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Proc. R. Soc. Lond. A 1999 **455**, 1813-1828

doi: 10.1098/rspa.1999.0381

References

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On the theory of advective effects on biological dynamics in the sea. II. Localization, light limitation, and nutrient saturation

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Received 27 October 1998; accepted 5 January 1999

The theory of advective effects is extended to include localization effects, due both to the attenuation of light with depth in the ocean and to nutrient transport into the euphotic zone of finite duration in time and/or over a limited horizontal domain. Nutrient uptake is also generalized to nonlinear Michaelis–Menten kinetics. The characteristic curves are solved for explicitly, and a symbolic general solution is obtained for arbitrary biological dynamics. Some exemplary results are presented for the effect of light, nutrient, and grazing limitations on primary productivity in an *NPZ* model. The theory is now applicable to further studies of more realistic oceanic processes.

Keywords: advection; reaction dynamics; *NPZ* dynamics; euphotic zone; upwelling

1. Introduction

Interactive physical–biological dynamical processes in the sea are of central importance to fundamental and applied research in many areas of interdisciplinary ocean science today, including, for example, the dynamics of ecosystems and biogeochemical cycles. Three major interactive processes are physiological thermodynamics (the effects of environmental conditions upon biological rates), diffusion and mixing, and advection. This study is focused on the advective process and attempts to provide an idealized general theoretical framework for the exploration of effects of various phenomenological flow fields that occur in the ocean over a broad range of time and space scales. It is intended to complement related process research based upon experimentation and simulation. Additionally, this theoretical approach may be of some general interest for applications to analogous problems of the reactive dynamics of advected tracers in other fluids, e.g. in chemical and engineering problems.

The first part of this study (Robinson 1997, hereafter referred to as Part I) introduced a biological dynamical model consisting of growth, self-interaction and bilinear interactions among n -state variables occurring in the presence of a stretching deformation flow field. A general theoretical approach via the theory of characteristics was formulated and some solutions were obtained for dynamical processes homogeneous in space and impulsive in time. In this second part, the nonlinear dynamics is extended to include the Michaelis–Menten nonlinear formulation for the uptake of nutrients by phytoplankton. The ocean is divided into an upper ocean, where sunlight is available for photosynthesis (euphotic zone), and a deeper ocean, which is not illuminated (aphotic zone). Kinematic flow fields are introduced that allow for the

localization of advective effects both horizontally and in time. A general solution is obtained for these kinematics and dynamics, and some idealized illustrative examples are presented. These developments should serve as the basis for theoretical studies of realistic oceanic processes.

Section 2 presents the model, §3 solves for the characteristics and §4 solves for the dynamics. Section 5 derives the general solution, §6 provides examples and §7 summarizes and concludes.

2. The model

The general model to be studied is that of equation (2.3) of Part I (which we will refer to as equation (I.2.3)) for n biological state variables ϕ_i in two spatial dimensions with diffusion neglected:

$$\frac{\partial \phi_i}{\partial t} + u \frac{\partial \phi_i}{\partial x} + v \frac{\partial \phi_i}{\partial y} = B_i(\phi_1, \dots, \phi_i, \dots, \phi_n). \quad (2.1)$$

The flow field is specified kinematically in terms of a stream function $\psi(x, y, t)$ such that (see equation (I.2.9))

$$u = -\frac{\partial \psi}{\partial y}, \quad v = \frac{\partial \psi}{\partial x}. \quad (2.2a)$$

$$\frac{D\phi_i}{Dt} \equiv \frac{\partial \phi_i}{\partial t} + u \frac{\partial \phi_i}{\partial x} + v \frac{\partial \phi_i}{\partial y} = \frac{\partial \phi_i}{\partial t} - \frac{\partial \psi}{\partial y} \frac{\partial \phi_i}{\partial x} + \frac{\partial \psi}{\partial x} \frac{\partial \phi_i}{\partial y}. \quad (2.2b)$$

and the continuity equation $u_x + v_y = 0$ for mass conservation in an almost incompressible Boussinesq fluid (Tritton 1988, Appendix to ch. 14) is satisfied. The kinematics of this section are applicable to general biological dynamics B_i .

