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A Spatial Model of Phytoplankton Patchiness

J. S. Wroblewski[1] and J. J. O'Brien[2]

[1] Department of Oceanography, Florida State University; Tallahassee, Florida, USA, and
[2] Office of Naval Research; Arlington, Virginia, USA

Abstract

The one-dimensional theory of critical-length scales of phytoplankton patchiness is developed to include phytoplankton growth and herbivore grazing as functions of time and space. The critical-length scale L_c for the patch is then determined by the initial spatial distribution and concentration of the limiting nutrient and herbivores in addition to the daily averaged values of the growth and loss processes. The response of an initial phytoplankton patch to the stresses of turbulent diffusion, nutrient depletion, light periodicity, and nocturnal or continuous herbivore grazing is investigated numerically for several oceanic conditions. Nocturnal grazing, while less stressful on primary production than continuous grazing, results in lower phytoplankton standing stocks. Increase in biomass of vertically migrating zooplankton results in a net loss of nutrient which might otherwise be egested, recycled, and utilized in the euphotic zone under continuous grazing conditions. The Ivlev constant is shown via sensitivity analysis to be a significant parameter ultimately influencing phytoplankton production. It is demonstrated numerically that diffusion of phytoplankton cells from areas of high concentration to low concentration prevents the local extinction of the standing stock, thereby rendering a positive herbivore grazing-threshold unnecessary for ecosystem stability.

Introduction

Recent advancement in instrumentation and methodology (Lorenzen, 1966; Clarke *et al.*, 1970; Platt, 1972; Walsh, 1972) has enabled oceanographers to obtain quasisynoptic mappings of the sea-surface chlorophyll distribution. These chlorophyll fields can be related to phytoplankton spatial heterogeneity or "patchiness". Theoretical investigations of the phenomenon of patchiness have been stimulated as a result.

The classical work of Kierstead and Slobodkin (1953) relates the competing physical and biological processes occurring within a phytoplankton patch. The complexity of plankton distributions stems from the interaction of near-deterministic biological rates of growth, death, and prey-predator interaction with the random character of eddies and small-scale turbulence in the ocean. Kierstead and Slobodkin derived a relationship between the length scale of a patch experiencing turbulent diffusion and the rate of growth of the phytoplankton required to balance the diffusive losses:

$$L_c = \pi(\nu/b)^{\frac{1}{2}} ,$$

where L_c is the size of the patch, ν is the diffusivity, and b is the phytoplankton growth rate. If for example b is 10^{-5} sec^{-1} and ν is 10^6 cm^2 sec^{-1}, then L_c is 10 km. A patch smaller than this size could not maintain itself against turbulent diffusion. Thus L_c is known as the "critical-length scale".

Recently Platt and Denman (1975) and Wroblewski *et al.* (1975) considered the effect of herbivore grazing on modifying this critical-length scale. Upon inclusion of an Ivlev grazing function (Parsons *et al.*, 1967) in the biological dynamics, the Kierstead-Slobodkin relationship becomes[1]:

$$L_C = \pi\left(\frac{\nu}{b-R\,\Lambda}\right)^{\frac{1}{2}},$$

where R is the maximum herbivore grazing ration (concentration sec^{-1}) and Λ is the Ivlev constant ($\mathrm{conc.}^{-1}$) for zooplankton grazing. Wroblewski *et al.* (1975) demonstrated the necessity of including nutrient limitation of the phytoplankton to achieve realistic solutions. In these previous simplified models all patch sizes ultimately grow with time without some limitation to growth.

The object of the present paper is to develop further the concept of a critical-length scale of patchiness by investigating the response of an initial patch to the combined stresses of turbulent diffusion, nutrient depletion, light periodicity, and continuous or nocturnal herbivore grazing. Parameter values characteristic of the wind-mixed, northeast Pacific Ocean during the spring and early summer seasons are used. A sensitivity analysis is performed on the model equations to determine the relative importance of the biological processes in determining the patch dynamics. The importance of the herbivore grazing-threshold and the Ivlev constant are determined in this manner.

Formulation of the Model

The Equations

The physical and biological processes which determine the phytoplankton concentration at any arbitrary point in the ocean may be expressed as:

$$\frac{\partial P}{\partial t} + u\frac{\partial P}{\partial x} + v\frac{\partial P}{\partial y} + w\frac{\partial P}{\partial z} = \frac{\partial}{\partial x}\left(\nu_h\frac{\partial P}{\partial x}\right) + \frac{\partial}{\partial y}\left(\nu_v\frac{\partial P}{\partial y}\right) + \frac{\partial}{\partial z}\left(\nu_v\frac{\partial P}{\partial z}\right) + V_m\,SP - QP. \quad (1)$$

The dependent variable P is the concentration (e.g. units of cells/l or µg atom limiting nutrient/l) of phytoplankton. The velocity components u, v, and w are the x-directed, y-directed (horizontal) and z-directed (vertical) vectors, respectively of the organized water motion.

It has been assumed that turbulent transport of P can be approximated by a Fickian diffusion law (Fofonoff, 1962). The first three terms to the right of the equal sign are the turbulent dispersion terms where ν_h and ν_v are the horizontal and vertical eddy diffusivities, respectively.

The term $V_m\,SP$ represents the growth of phytoplankton; V_m is the maximum specific growth rate; S is the function which details the growth formulation. The term QP represents the collective losses of phytoplankton due to such processes as predation by herbivores, extracellular release, respiration, and death.

If we consider for simplicity only the horizontal x direction, assume a constant value of ν_h consistent with the patch length scale to be investigated, and neglect advection, Eq. (1) reduces to

$$\frac{\partial P}{\partial t} = \nu_h\frac{\partial^2 P}{\partial x^2} + V_m\,SP - QP. \quad (2)$$

The circumstances under which advection cannot be neglected in phytoplankton spatial models are discussed by O'Brien and Wroblewski (1973a).

The function S in Eq. (2) is chosen to be a Michaelis-Menton formulation of uptake of the biologically limiting nutrient N by the phytoplankton (Dugdale, 1967). The term $V_m\,SP$ then becomes:

$$\frac{V_m\,NP}{k+N},$$

where V_m is the maximum uptake rate of the nutrient N by P, and k is the Michaelis half-saturation constant, i.e., the concentration of N supporting half the maximum uptake rate. It is assumed that the phytoplankton community is dominated by one or more species with this k value. Phytoplankton and herbivore biomass will henceforth be discussed in units of concentration of the biologically limiting nutrient, e.g. nitrogen.

We separate the loss term, $-QP$ into a herbivore grazing function and a second term, $-BP$, to represent the losses of phytoplankton biomass due to extracellular release and senescent cell autolysis.

The grazing of herbivores, Z, on the phytoplankton, P, is assumed to follow a modified Ivlev function (Parsons *et al.*, 1967):

$$g(P,Z) = R_m Z\,(1 - \exp[-\Lambda(P - P_t)])\,;\quad P > P_t$$
$$g(P,Z) = 0 \qquad ;\quad P \le P_t\,,$$

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[1] The critical length may contain a factor of 2 depending on how the length scale of the phytoplankton patch is defined. For illustrative purposes let us represent two adjacent patches as an always positive sine curve with two periodic peaks. If each patch length L is taken as the patch width above the mean concentration, L_C is as given above. If, however, L is regarded as the distance between adjacent peaks, an assumption often made in spectral analysis of patchiness (Platt *et al.*, 1970), then $L_C = 2\pi\left(\frac{\nu}{b-R\,\Lambda}\right)^{\frac{1}{2}}$. See Wroblewski *et al.* (1975) for the derivation.

where R_m is the maximum rate of herbivore grazing (sec^{-1}), Λ is the Ivlev constant, and P_t is the threshold concentration of P below which the grazing behavior of the herbivores ceases. Actually we set $R_m = 0$ if $P < P_t$.

