Details of the distribution of temperature, dissolved nitrate + nitrite, and chlorophyll *a*, along a section westwards from the Scilly Isles, are shown in figures 1–3. Methods are described in J. H. Simpson, P. B. Tett, M. L. Argote-Espinosa, A. E. Edwards, K. J. Jones & G. Savidge (unpublished paper).

As far as possible, model parameters (table 2) were chosen from relevant values in the literature, to provide a more severe test of the model than if it were parametrized from local data.

Diffusivities were computed from observed vertical temperature gradients on the assumption of no horizontal transport of heat and with the use of an estimate by Pingree *et al.* (1975) of 2 kcal cm^{-2} $month^{-1}$† for the mean heat flux down the water column in summer.

The simulations involved nitrogen as the limiting nutrient and chlorophyll *a* as a measure of biomass. It was thus necessary to convert carbon-based parameters to a chlorophyll basis, and a carbon: chlorophyll ratio of 50:1 (g:g) was used, after Steele's (1956) ratio of 54:1.

The model was run for 40 simulated days at each station, by which time a steady state had been reached. Predicted distributions of dissolved nitrate + nitrite (figure 4) and chlorophyll *a* (figure 5) look in general like sections across fronts and resemble in particular the observed distributions. This is perhaps unremarkable for the nutrient, for which the choice of lower boundary conditions forced a deep-water nitrogen concentration close to that observed. Observed and predicted chlorophyll *a* concentrations were however strongly correlated (Spearman's coefficient of rank correlation = 0.78, 28 d.f., $p < 0.001$) despite the 'universal' parameterization of biological terms in the model.

Predicted column production (table 1) ranged from about 0.2 g C m^{-2} day^{-1} at the strongly stratified station at the western end of the section, to about 1.7 g C m^{-2} day^{-1} in the more complex water column a few kilometres to the north of the Scilly Isles.

DISCUSSION

Mathematical models can function as refutable reviews of knowledge on a particular topic. A choice of what processes to include, how to describe these processes, and what values to give parameters, can be tested by comparing prediction with observation. In so far as my model is successful it represents an adequate (although not the only possible) summary of the literature concerning processes governing phytoplankton production at fronts. The model's novelty resides partly in its simplicity, which looks back to the models of Riley (1946) and Sverdrup (1953), partly in its hypothesis of alternate limitation by light and nutrient, which derives from Blackman's (1905) modification of Liebig's 'Law of the Minimum', and partly in the use of a cell-nutrient-quota-determined function for growth, taken from the work of Droop (1968, 1977). Given suitable boundary conditions the model ought to be applicable to any ocean in which vertical turbulent diffusion dominates transport processes. Other one-dimensional models with a dominant vertical diffusion term (see, for example, Jamart *et al.* 1977) provide realistic predictions of chlorophyll

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† kcal = 4184 J.

distribution in a stratified ocean, and it seems likely that such models would also predict a biomass distribution in frontal regions with an accuracy similar to that of my model.

It is hard to find measurements of primary production to compare with those in table 1. The ^{14}C method might not be reliable when nutrients limit algal growth, and the incubator version of this method is likely to give imprecise estimates of production in sharply stratified water columns. Predicted production is in very rough agreement with incubator ^{14}C measurements in the English Channel (Boalch, Harbour & Butler 1978) and with incubator measurements made by G. Savidge during our *Challenger* cruise to the Scillies. The main test of the model must however come from a comparison between observed and predicted chlorophyll *a* distributions (figures 3 and 5).

Table 1. Production predicted at stations near Scilly Isles, July 1979

station	position	observed ϕ $J\,m^{-3}$	predicted production $g\,C\,m^{-2}\,day^{-1}$
F 4	50° 00′ N 6° 28′ W	16	1.70
FG 3	50° 03′ N 6° 37′ W	61	0.96
FG 2	50° 02′ N 6° 45′ W	46	1.13
FG 0	50° 03′ N 7° 00′ W	167	0.26
NW 1	50° 06′ N 7° 19′ W	161	0.20

There are several differences in detail between these. Observed chlorophyll concentrations average twice those predicted, and the regions of greatest observed chlorophyll concentration are broader, and penetrate deeper to the west, than the predicted chlorophyll maxima.