Upon substitution of these functions, Eq. (2) becomes

$$\frac{\partial P}{\partial t} = \nu_h \frac{\partial^2 P}{\partial x^2} + V_m \frac{NP}{k+N} - R_m Z\,(1 - \exp[-\Lambda\,(P-P_t)]) - BP. \qquad (3)$$

Similarly, we may derive a one-dimensional (horizontal) spatial equation for the growth and diffusion of the herbivores Z:

$$\frac{\partial Z}{\partial t} = \nu_h \frac{\partial^2 Z}{\partial x^2} + R_m Z\,(1 - \exp[-\Lambda\,(P-P_t)]) - \Gamma Z\, g(P,Z)\,, \qquad (4)$$

where the increase of herbivore biomass is dependent on the grazing function $g(P,Z)$ and an egestion term $-\Gamma Z\, g(P,Z)$ linearly related by Γ to the grazing function. Note that as grazing, $g(P,Z)$, increases with the concentration of phytoplankton, egestion, $\Gamma Z\, g(P,Z)$, increases proportionately. The fraction of the grazing ration which is egested is ΓZ. We ignore carnivore grazing and limit the food chain to two links for simplicity. The turbulent diffusion term is similar to that of the phytoplankton. The value of ν_h for the zooplankton population is assumed to be the same as for phytoplankton. Actually, it may be smaller or even zero, as adult herbivores may swim to maintain a patch density.

We include an equation for the diffusion, uptake, and recycling of the biologically limiting nutrient N:

$$\frac{\partial N}{\partial t} = \nu_h \frac{\partial^2 N}{\partial x^2} - V_m \frac{NP}{k+N} + BP + \Gamma Z\, g(P,Z). \qquad (5)$$

Notice that upon neglecting the effect of diffusion,

$$\frac{\partial P}{\partial t} + \frac{\partial Z}{\partial t} + \frac{\partial N}{\partial t} = 0,$$

i.e., the total amount of biologically limiting nutrient in the oceanic region is conserved in this model.

Our formulation of the included processes is simplistic. The assumption of immediate regeneration of the unassimilated material egested by herbivores is not realistic, as zooplankton form fecal pellets which may sink out of the euphotic zone. Important processes such as the formation, sinking, and decomposition of fecal pellets, phytoplankton cell sinking, vertical mixing, and light attenuation with depth have been deliberately ignored in focusing our attention on the horizontal dynamics of phytoplankton patchiness. Inclusion of these factors would require a vertical dimension in the model which is beyond the scope of the present discussion.

The conditions we are attempting to model have influenced our formulation of the biological dynamics. Phytoplankton growth in the oceanic region near "Ocean Station Papa" is most likely limited by light rather than the availability of nutrients during the spring and early summer (McAllister, 1969; McGowan and Williams, 1973). Formulation of diurnal light limitation of phytoplankton growth is introduced later in the paper. Our zooplankton-nutrient dynamics are not meant to describe a nutrient-limited ocean. Where phytoplankton standing stocks are small due to depletion of nutrients, as in the central gyre of the North Pacific, zooplankton grazing and egestion rates are small. An important source of nutrients for phytoplankton growth may then be the metabolic excretory products of zooplankton, e.g. urea-nitrogen (Eppley *et al.*, 1973). A term would then be needed to model the cycling of herbivore metabolites into nutrient available to the phytoplankton.

As the time scale we are dealing with here is at most several weeks, the zooplankton are allowed to increase in body size and grazing capacity, but no increase in the number of individual grazers is allowed. At first the zooplankton (early copepodite stages) assimilate a large proportion of the grazing ration. As they grow and attain their nutritional requirement, more of the ingestion ration is egested. This concept follows from the data presented by Corner *et al.* (1967) on the growth rate, as daily increments in body nitrogen, of *Calanus finmarchicus*. Our formulation of the egestion term simulates increasing egestion rate with increasing zooplankton body nitrogen. Fig. 1 displays the egestion rate $\Gamma Z R_m\,(1\text{-}\exp[-\Lambda\,(P-P_t)])$ as a function of phytoplankton concentration and zooplankton biomass.

Eqs. (3) - (5) contain explicitly the positive parameters ν_h, V_m, k, R_m, Λ, P_t, B, and Γ and implicitly the initial concentrations of P, Z, and N. O'Brien and Wroblewski (1973b) discuss the benefits of nondimensional oceanographic physical-biological equations. Essentially, scaling reduces the number of parameters. Also, the solution of the one nondimensional case is equivalent to solving several cases with specified values for the scaling parameters.

Since we are interested in the competing processes of biological growth and turbulent diffusion on the same time scale, we choose to scale time by the maximum specific growth rate V_m. Thus,

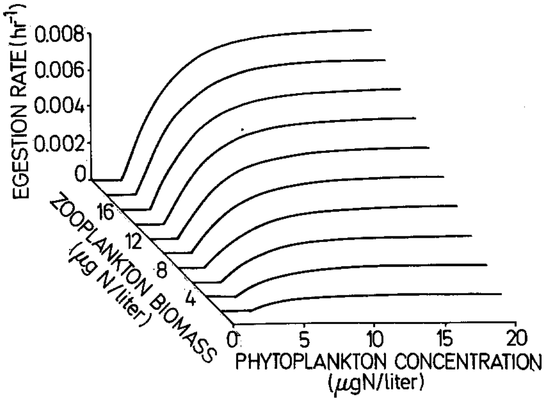

Fig. 1. Herbivore egestion rate $\Gamma Z R_m(1-\exp[-\Lambda(P-P_t)])$ as function of phytoplankton concentration, P, and zooplankton biomass, Z. Dimensional parameters are $\Gamma = 0.05(\mu gN/l)^{-1}$, $R_m = 0.008\ h^{-1}$, $\Lambda = 0.30(\mu gN/l)^{-1}$, $P_t = 2.5\ \mu gN/l^{-1}$. Note, for a fixed Z, egestion rate is a constant proportion of ingestion rate, $R_m(1-\exp[-\Lambda(P-P_t)])$

Table 1. Definition of symbols and scaling relationships

Dimensional quantity	Definition	Scaling factor	Nondimensional quantity
P	Phytoplankton	P/N_t	P'
Z	Zooplankton	Z/N_t	Z'
N	Limiting nutrient	N/N_t	N'
x	Distance	$x/(\nu_h/V_m)^{\frac{1}{2}}$	x'
t	Time	tV_m	τ
R_m	Zooplankton maximum grazing ration	R_m/V_m	β
P_t	Zooplankton grazing threshold	P_t/N_t	P^*
k	Michaelis constant	k/N_t	α
B	Phytoplankton nutrient loss coefficient	B/V_m	ψ
Γ	Zooplankton egestion coefficient	ΓN_t	γ
Λ	Ivlev constant	ΛN_t	λ
V_m	Phytoplankton maximum specific growth rate	-	-
ν_h	Horizontal eddy diffusivity	-	-
N_t	Total amount of biologically limiting nutrient in the system	-	-

$t = \tau/V_m$, where t has units of seconds, τ is nondimensional, and V_m has units of seconds^{-1}. Let P, Z, and N be scaled by N_t, the conserved total amount of biologically limiting nutrient (conc.) in the oceanic region of concern. Also let

$$x = x'\ (\nu_h/V_m)^{1/2} \qquad \alpha = k/N_t$$
$$\beta = R_m/V_m \qquad \gamma = \Gamma N_t$$
$$\lambda = \Lambda\ N_t \qquad \psi = B/V_m$$
$$P^* = P_t/N_t\ ,$$

where primed quantities are dimensionless.

Then Eqs. (3) - (5) may be rewritten:

$$\frac{\partial P'}{\partial \tau} = \frac{\partial^2 P'}{\partial x'^2} + \frac{N'P'}{\alpha + N'} - \beta Z'\ [1-\exp(-\ \lambda P' + \lambda P^*)] - \psi P' \qquad (6)$$

$$\frac{\partial Z'}{\partial \tau} = \frac{\partial^2 Z'}{\partial x'^2} + \beta Z'\ [1-\exp\ (-\ \lambda P' + \lambda P^*)] - \gamma\beta Z'^2[1-\exp(-\lambda P' + \lambda P^*)] \qquad (7)$$

$$\frac{\partial N'}{\partial \tau} = \frac{\partial^2 N'}{\partial x'^2} - \frac{N'P'}{\alpha + N'} + \psi P' + \gamma\beta Z'^2\ [1-\exp\ (-\lambda P' + \lambda P^*)] \qquad (8)$$

Hereupon we drop the primes for convenience. However, it should be remembered that all terms in Eqs. (6) - (8) are nondimensional. To transform back to dimensional units one multiplies the nondimensional quantities by the scaling parameters. For example, one time unit equals V_m^{-1} in hours. One must bear in mind these scaling relationships (Table 1) when comparing the model solutions with real observations.

Note that by scaling, the eddy diffusivity coefficient ν_h is no longer explicit in the model equations. However, interpretation of the model solution still depends on the value of ν_h. As ν_h is a function of length scale (Okubo, 1971), the initial phytoplankton patch size dictates the proper value. We are fundamentally interested in the response of the patch (whether it will grow, be maintained, or decay) on a short time scale. Our assumption of a constant ν_h is no longer valid as the patch size changes by several orders of magnitude from its initial size, thus limiting our solutions in time.

Biological and Physical Parameter Values

We choose to solve Eqs. (6) - (8) over several phytoplankton doubling times. Using data presented by McAllister (1969), the maximum springtime growth rate of phytoplankton at "Ocean Station Papa" (50°N;145°W) is approximately 1.0 doubling day^{-1} or $V_m = 1.15 \times 10^{-5}$ sec^{-1}. Then $\tau = 1$ would correspond to 1 day.

Since $\beta = R_m/V_m$, i.e., the ratio of herbivore grazing rate to the phytoplankton growth rate, we investigate the parameter range $0<\beta<1.2$. Note that $\beta>1.0$ denotes that the herbivores are consuming more phytoplankton than are produced in one day.

In our model we choose $P_t = 0.3$ µgN l^{-1} and $N_t = 30$ µgN l^{-1}. Thus, the grazing threshold P^* is 1% of the phytoplankton concentration if all the biologically limiting nutrient N_t were tied up in the phytoplankton standing stock. Steele (1974a, b) has discussed the importance of the zooplankton grazing threshold in nonspatial marine ecosystem models. Parameter P^* prevents the phytoplankton from being grazed to extinction and thus enhances the stability of the biological dynamics. The grazing threshold no doubt plays a role in determining the stock of phytoplankton, but the unimportance of P_t^* for stability in spatial models is demonstrated later in this paper.

The model value chosen for the Ivlev constant, λ, is 1.0. Dimensional Λ becomes a small number, 0.033 $(\mu gN/l)^{-1}$, as in nature (McAllister, 1970).

In his 1969 paper, McAllister provides data on primary production in the euphotic zone and zooplankton stocks in the upper 150 m at northeast Pacific "Ocean Station Papa" measured concurrently over a period of 6 years. The ratio of phytoplankton to zooplankton standing stocks given in mg C m^{-2} appears to be close to 1 in the spring, although production varies greatly with season. Work by Taniguchi (1973) demonstrates this ratio is reasonable at this latitude in the Pacific Ocean. If we assume a C/N ratio of 6 for phytoplankton (Strickland, 1960) and 10 for zooplankton (Corner and Cowey, 1964) this observed ratio of phytoplankton to zooplankton standing stock would give a P/Z ratio in terms of nitrogen of 1.7. With the nondimensional zooplankton egestion parameter, γ, set equal to 2.3 in our model, we get a steady-state P/Z ratio of 1.2 (Fig. 2a).

Typically the Michaelis constant k is a small fraction of the concentration of limiting nutrient at which the specific uptake rate is maximum (Dugdale, 1967; Eppley *et al.*, 1969). Thomas (1970) estimated k to be 0.75 µg-at NO_3-N l^{-1} in nitrate-limited eastern Pacific waters and we assume a similar value applies near "Ocean Station Papa". As N_t is taken to be 30 µg-at NO_3-N l^{-1}, the range of α is 10^{-1} to 10^{-2}. Higher values of α correspond to less efficient uptake of nutrient by the phytoplankton.

Parsons and Seki (1970), reviewing the literature on phytoplankton extracellular release, have estimated that an average 15% of the total daily production is excreted from the cell. McAllister (1969) used a respiratory loss rate of 12% per day. In our model we may calculate the daily percent change in P due to the loss term $-\psi P$ as

$$\frac{P_{t_0} - P_{t_0+1}}{P_{t_0}} \times 100 =$$

$$\frac{P_0\,[\exp(-\psi t_0) - \exp(-\psi(t_0+1))]}{P_0 \exp(-\psi\, t_0)} \times 100 =$$

$$100\,[1 - \exp(-\psi)].$$

By choosing $\psi = 0.2$, the phytoplankton lose 18‰ of their biomass daily due to extracellular release and cell autolysis.

While phytoplankton patch sizes range from millimeters to tens of kilometers (Platt *et al.*, 1970), we are interested in the common oceanic patch size of the order 1 km. Thus an appropriate value for ν_h is of the order 10^4 cm^2 sec^{-1} (Okubo, 1971).

Before we begin our discussion of patch dynamics we solve Eqs. (6) - (8) without spatial dependence. We obtain the steady-state values for P, Z, and N using the parameter values given in Fig. 2a to be used in the following sensitivity analysis.

Sensitivity Analysis of Biological Dynamics

We employ the technique of sensitivity analysis to determine which of the model's parameters are most important in determining the biological dynamics within a patch. Given the steady-state solution to the model equations, the displacement from equilibrium the model experiences upon variation in a parameter value is defined as the model's sensitivity to the parameter (Tomović, 1963). If the solution changes substantially with a small variation in a particular parameter, then the value of that parameter is important and must be estimated with precision (Smith, 1970).

Analytical sensitivity analysis involves derivation of partial differential equations describing the rate of change of the dependent variables (P, Z, N) with respect to change in the model parameters. These simultaneous equations are then solved for the values of the partial derivatives, e.g. $\frac{\partial P}{\partial \alpha}$, $\frac{\partial Z}{\partial \beta}$, etc.

Consider the steady-state form of Eqs. (6) - (8). If we neglect the turbulent diffusion terms, these three equations sum to zero. Therefore, we use