Some of these differences might be reduced by local parameterization. The optical attenuation coefficient, λ, was fixed at $0.15\,m^{-1}$ for all simulations, resulting in a compensation depth of about 36 m. The greatest depth at which light-limited growth exceeded grazing in the simulations was about 28 m. Increasing transparency of the water column towards the western end of the section might allow light-limited growth to occur deeper, and, if taken into account in simulations, might predict a chlorophyll distribution closer to that observed at station NW 1.

Other differences might be the fault of the model. Algal sinking (Steele & Yentsch (1960) and many subsequent models) could account for the observed chlorophyll maximum lying deeper than predicted at station NW1. Horizontal transport of nutrient-rich water might account for the greater and broader chlorophyll maximum at stations FG3 and FG2. Another explanation involves vertical migration of the dinoflagellate *Gyrodinium aureolum*, which dominated phytoplankton biomass in this region in July 1979, perhaps interacting with convergence cells (Savidge 1976; James 1978). Cullen & Epley (1981) review observations on the deep chlorophyll maximum in thermally stratified water in the southern Californian Bight, and suggest that, in this region lacking strong tidal mixing, behavioural aggregation is more important than either sinking or physical transport of phytoplankton.

Nevertheless, the proportionate success of the present model in predicting chlorophyll distribution from the temperature section in figure 1 indicates the biological importance, although not the complete dominance, of vertical turbulent diffusion in the frontal region around the Scilly Isles, and thus helps to confirm the hypothesis of Pingree *et al.* (1975).

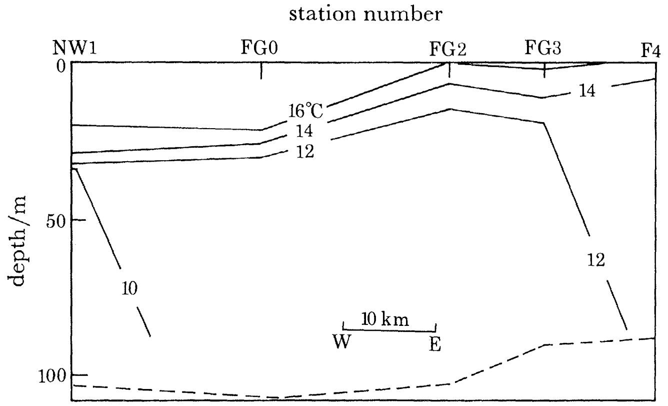

Figure 1. West–east temperature (°C) section near Scilly Isles, July 1979; from CTD measurements.

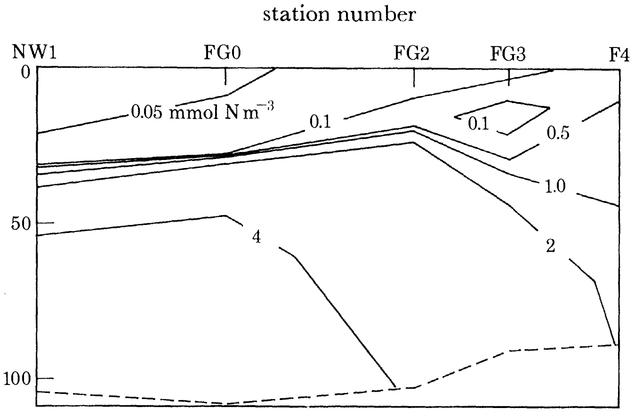

Figure 2. West–east section of dissolved nitrate + nitrite (mmol N m^{-3}) near Scilly Isles, July 1979; from discrete samples.