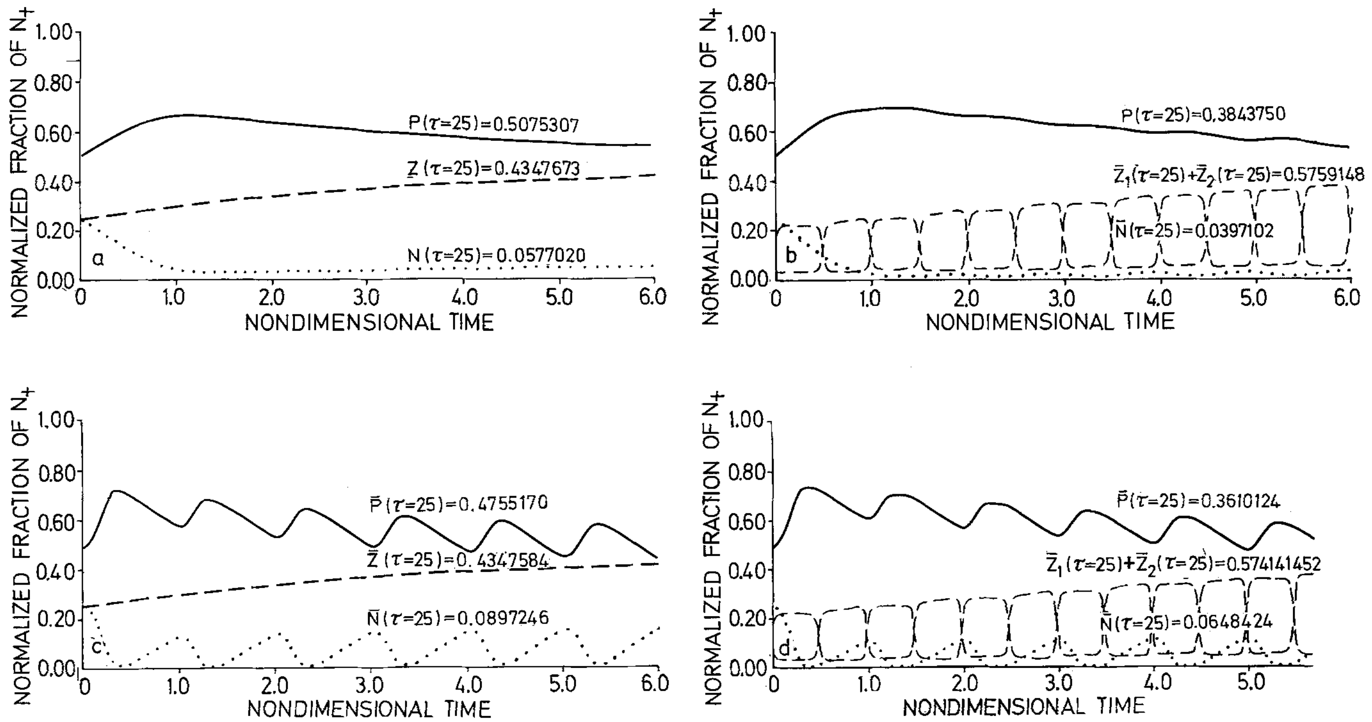

Fig. 2. (a) Time-dependent standing-stock concentrations of phytoplankton P (solid line), zooplankton Z (dashed line), and nutrient N (dotted line). Abscissa is nondimensional time ($t=\tau/V_m$); ordinate is concentration of the biotic component as a fraction of total amount of biologically limiting nutrient in the system, N_t. The 7-digit, steady-state values are used in the sensitivity analysis. The nondimensional biological parameter values for this solution are: $\alpha=0.05$, $\beta=1.0$, $\gamma=2.3$, $\psi=0.2$, $\lambda=1.0$, $P^*=0.01$. (b) Same as (a), except herbivore grazing is function of time. Zooplankton component Z is partitioned into grazing, euphotic zone herbivores Z_1 and non-grazing, non-excreting, aphotic zone herbivores Z_2. $\bar{P}$ is steady-state standing stock of phytoplankton averaged over 1 doubling time. $\bar{N}$ is steady-state nutrient concentration, and $\bar{Z}_1$, and $\bar{Z}_2$ are steady-state zooplankton fractions each averaged over 1 nondimensional day. (c) Same as (a), except nutrient uptake by phytoplankton is a function of time. $\bar{P}$, $\bar{Z}$, and $\bar{N}$ are steady-state concentrations averaged over 1 nondimensional day. (d) Same as (b), except nutrient uptake by phytoplankton is a function of time. See text for details

only the steady-state Eqs. (9) - (10) for P and Z below and the closure relationship (11) in the sensitivity analysis:

$$\frac{NP}{\alpha+N} - \beta Z[1-\exp(-\lambda P+\lambda P^*)] - \psi P = 0, \tag{9}$$

$$\beta Z[1-\exp(-\lambda P+\lambda P^*)] - \gamma\beta Z^2[1-\exp(-\lambda P+\lambda P^*)] = 0. \tag{10}$$

$$N+P+Z=1. \tag{11}$$

We first differentiate Eqs. (9) - (11) with respect to each biological parameter. The results are represented by a square coefficient matrix A. For example, differentiation of Eqs. (9) - (11) with respect to α yields:

$$\begin{bmatrix} A_{11} & A_{12} & A_{13} \\ A_{21} & A_{22} & A_{23} \\ A_{31} & A_{32} & A_{33} \end{bmatrix} \begin{bmatrix} \frac{\partial P}{\partial\alpha} \\ \frac{\partial Z}{\partial\alpha} \\ \frac{\partial N}{\partial\alpha} \end{bmatrix} = \begin{bmatrix} \frac{NP}{(\alpha+N)^2} \\ 0 \\ 0 \end{bmatrix},$$

where $A_{11} = \frac{N}{\alpha+N} - \psi - \beta\lambda Z\exp(-\lambda P+\lambda P^*)$

$$A_{12} = \beta\exp(-\lambda P+\lambda P^*) - \beta$$

$$A_{13} = \frac{P}{\alpha+N} - \frac{NP}{(\alpha+N)^2}$$

$$A_{21} = \lambda\beta Z\exp(-\lambda P+\lambda P^*)[(1-\gamma Z)]$$

$$A_{22} = \beta - \beta\exp(-\lambda P+\lambda P^*) - 2\gamma\beta Z[1-\exp(-\lambda P+\lambda P^*)]$$

$$A_{23} = 0$$

$$A_{31} = A_{32} = A_{33} = 1.$$

Matrix A is always the same upon differentiation with respect to any parameter. We can evaluate $\frac{\partial P}{\partial\alpha}$, $\frac{\partial Z}{\partial\alpha}$, and $\frac{\partial N}{\partial\alpha}$ by using Gaussian elimination to solve for A^{-1}, the matrix inverse, and multiplying A^{-1} by the column vector specific to each parameter.

Table 2. Sensitivity analysis. Partial derivative values of phytoplankton *P*, zooplankton *Z*, and nutrient *N* differentiated with respect to biological parameters and normalized by parameter/component ratio (e.g. $\frac{\alpha}{P}\frac{\partial P}{\partial \alpha}$). Steady state $P = 0.507$, $Z = 0.435$, $N = 0.058$. Parameters $\lambda = 0.05$, $\beta = 1.0$, $\gamma = 2.3$, $\psi = 0.2$, $\lambda = 1.0$, and $P^* = 0.01$

	P	Z	N
α	-0.117	-1.85×10^{-9}	1.034
β	-0.159	1.75×10^{-8}	1.396
λ	-0.125	1.38×10^{-8}	1.099
ψ	-0.095	-1.48×10^{-9}	0.831
γ	1.044	-1.000	-1.650
P^*	0.002	-2.72×10^{-10}	-0.022

Table 3. Relative sensitivity analysis. Table 2 values divided by γ/N $(\partial N/\partial \gamma)$ x 100, then ranked with decreasing magnitude. Summation of the assignments by rows is given in fourth column

	P	Z	N	Σ
α	10	16	5	31
β	8	14	2	24
λ	9	15	3	27
ψ	11	17	7	35
γ	4	6	1	11
P^*	13	18	12	43

The values in Table 2 are the evaluated partial derivatives of *P*, *Z*, and *N* differentiated with respect to the parameters α, β, λ, ψ, γ, and P^*, and normalized by the ratio of the parameter to the model component. That is, the first value in Table 2 is $\frac{\alpha}{P}\frac{\partial P}{\partial \alpha}$.

The sensitivity of greatest magnitude (-1.650) is that by *N* for γ. Thus, for a 1% increase in the zooplankton egestion coefficient, the steady-state nutrient concentration would decrease by 1.65%. Higher values of γ mean less assimilation and lower zooplankton biomass. This in turn results in less grazing and higher phytoplankton standing stock, which reduces the amount of dissolved nutrient *N*.

Finally, as a measure of the overall importance of the parameters, we order the 18 sensitivities of Table 2 relative to $\frac{\gamma}{N}\frac{\partial N}{\partial \gamma}$. Table 3 lists the assignments. If we sum across the rows in Table 3, we have an indication of the overall influence of the parameter on the biological dynamics. We see that the zooplankton egestion parameter γ has the foremost effect on the biological solutions. The grazing threshold P^* is the least influential parameter. It is noteworthy that the most important parameters (γ, β, and λ) are those of the herbivore dynamics, both ingestion and egestion. The Ivlev parameter λ has importance in both processes as it is found in both terms. The grazing threshold P^* has importance only when the phytoplankton concentration becomes very small, as may occur if $\beta > 1$, or if the phytoplankton become nutrient-limited.

The fundamental importance of V_m, the growth rate of the phytoplankton, should not be forgotten. V_m is implicit in the sensitivity analysis via the scaling parameters. For example, a change in β implies a change in either V_m or in the maximum grazing ration R_m. As $t = \tau/V_m$ we are in essence investigating all other processes relative to the growth time scale of the phytoplankton.

If we had not neglected the turbulent diffusion terms in our sensitivity analysis and the steady-state solution was not spatially homogeneous, the matrix *A* above would be larger by a factor equal to the number of spatial model grid points. The diffusion term links the solution at each grid point to the values of *P*, *Z*, and *N* at the neighboring points. Rather than solving this large matrix, a numerical sensitivity analysis of dimensional equations (3) - (5) can be performed to demonstrate the influence of the eddy coefficient ν_h on the spatial solutions. We find as expected *a priori*, an increase in the value of ν_h results in decreased gradients.

Investigation of the Model

We now return to the main thesis of this paper. We are interested in the response of an initial phytoplankton patch to the combined stresses of turbulent diffusion, nutrient depletion, and zooplankton grazing. The time-dependent, spatial solutions to Eqs. (6) - (8) which follow were numerically computed and displayed graphically using a CDC6400 computer.

There are many solutions to Eqs. (6) - (8), dependent upon the initial conditions. We have chosen to explore several cases with the following environmental conditions and stresses to which the phytoplankton patch is exposed:

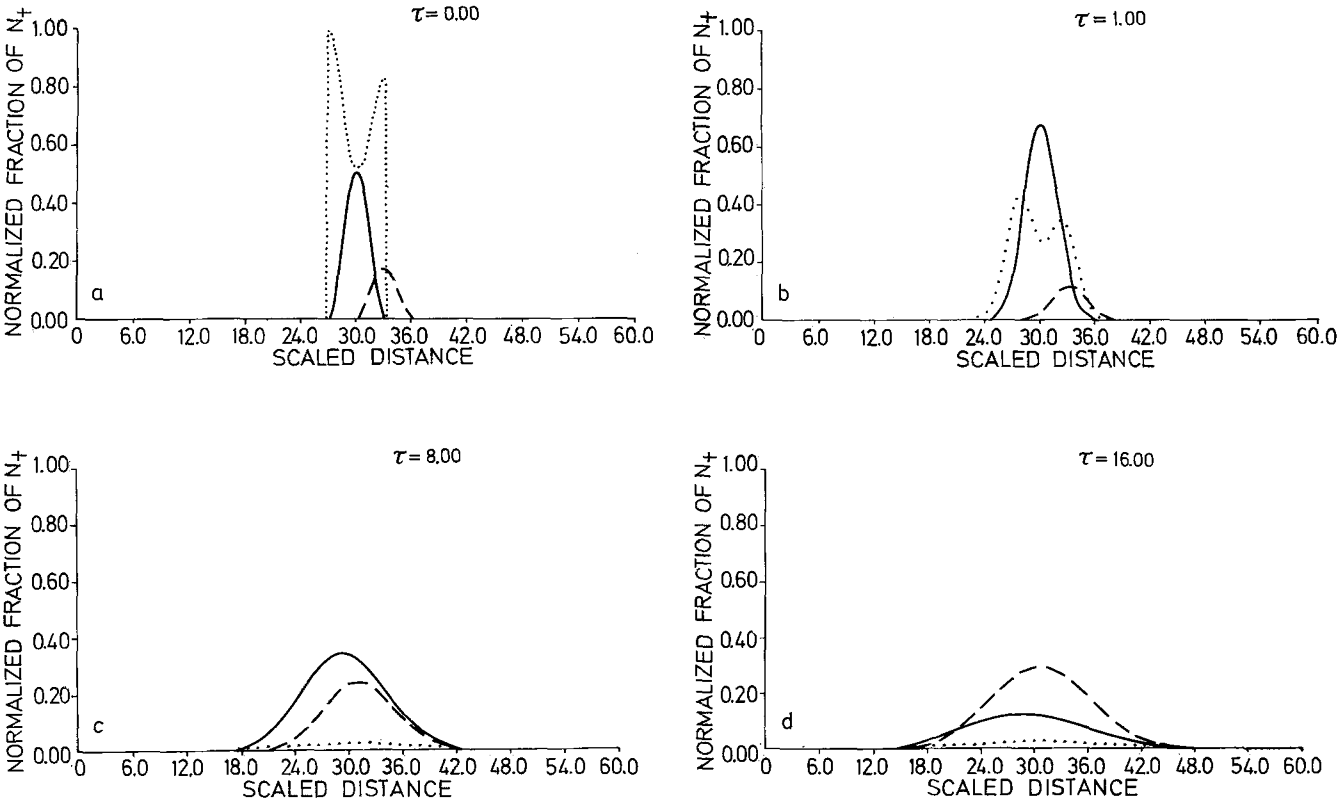

Fig. 3. (a) Initial conditions for Case A. Solid line delineates a phytoplankton patch; dotted line represents concentration and spatial distribution of the limiting nutrient; dashed line outlines a zooplankton patch. Ordinate is same as in Fig. 2. Each nondimensional spatial unit (abscissa) represents 0.5 km, since $x = x' (\nu_h/V_m)^{\frac{1}{2}}$, $\nu_h = 3 \times 10^4$ cm^2 sec^{-1} and $V_m = 1.15 \times 10^{-5}$ sec^{-1}. (b) - (d) Time-dependent spatial solution of Eqs. (6) - (8) with the above initial conditions and same parameter values as in Fig. 2a. Stresses upon the phytoplankton patch are nutrient limitation, continuous herbivore grazing, and turbulent diffusion. Since V_m = 1 day^{-1}, time $\tau = 1$ is one day (b), $\tau = 8$ is eight days (c), and $\tau = 16$ is sixteen days (d)

Case A. (1) A nutrient-patchy ocean surface; (2) continuously grazing herbivores; (3) turbulent diffusion.

Case B. (1) A nutrient-rich ocean surface as after wind mixing; (2) continuously grazing herbivores; (3) turbulent diffusion.

Case C. (1) A nutrient-rich ocean surface; (2) continuous versus nocturnally grazing, vertically migrating herbivores; (3) turbulent diffusion.

Case D. (1) A nutrient-rich ocean surface; (2) nocturnally feeding grazers; (3) diurnal light limitation of phytoplankton growth; (4) turbulent diffusion.

Case A

The initial conditions for Case A are shown in Fig. 3a. The solid line represents the phytoplankton patch. The dashed line outlines a zooplankton patch adjoint to one boundary of the phytoplankton patch. The dotted line shows the concentration and spatial distribution of the biologically limiting nutrient. In this and the following figures, each nondimensional spatial unit is approximately 0.5 km, since $x = x'(\nu_h/V_m)^{\frac{1}{2}}$, and we have chosen $\nu_h = 3 \times 10^4$ cm^2 sec^{-1} and $V_m = 1.15 \times 10^{-5}$ sec^{-1}. Thus, the initial phytoplankton patch is 6 units or approximately 3 km in length. The next several figures (Fig. 3b, c, d) show the time-dependent spatial solutions of Eqs. (6) - (8) computed with these initial conditions and the parameter values specified in Fig. 2a. Notice the phytoplankton patch grows as the concentration of limiting nutrient declines. At time $\tau = 8.0$ (Fig. 3c), the nutrient has fallen to a low concentration and the continuously grazing zooplankton have increased in biomass at the expense of the phytoplankton. All the while diffusion has acted to disperse the patches.