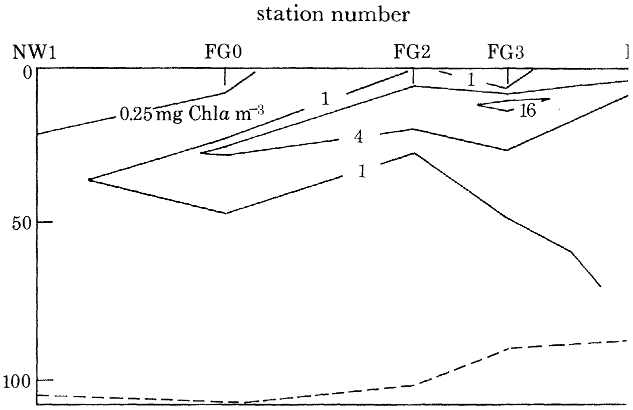

Figure 3. West–east section of chlorophyll *a* (mg m^{-3}) near Scilly Isles, July 1979; from discrete samples corrected for pheopigments.

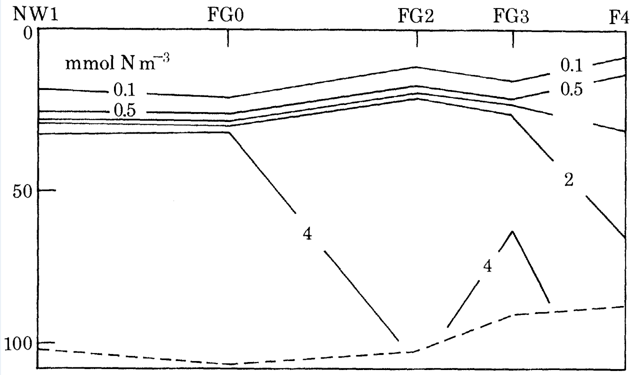

Figure 4. West–east section of predicted concentration of dissolved nitrate + nitrite (mmol N m^{-3}) near Scilly Isles, July 1979; (cf. figure 2).

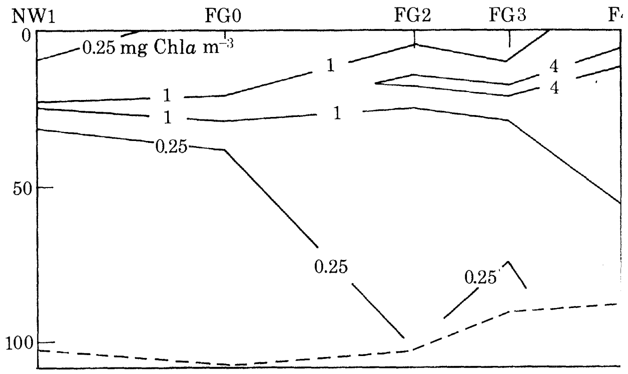

Figure 5. West–east section of predicted chlorophyll *a* concentration (mg m^{-3}) near Scilly Isles, July 1979 (cf. figure 4).

To take these conclusions further requires the testing of the model in several frontal regions, a programme with at least three difficulties.

(i) The parameterization of diffusivity: a problem for physical oceanographers.

(ii) The choice of suitable boundary conditions for dissolved nutrients. This is mainly a chemical problem. At what rate are mineral nutrients released from possibly organically enriched sediments in frontal regions?

(iii) The relation between chlorophyll *a* content and algal biomass, which probably depends on nutrient status and recent illumination (Tett *et al.* 1975).

The predictions in figures 4 and 5 are for steady states, and the agreement between observed and predicted chlorophyll distributions does suggest that physical conditions remain stable for the several tens of days necessary to bring about an equilibrium in algal growth rates. There are, however, faster processes at fronts, and these might entail transient algal growth (see Pingree 1978; Simpson *et al.* 1979). In early summer, fronts and their phytoplanktonic populations must develop together, a topic that can be explored theoretically by combining a phytoplankton growth like mine or those of Radach & Maier-Raimer (1975), Steele & Henderson (1976), or Jamart *et al.* (1977) with a one-dimensional physical model for temperature and diffusivity structure, such as that of James (1977). The equivalent experiment involves following the physical and biological structure of a front over several months.

Finally, it is worth emphasizing that, although 'vertical-process' models are applicable to many parts of the ocean, fronts are good places to test them because of the fronts' proximity to land and because of the strong frontal gradients in physical, chemical and biological properties.