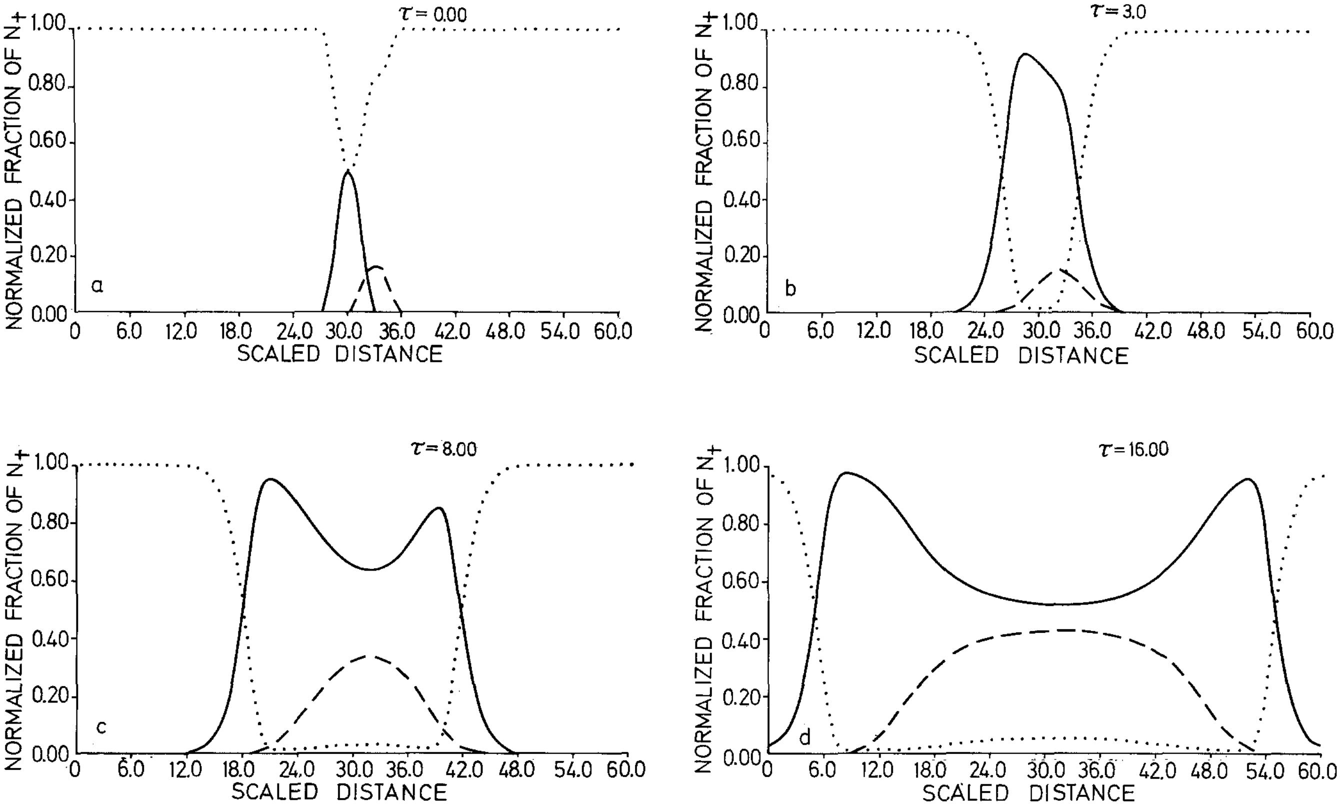

Fig. 4. (a) Initial conditions for Case B. Line representations, initial conditions, and parameter values as in Fig. 3, except for abundance of nutrient beyond the phytoplankton patch edges. The initial phytoplankton patch size is 3 km. (b) - (d) Time-dependent spatial solution of Eqs. (6) - (8) with the above initial conditions and same parameter values as in Fig. 2a. Stresses upon the phytoplankton patch are continuous herbivore grazing, and turbulent diffusion. Time τ is in days

The displacement of the patch centers is due to the initial conditions. The solution at τ = 16.0 or 16 days (Fig. 3d) shows little of the phytoplankton patch remaining, the area now dominated by a zooplankton patch. The small amount of nutrient present is mainly due to zooplankton egestion.

Case B

Case B simulates an oceanic region where nutrient is plentiful and spatially homogeneous. Otherwise the initial conditions (Fig. 4a) and parameter values are the same as in Case A. The immediate result is a bloom of the phytoplankton, with the patch proliferating as it is diffused into nutrient-rich water (Fig. 4b, c, d). A dip in the phytoplankton patch concentration appears with time as the zooplankton patch causes heavy grazing (Fig. 4c). The zooplankton may even split the original phytoplankton patch into two patches if the grazing is heavy enough, i.e., if $\beta > 1.0$.

A second noteworthy result of this case is the appearance of abrupt gradients between the phytoplankton patch edges and the nutrient field. In both coastal and oceanic regions, discontinuities in the distribution of phytoplankton are often so extreme that the edges of patches can be seen with the naked eye (Bainbridge, 1957; Platt *et al.*, 1970; Beers *et al.*, 1971). Strong gradients in the nutrient field near the edge of a phytoplankton patch is a model prediction which could easily be tested with observational data.

Case C

To investigate the effect of a continuous versus a nocturnal herbivore grazing stress, we have simulated the diurnal migration of zooplankton into the oceanic surface waters. Let the total herbivore biomass z be partitioned into two fractions, z_1 and z_2. Fraction z_1 is that portion of z located in the surface waters where it can graze on the phytoplankton patch. Fraction z_2 is the remaining portion of z which has vertically migrated downward where it can no longer graze on the phytoplankton. In essence, z_2 is removed temporarily from the biological dynamics.

Eq. (7) describing the change of herbivore biomass z with time becomes

$$\frac{\partial z_1}{\partial \tau} = \frac{\partial^2 z_1}{\partial x^2} + \beta z_1 \left[1-\exp(-\lambda P + \lambda P^*)\right](1-\gamma z_1)$$

$$+ \Phi z_2 \exp[-(\tau-\tau_2)^2/\sigma^2] - \Phi z_1 \exp[-(\tau-\tau_1)^2/\sigma^2], \quad (12)$$

and $$\frac{\partial z_2}{\partial \tau} = \Phi z_1 \exp[-(\tau-\tau_1)^2/\sigma^2]$$

$$- \Phi z_2 \exp[-(\tau-\tau_2)^2/\sigma^2], \quad (13)$$

where τ is again nondimensional time, τ_2 is that point within the nondimensional day about which ascent into the surface waters is centered, and τ_1 is the period about which descent from the surface is centered. Parameter σ is the fraction of the nondimensional day over which the migrational transition takes place. If $\sigma = 1.0$, then 95% of these zooplankton complete their vertical migration within 4 h. The transition period is centered about analogous sunset and dawn periods within a nondimensional day (Fig. 5).

Parameter Φ determines what portion of the total herbivore biomass z undergoes migration. The standing stock of grazers in oceanic regions is generally composed of both omnipresent herbivores and nocturnal feeders who vertically migrate to the surface (Banse, 1964). McAllister (1961) suggests that the nighttime abundance of grazers in the upper 50 m at "Ocean Station Papa" is about three times that of the daylight hours. Choosing a model value of $\Phi = 0.4$, whereby 66% of the total zooplankton migrate, would closely model the observational data. However, to test the maximal effects of vertical migration on phytoplankton patchiness, we have used $\Phi = 1.0$, whereby 85% of the zooplankton migrate (Fig. 5).

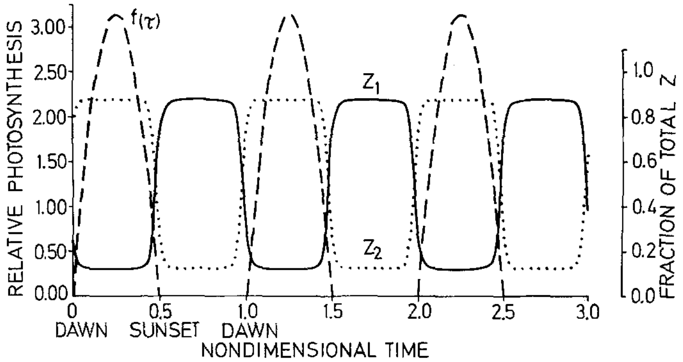

Fig. 5. Relative photosynthesis $f(\tau)$ and vertical migration pattern of euphotic zone herbivores z_1, and aphotic zone herbivores z_2 as functions of time of day. One doubling of phytoplankton per day is assumed. See text for details

In Case C, then, we compare the effect of continual grazing versus a periodic grazing stress on a phytoplankton patch in oceanic waters initially unlimited by nutrient. We first solve the model using the continual grazing scheme of Eq. (7). The initial conditions and parameter values used are the same as in Fig. 4, except the zooplankton spatial distribution is homogeneous with an initial concentration of 0.20. There is also a low (0.07) ambient phytoplankton concentration present. The growth of the initial phytoplankton patch in time is shown in Fig. 6a. As the initial patch is partially grazed, the ambient concentration of P grows. After 4.5 doubling times, the locale of the initial patch has an even lower P concentration than its surroundings. The corresponding time sequence of nutrient distributions is shown in Fig. 6b. Concentration of the limiting nutrient decreases everywhere as P increases. The increase in zooplankton biomass z (not shown) is greatest in the area of the initial phytoplankton patch.

Now we solve our model using Eqs. (12) and (13) in place of Eq. (7). The vertically migrating herbivores are allowed to graze for only half the nondimensional day. By reducing the grazing stress in this manner, one would expect a higher phytoplankton standing stock. However, this is not the case. The steady-state P concentration is in fact reduced by 24% for the case of vertically migrating herbivores below that concentration of P when the zooplankton were always present. This result is due to the removal of z_2 from the biological dynamics. The zooplankton having vertically migrated out of the surface patch are no longer recycling nutrient back into the water column. The steady-state concentration of dissolved nutrient N (averaged over the nondimensional day) is 31% lower. The total production of $z = z_1 + z_2$ is