I am grateful to D. Booth, M. Droop, A. Edwards, K. Jones, T. Lederman and J. Simpson for their contributions to the development of the ideas expressed in this paper, and to the Natural Environment Research Council for their support of the practical and theoretical work.

APPENDIX. OPERATION OF THE MODEL

(*a*) *Effective layer thickness for photosynthesis in a turbulent water column*

Equation (7) requires a value for H, the effective thickness of the layer through which phytoplankton at depth z are mixed by turbulence. I assumed that $K_z \Delta t$ was the depth variance of a normal distribution of algal cells which at the beginning of time-step Δt were at a single depth. Thus the average layer thickness is

$$H = 2.3(K_z \Delta t)^{\frac{1}{2}}. \tag{13}$$

$K_z \Delta t$ must be small so that H represents an effectively homogeneous layer. The avoidance of numerical problems required $\Delta t = 0.004$ day; the greatest values of H were thus less than 6 m.

Equation (13) can be rearranged to obtain a mixing time scale t' for a layer of known thickness H':

$$t' = H'^2/5.3 K_z \tag{14}$$

(cf. Pingree *et al.* 1975).

(*b*) *Parametrization of diffusivity*

Diffusivity was estimated from the observed vertical temperature gradient, by assuming a downwards heat flux of 700 kcal m^{-2} day^{-1} on the basis of the figure in Pingree *et al.* (1975) of 2 kcal cm^{-2} month^{-1} for summer in the approaches to the English Channel. In the deep water of stations FG 3 to NW 1 the observed temperature gradient was considerably less than 0.01 K m^{-1}, which was the limit of the precision of available data. As Pingree & Griffiths (1977) have shown, the temperature gradient in the bottom mixed layer approaches the adiabatic, with potential temperature gradients of the order of 10^{-4} K m^{-1} corresponding to a diffusivity of 7000 m^2 day^{-1}. Such a diffusivity requires simulation with an impracticably small time step to avoid numerical instability. Thus the minimum temperature gradient entered into the simulation was 0.0005 K m^{-1}, corresponding to a diffusivity of 1400 m^2 day^{-1}. Both this and the higher value of diffusivity correspond to mixing time-scales (equation (14)) for a 60 m bottom-mixed layer of less than 1 day, and are thus roughly equivalent as far as algal growth and nutrient uptake are concerned. The latter processes have time-scales of 1 day or greater (see Tett *et al.* 1981).

(*c*) *Boundary conditions for dissolved nutrients*

Boundary conditions for phytoplankton biomass and nutrient, and for dissolved nutrient at the upper boundary, were set so that

$$\frac{\partial x}{\partial z} = \frac{\partial N}{\partial z} = \frac{\partial s}{\partial z} = 0. \tag{15}$$

It was; however, necessary to provide an imput of nutrient into the bottom of the water column. I therefore postulated a sediment surface nutrient concentration of 6 mmol N m^{-3} and a diffusivity of 50 m^2 day^{-1}. Separately these parameter values are dubious but together they resulted in realistic final nutrient concentrations in the bottom-mixed layer, and under steady-state conditions gave seabed nutrient fluxes of 2.5 to 35 mmol N m^{-2} day^{-1}. These are, however, larger than the values used by Steele & Henderson (1976) (1 mmol m^{-2} day^{-1}) or estimated by Billen (1978) (2 mmol m^{-2} day^{-1}) or Rutgers van der Loeff (1980) (1.2 mmol m^{-2} day^{-1}) for offshore sediments in the North Sea. This topic requires further theoretical and practical examination.

(*d*) *Numerical problems in operating the model*

Radach & Maier-Reimer (1975) and Steele & Henderson (1976) discuss the advantages of integrating a set of equations such as (9)–(11) with respect to depth, thus making it possible to replace diffusion terms by mixing rates between layers. This is attractive to algologists, evoking chemostat analogies in which mixing rates equal dilution rates, and was the approach adopted by Dugdale (1967) in his influential paper. The earlier version of the present model (Tett *et al.* 1981) used the integrated form, and layers whose thickness was variable within the constraint that their mixing time-scale should not exceed 1 day. The first simulations with equations (9)–(11) were performed after integration with respect to both depth and time, giving for biomass

$$x_{t+\Delta t} = x_t \exp\left(-[x^*/x_t H' + \mu - g]\,\Delta t\right), \tag{16}$$

where x^* is the net rate of biomass diffusion into or from a layer (see Tett *et al.* 1981), and $x^*/x_t H'$ is a specific rate of gain or loss of biomass by diffusion equivalent to dilution rate in a chemostat.

This form enabled the model to be run for a two- to five-layered water column on a Hewlett-Packard 41 C pocket programmable calculator, with a time-step of 0.25 day^{-1}. These simulations did not, however, provide sufficient resolution, and a program was written in HPL for a Hewlett-Packard 9825B desk-top minicomputer to use a forward-difference procedure with equations (9)–(11) in their original forms. It was necessary to ensure that $\Delta t \leqslant \frac{1}{2}\Delta z^2/K_z$ for stability (James 1977; Steele & Henderson 1978). With $\Delta z = 4$ m and $K_z \leqslant 1400$ m^2 day^{-1}, a Δt of 0.004 day was used.

Table 2. Variables, parameters, units, values and sources

(a) *State, intermediate and driving variables*

symbol	definition	expressed as
H	layer thickness for photosynthesis (eqn (13))	m
I	photosynthetically effective irradiance (eqn (4))	$\mathrm{W\,m^{-2}}$
K_z	vertical turbulent diffusivity	$\mathrm{m^2\,day^{-1}}$
N	phytoplankton particulate nutrient (eqn (10))	$\mathrm{mmol\ N\ m^{-3}}$
P^{B}	biomass-related gross photosynthesis (eqn. (7))	$\mathrm{day^{-1}}$
$P^{\square}$	column primary production (eqn (12))	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$
Q	phytoplankton nutrient content ($Q = N/x$)	$\mathrm{mmol\ N\ (mg\ Chl)^{-1}}$
s	dissolved nitrate + nitrite (eqn (11))	$\mathrm{mmol\ N\ m^{-3}}$
u	phytoplankton nutrient uptake rate (eqn (6))	$\mathrm{mmol\ N\ (mg\ Chl)^{-1}\ day^{-1}}$
x	phytoplankton biomass (eqn (9))	$\mathrm{mg\,Chl\,m^{-3}}$
μ	phytoplankton specific growth rate (eqn (8))	$\mathrm{day^{-1}}$

(b) *Parameters*

symbol	definition	value used
e	excreted proportion of grazed phytoplankton nutrient	0.5 (Tett *et al.* 1981)
g	phytoplankton-specific zooplankton grazing rate	$0.25\ \mathrm{day^{-1}}$
I_0	24 h mean (sub)surface photosynthetically effective irradiance	$120\ \mathrm{W\,m^{-2}}$ (Parsons *et al.* (1977); Nanaimo, 50° N, summer)
k_Q	phytoplankton subsistence quota for nitrogen (equation (5))	$0.2\ \mathrm{mmol\ N\ (mg\ Chl)^{-1}}$ (Caperon & Meyer (1972); mol N: mol C = 0.051)
k_s	half-saturation constant for nitrogen uptake by phytoplankton (equation (6))	$2\ \mathrm{mmol\ N\ m^{-3}}$ (Parsons *et al.* (1977); coastal species)
R^{B}	biomass-related phytoplankton respiration rate	$0.1\ \mathrm{day^{-1}}$ (Di Toro *et al.* 1971)†
u_{m}	maximum uptake rate for nitrogen (equation (6))	$1\ \mathrm{mmol\ N\ (mg\ Chl)^{-1}\ day^{-1}}$
α	24 h mean photosynthetic efficiency of phytoplankton	$0.19\ \mathrm{day^{-1}\ (W\,m^{-2})^{-1}}$ (Platt 1975)†
λ	optical attenuation of seawater	$0.15\ \mathrm{m^{-1}}$ (Jerlov 1968)†
μ'_{m}	maximum specific growth rate for phytoplankton (equation (5))	$1\ \mathrm{day^{-1}}$

† For discussion see Tett *et al.* (1981).