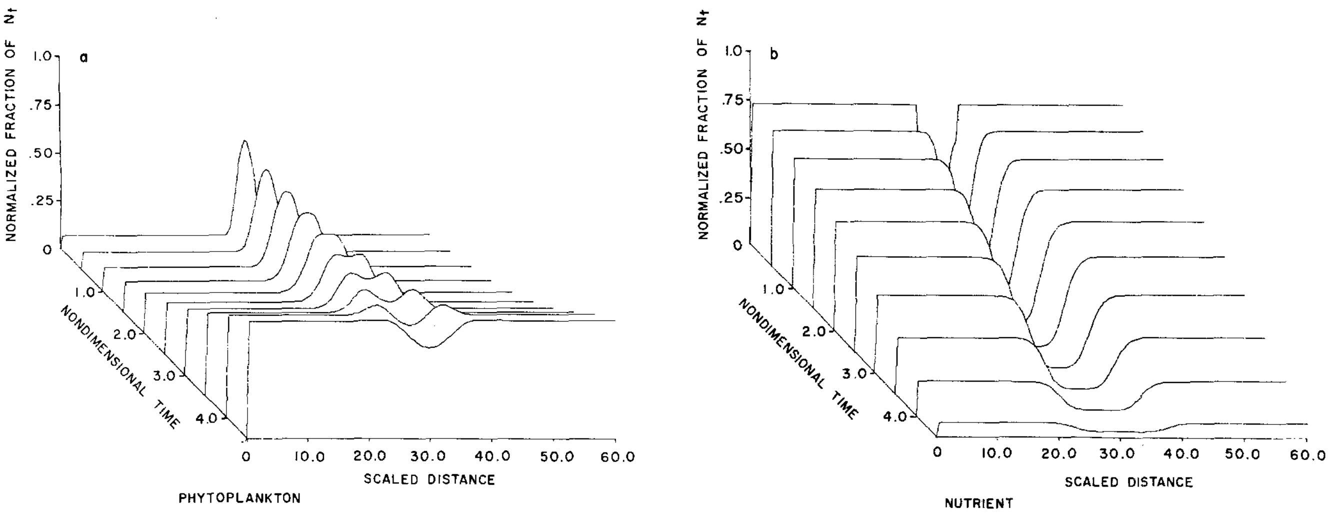

Fig. 6. Case C. Time-dependent spatial solution of Eqs. (6) - (8) with initial conditions of Fig. 4a, except zooplankton spatial distribution is homogeneous with initial concentration of 0.20. The initial phytoplankton patch size is 3 km with a low (0.07) ambient concentration of phytoplankton also present. Stresses upon the phytoplankton patch are continuous herbivore grazing and turbulent diffusion. (a) Spatial distribution and concentration of phytoplankton with time; (b) spatial distribution and concentration of limiting nutrient with time

32% higher, as the Z_2 herbivore biomass acts as a sink for half the nondimensional day. These results are shown without spatial dependence in Fig. 2b.

If the Z_2 zooplankton were allowed to excrete metabolites, the surface concentration of P and N would be even lower, as the vertical migration and excretion processes would constitute a continual loss of limiting nutrient from the euphotic zone. This nutrient loss would have to be compensated for by upwelling or vertical mixing to maintain a phytoplankton population in the euphotic zone.

The spatial solution of Case C with nocturnal grazing is not shown for brevity, as the spatial structure of the phytoplankton patch is not much different than the solution with continuous grazing. The time-dependent grazing stress causes slight oscillations in the phytoplankton concentration.

Case D

We next investigate the combined effect of diurnal light limitation of phytoplankton growth and continuous versus nocturnal grazing stresses. To simulate diel variation in photosynthesis, we multiply the phytoplankton nutrient uptake term by the function

$$f(\tau) = \frac{\pi}{2\Theta} \sin(\pi\tau/\Theta),$$

where τ is nondimensional time equal to tV_m and Θ represents the daylength fraction of one nondimensional day. During the remainder of the nondimensional day, we set $f(\tau) = 0$ to simulate no growth at night. Note that if N is constant and there is no grazing, the total phytoplankton growth over one nondimensional day is the same with or without multiplication of the uptake term by this function, since

$$\int_0^\Theta f(\tau) = 1.$$

The function acts to condense the daily phytoplankton growth into the Θ fraction of a nondimensional day, assuming dawn begins at $\tau = 0$.

The solution of Eqs. (6) - (8) utilizing this function is shown in Fig. 2c. While the potential uptake of nutrient over one nondimensional day is the same, the steady-state concentration of phytoplankton (averaged over the nondimensional day) is 6% lower than without the diel variation. This results from the extracellular release term $-\psi P$ and the near depletion of nutrients during the growth period. The loss of nutrient by $-\psi P$ is greatest when P is highest in the day, but continues to decrease P during the night when P is not growing. The daily averaged increase of dissolved nutrient in the diurnal photosynthesis case is also 6%. We can eliminate zooplankton grazing as the cause of the lower steady-state P as the concentration of Z with time is identical to that where $f(\tau) = 1$ for all time (Fig. 2a).

If we combine the stresses of diel variation in photosynthesis and noctur-

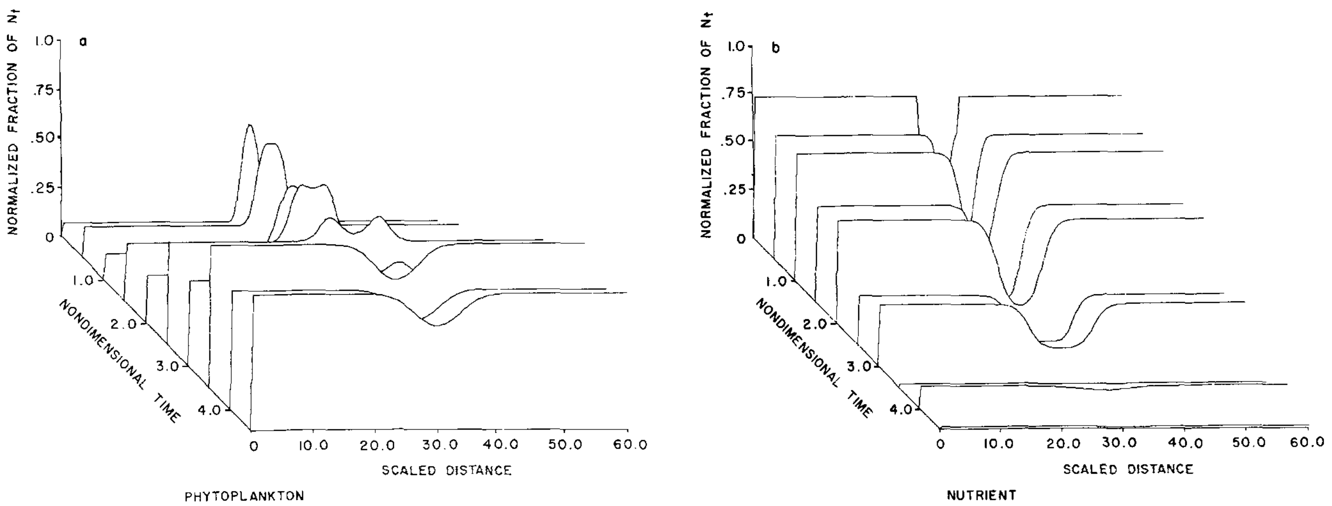

Fig. 7. Case D. Time-dependent spatial solution of Eqs. (6), (8), (12), and (13) with same initial conditions as Case C. Nutrient uptake by phytoplankton and herbivore grazing are functions of time. Stresses upon the phytoplankton patch are periodic growth, nocturnal herbivore grazing, and turbulent diffusion. (a) Spatial distribution and concentration of phytoplankton with time; (b) spatial distribution and concentration of limiting nutrient with time

nal grazing zooplankton (see Fig. 5 for the phase of the functions), we obtain the daily averaged steady-state values of *P*, *Z*, and *N* shown in Fig. 2d. The phytoplankton concentration is reduced 29% below that where neither stress is applied. This decrease is close to but not exactly an additive effect of the individual stresses (24% + 6% decreases in *P*), due to the nonlinear nature of the biological dynamics. The total zooplankton standing stock is approximately that for the vertical migration, constant *P* growth case (Fig. 2b). The dissolved nutrient concentration is less than that expected solely with diurnal variation of photosynthesis (Fig. 2c). The amount of nutrient being recycled is reduced as zooplankton vertically migrate out of the euphotic zone.

The spatial solution of Case D uses the same initial conditions as in Case C. The effect of diel variation of phytoplankton growth and a periodic grazing stress is reflected in the oscillating phytoplankton patch concentrations (Fig. 7a) and nutrient concentrations (Fig. 7b).

Discussion

We have used parameter values in our model characteristic of the springtime, northeast Pacific Ocean in order to compare our results with the investigations of McAllister (1961, 1969) at "Ocean Station Papa". While McAllister's (1969) analytical model of phytoplankton and zooplankton production was in terms of carbon, the two models have basically similar growth and loss terms.

Both models show that diurnal variation of phytoplankton growth leads to a high plant stock by sunset but also a large loss due to extracellular release (or plant respiration in McAllister's carbon model) during the night.

McAllister was concerned with demonstrating that different grazing schemes result in large differences in secondary production. He showed that nocturnal grazing on light-limited phytoplankton increases the herbivore production over that produced by continual grazing via "better utilization of the growth potential of the phytoplankton". Nocturnally grazing herbivores consume a portion of the primary production which otherwise would be lost during the night through respiration (or extracellular excretion). Nocturnal grazing also permits unhindered growth of the phytoplankton during the day.

Our results were similar to McAllister's in that nocturnal grazing increased the steady-state herbivore production (here by 32%) over that produced with continual grazing on plants growing only during the day. While McAllister assumed an abundance of nutrients at all times, our model shows these relationships may also hold as nutrients become depleted in the euphotic zone. However, our formulation of the zooplankton nutrient dynamics is not realistic in a nutrient-limited ocean.

The present study shows one consequence of nocturnally grazing, vertically migrating zooplankton behavior is to reduce the amount of herbivore egested nutrient in the euphotic zone during the daylight hours. As the herbivores are only allowed to egest nutrient while they graze in the euphotic zone, the act of vertical migration temporarily removes the zooplankton biomass from the system, resulting in less nutrient involved in recycling and uptake. This lowered nutrient availability results in a smaller standing stock of phytoplankton unless upwelling insures a nutrient-unlimited environment. The effect is enhanced if the migrators are allowed to excrete metabolites while in the lower layer, constituting a continual loss of nutrient from the euphotic zone. Increases in ammonia below the euphotic zone in the nutrient-limited central gyre of the North Pacific have been observed (Eppley *et al.,* 1973), suggesting this process may indeed exist.

With an understanding of the dynamics of our model, we now return to the main thesis of our paper, namely that of determining the critical-length scale for a patch of phytoplankton experiencing the stresses of nutrient depletion, diel periodicity in growth rate, continuous and/or nocturnal herbivore grazing, and turbulent diffusion.

As stated previously, the critical size of a one-dimensional patch undergoing dissipation by turbulence and continuous, Ivlev type, herbivore grazing is given by

$$L_c = \pi \left(\frac{\nu}{b - R\Lambda} \right)^{1/2} .$$

Using data derived from McAllister (1969, 1970), and assuming for the moment that b and R are constant with time and space, L_C for "Ocean Station Papa" during spring when grazing is highest is of the order

$$\tau \left[\frac{3 \text{ x } 10^4 \text{ cm}^2 \text{ sec}^{-1}}{(1.15 \text{ x } 10^{-5} \text{ sec}^{-1}) - (1.8 \text{ x } 10^{-5} \text{ mgCm}^{-3} \text{ sec}^{-1})(0.02 \text{ m}^3 \text{mgC}^{-1})} \right]^{\frac{1}{2}},$$

or 1.5 km.

If b and R become functions of time and space, L_C is no longer given exactly by this expression. The critical length in this case may necessarily be determined from the solution of a model explicitly describing the biological dynamics and the initial conditions.

In the simulations presented, all initial phytoplankton patch sizes have been well above this critical length, and all initial patches have grown. We can set our initial patch size slightly less than L_C, and again observe the responses of the model to the considered stresses.

In all cases where the spatial variation of b and R are such that $L < L_C$, we find the initial phytoplankton patch decays with time. Fig. 8 illustrates the effect of the time-dependent stresses on the rate of decline of the patch. The lower solid line shows the concentration of phytoplankton at the patch center with time for the case of continuous grazing and growth. The upper solid line represents the patch center concentration of P where the grazing stress is 95% nocturnal and 5% continuous. The dashed curves demonstrate the effect of diel periodicity in phytoplankton growth on the rate of decay of the patch. The lower dashed line is the patch center concentration where the grazing stress is again continuous. The upper dashed curve is for the nocturnal grazing condition. The value of β used in Fig. 8 is 1. If we had used a much lower wintertime value for β there would be little difference in the decay curves comparing nocturnal to continual grazing-stress conditions.

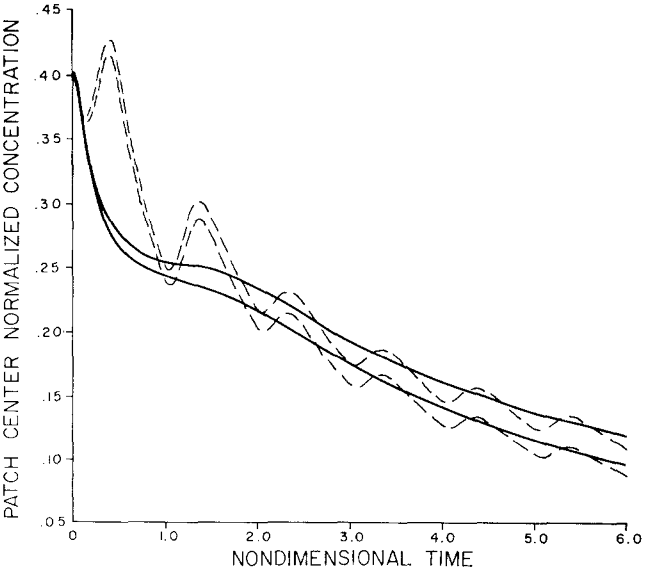

Fig. 8. Effect of time-dependent stresses upon rate of decay of a phytoplankton patch whose initial length scale is less than critical length L_C. Lower solid line denotes concentration of phytoplankton at the patch center with time for the case of continuous herbivore grazing and continuous plant growth. Upper solid line is for the case of nocturnal grazing and continuous plant growth. Lower dashed curve results from diel variation in nutrient uptake and continuous herbivore grazing. Upper dashed curve shows rate of decay of the patch under nocturnal grazing and diel periodicity in phytoplankton growth. Time, τ, is in days

Conclusions

We may conclude from Fig. 8 that time-dependence in phytoplankton growth and in the grazing stress affects the rate of decay of the patch. If the patch size is near the critical length, whether that patch initially grows or decays depends on the magnitude and phase of the stresses. However, it is the time-integrated magnitude of the growth and grazing functions plus the spatial distribution of herbivores and concentration of limiting nutrient which determine L_c and ultimately decide the fate of the patch.

There has been recent interest in the ability of the herbivore grazing threshold to impart stability to marine ecosystem models (Steele, 1974a, b). The grazing threshold is highly species-specific and is a measure of the ability of the animal to efficiently graze upon low phytoplankton concentrations (Frost, 1972, 1975). Both the spatial and non-spatial models described here are numerically stable with P^* set to zero. The spatial models run with $P^* = 0$ and $\beta >> 1$ show an interesting result. The phytoplankton cannot locally be grazed to extinction. Diffusion keeps a seed population continually present. The phytoplankton at a particular point can only become zero if $P = 0$ everywhere.

We maintain the same conclusion as to the insignificance of P_t for stability would be made if Steele's (1974a) biological dynamics were modeled spatially with a diffusion term. Our model formulation is similar enough to Steele's to allow comparison of results on a short time-scale. The phytoplankton growth and herbivore grazing functions used in both models are identical, as is the egestion rate for a fixed zooplankton biomass.

In one-box models (e.g. the time-dependent, non-spatial ecosystem model of Steele's) the system is called unstable if a fundamental dependent variable (phytoplankton, zooplankton, fish, etc.) reaches zero. Such a catastrophic event rarely occurs in nature, as a seed stock is often present to permit recovery of the system. In spatial models where advection, and/or diffusion is included, this instability occurs only if the dependent variable becomes zero in every spatial box. This is not to be expected, for as the variable locally approaches zero its gradient becomes so high that diffusion brings a seed concentration back into the box. In this sense, one-box modelers use a positive grazing threshold to parameterize dissipative turbulent diffusion not explicitly formulated in their models.

The actual importance of a grazing threshold in maintaining stable populations of phytoplankton in the ocean is unknown. However, it may rather be the inhomogeneities in the physical and chemical environment, together with the patchiness of the herbivores, which insure the patchy character of the phytoplankton and, in turn, the stability of the system.

While this model incorporates a formulation of vertical zooplankton migration, no attempt has been made to account for effects such as vertical mixing, cell sinking, and light extinction with depth upon the maintenance of a phytoplankton patch. Critical-length scale theory needs extension to the vertical dimension for a more complete understanding of patchiness.

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J.S. Wroblewski
Department of Oceanography
Florida State University
Tallahassee, Florida 32306
USA

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