(e) *Other parameter values*

Table 2 lists parameter values used in the model. Some of these have been converted by assuming a carbon: chlorophyll ratio of 50:1. Values for which no source are given were estimated, before simulation, from experience with experiments on enclosed natural phytoplankton such as that described by Jones *et al.* (1978).

References (Tett)

Bainbridge, R. 1957 *Biol. Rev.* **32**, 91–115.

Billen, G. 1978 *Estuar. coast. mar. Sci.* **7**, 127–146.

Blackman, F. F. 1905 *Ann. Bot.* **19**, 281–295.

Boalch, G. T., Harbour, D. S. & Butler, E. I. 1978 *J. mar. biol. Ass. U.K.* **58**, 943–953.

Caperon, J. & Meyer, J. 1972 *Deep Sea Res.* **19**, 601–618.

Cullen, J. J. & Eppley, R. W. 1981 *Oceanologica Acta* **4**, 23–32.

Di Toro, D. M., O'Connor, D. J. & Thomann, R. V. 1971 In *Nonequilibrium systems in natural water chemistry* (ed. J. D. Hem), pp. 131–180. Washington, D.C.: American Chemical Society.

Droop, M. R. 1968 *J. mar. biol. Ass. U.K.* **48**, 689–733.

Droop, M. R. 1977 *J. Protozool.* **24**, 528–531.
Dugdale, R. C. 1967 *Limnol. Oceanogr.* **12**, 685–695.
Jamart, B. M., Winter, D. F., Banse, K., Andserson, G. C. & Lam, R. K. 1977 *Deep Sea Res.* **24**, 753–773.
Jamart, B. M., Winter, D. F. & Banse, J. 1979 *J. Plankt. Res.* **1**, 267–290.
James, I. D. 1977 *Estuar. coast. mar. Sci.* **5**, 339–353.
James, I. D. 1978 *Estuar. coast. mar. Sci.* **7**, 197–202.
Jerlov, N. G. 1968 *Optical oceanography* (194 pp.). New York: Elsevier.
Jones, K. J., Tett, P., Wallis, A. C. & Wood, B. J. B. 1978 *J. mar. biol. Ass. U.K.* **58**, 923–941.
Okubo, A. 1978 In *Oceanic fronts in coastal processes* (ed. M. J. Bowman & W. E. Esaias), pp. 23–28. Berlin: Springer-Verlag.
Parsons, T. R., Takahashi, M. & Hargrave, B. 1977 *Biological oceanographic processes* (2nd edn) (332 pp.). Oxford: Pergamon.
Pingree, R. D. 1978 *J. mar. biol. Ass. U.K.* **58**, 955–963.
Pingree, R. D. & Griffiths, D. K. 1977 *Estuar. coast. mar. Sci* **5**, 399–413.
Pingree, R. D., Holligan, P. M. & Mardell, G. T. 1978 *Deep Sea Res.* **25**, 1011–1028.
Pingree, R. D., Pugh, P. R., Holligan, P. M. & Forster, G. R. 1975 *Nature, Lond* **258**, 672–677.
Platt, T. 1975 *10th European Symp. Mar. Biol.* vol. 2, pp. 477–484. Wetteren, Belgium: Universa Press.
Radach, G. & Maier-Reimer, E. 1975 *Mém. Soc. r. Sci. Liège*, Ser. 6, **7**, 113–146.
Riley, G. A. 1946 *J. mar. Res.* **6**, 54–73.
Rutgers van der Loeff, M. M. 1980 *Neth. J. Sea Res.* **14**, 144–171.
Savidge, G. 1976 *Estuar. coast. mar. Sci.* **4**, 617–625.
Simpson, J. H., Allen, C. & Morris, N. C. G. 1978 *J. geophys. Res.* **83**, 4607–4614.
Simpson, J. H., Edelsten, D. J., Edwards, A., Morris, N. C. G. & Tett, P. B. 1979 *Estuar. coast. mar. Sci.* **9**, 713–726.
Simpson, J. H. & Pingree, R. D. 1978 In *Oceanic fronts in coastal processes* (ed. M. J. Bowman & W. E. Esaias), pp. 29–44. Berlin: Springer-Verlag.
Steele, J. H. 1956 *J. mar. biol. Ass. U.K.* **35**, 1–33.
Steele, J. H. & Henderson, E. W. 1976 *Scotl. Dept Agric. Fish., Fish Res. Rep.* **5**, 1–27.
Steele, J. H. & Yentsch, C. S. 1960 *J. mar. biol. Ass. U.K.* **39**, 217–226.
Sverdrup, H. U. 1953 *J. Cons. perm. int. Explor. Mer.* **18**, 287–295.
Tett, P., Cottrell, J. C., Trew, D. O. & Wood, B. J. B. 1975 *Limnol. Oceanogr.* **20**, 587–603.
Tett, P., Edwards, A. & Jones, K. 1981 *Estuar. coast. mar. Sci.* (Submitted.)

Discussion

D. J. CRISP, F.R.S. (*N.E.R.C. Unit, Marine Science Laboratories, Menai Bridge, Gwynedd LL59 5EH, U.K.*) Conformity with observed data does not necessarily validate the underlying processes assumed in the simulation. For example, multiple regression equations can often provide a close fit to sets of observed data though based only on pragmatically derived arbitrary constants.

Stronger evidence would be attributable to the processes assumed if there were few arbitrary constants and the productivity model had been applied to a number of independent fronts.

Would the speaker care to comment?

P. TETT. The aim was to show that it is *possible* to explain much of the distribution of chlorophyll at a front as a result solely of vertical mixing of nutrients and biomass. I agree that conformity of predictions with observations does not necessarily validate the assumptions of a simulation, and that further testing is needed with other data sets. The model was not, however, applied in the same way that a multiple regression can be fitted to data. Instead, the temperature structure of the water column was used to derive the model. With the exception of the lower boundary condition for dissolved nutrient, other parameter values were chosen in advance. The model was thus subject to a harder test than if parameters such as photosynthetic efficiency or nutrient subsistence quota had been adjusted to obtain a better fit of the simulation to the data.

G. E. FOGG (*Marine Science Laboratories, University College of North Wales, Menai Bridge, Gwynedd LL59 5EH, U.K.* I wonder whether a mechanism such as that proposed by Dr Tett, producing increased phytoplankton population at a front, may be a trigger rather than the chief process sustaining production. Once organic matter accumulates at a front, whether it be as a result of passive advection of living or non-living particulate matter, or of enhanced phytoplankton growth, then animals may actively move into it. It is well known that fish and seabirds congregate at fronts and there is evidence that zooplankton populations are higher at fronts too (Floodgate *et al.* 1981). These animals will excrete substances available as nutrients and will thereby promote phytoplankton growth so that there is biological amplification of an increase initially promoted by physical conditions. Two effects should be distinguished: (i) concentration of nutrients from a wide area into the front, and (ii) increased rates of nutrient cycling within the front. Some evidence that these effects occur was found in studies of area accumulation and breakdown at a front in Liverpool Bay. In early summer urea concentrations at this front were about $1\ \mu g\ l^{-1}$ as compared with $0.1\ \mu g\ l^{-1}$ elsewhere, and rates of urea breakdown by bacteria and phytoplankton were several times higher at the front than on either side of it (Floodgate *et al.* 1981).

Reference

Floodgate, G. D., Fogg, G. E., Jones, D. A., Lochte, K. & Turley, C. M. 1981 *Nature, Lond.* **290**, 133–136.

P. TETT. I accept much of Professor Fogg's comment, in so far as it was necessary to include a term in my model for the excretion of nutrients by zooplankton. I disagree in that, in the model, enhanced vertical diffusion of nutrients is the only process capable of *sustaining* high production, since not all phytoplankton nutrients eaten by zooplankton are then excreted. The model explains much enhanced frontal production without postulating horizontal transport of nutrients, but that is not to say that concentration of nutrients through animal movement does not take place or is not significant.