For the study of light limitation and to illustrate the effects of flow kinematics on biological dynamics we adopt the general *NPZ* model of Part I, §4*d*, but with Michaelis–Menten kinetics of nutrient uptake and light attenuation (Parsons *et al.* 1984; Kirk 1994). Then for phytoplankton ($\phi_1 = P$), zooplankton ($\phi_2 = Z$) and nutrient ($\phi_3 = N$), the governing equations are (with reference to (I.2.10) and (I.4.11))

$$\frac{DP}{Dt} = U - a_{21}PZ, \quad (2.3a)$$

$$\frac{DZ}{Dt} = a_{21}PZ, \quad (2.3b)$$

$$\frac{DN}{Dt} = -U, \quad (2.3c)$$

where

$$U \equiv \frac{a_{13}\lambda(y)PN}{K + N}. \quad (2.3d)$$

The independent variable $0 < y < \infty$ represents depth into the ocean from the sea surface; $\lambda(y)$ is a non-dimensional light attenuation coefficient. The base of the euphotic zone is located at $y = y_e$ with $\lambda(y > y_e) \equiv 0$. The interaction coefficient a_{21} (dimensions $[l^3(mt)^{-1}]$, where m, l and t are units of mass, length and time, respectively) is the zooplankton grazing rate; a_{13} ($[t^{-1}]$) is the phytoplankton maximum

specific rate of growth, and $K([\text{ml}^{-3}])$ is the half-saturation constant for nutrient uptake.

The dependent variables N, P, Z ($[\text{ml}^{-3}]$) are all dimensionalized by a biomass density M , where M is to be chosen as a characteristic value of N advected into the euphotic zone during any injection event of interest. The independent variables (x, y, t) are scaled, respectively, by $(x_0, y_0 = y_e, t_0 = K(Ma_{13})^{-1})$, where x_0 is a horizontal length characterizing a localized upwelling event. The horizontal and vertical velocities (u, v) are scaled, respectively, by $(u_0, v_0$ with $u_0 = v_0x_0y_0^{-1}$), which yield a non-dimensional continuity equation $u_x + v_y = 0$. This implies a scaling of $\psi_0 = u_0y_0 = v_0x_0$.

The kinematic flow field is chosen such that the horizontal velocity is independent of y and the product of a function of x times a function of t . As in Part I, both dimensional and non-dimensional variables are represented by the same symbols. Thus non-dimensionally,

$$\psi = -yf(t)g(x), \quad u = fg, \quad v = -yf\frac{dg}{dx}, \quad (2.4 a)$$

$$\frac{D}{Dt} = \frac{\partial}{\partial t} + \alpha \left[-\frac{\partial\psi}{\partial y} \frac{\partial}{\partial x} + \frac{\partial\psi}{\partial x} \frac{\partial}{\partial y} \right], \quad (2.4 b)$$

$$\frac{DP}{Dt} = U - \beta PZ, \quad (2.4 c)$$

$$\frac{DZ}{Dt} = \beta PZ, \quad (2.4 d)$$

$$\frac{DN}{Dt} = -U, \quad (2.4 e)$$

$$U = \frac{\lambda(y)NP}{1 + \delta N}. \quad (2.4 f)$$

The three non-dimensional parameters characterizing advection (α), grazing (β), and uptake kinetics (δ) are defined by

$$\alpha \equiv \frac{v_0t_0}{y_0} = \frac{u_0t_0}{x_0} = \frac{v_0K}{y_e a_{13}M}, \quad \beta \equiv a_{21}t_0 = \frac{a_{21}K}{a_{13}M}, \quad \delta \equiv \frac{M}{K}. \quad (2.4 g)$$

3. Kinematics and characteristics

For the flow system given by the stream function of equation (2.4 a), the characteristic equations (I.2.12 a) take the form

$$\frac{dt}{ds} = 1, \quad (3.1 a)$$

$$\frac{dx}{ds} = \alpha u = \alpha f(t)g(x), \quad (3.1 b)$$

$$\frac{dy}{ds} = \alpha v = -\alpha y \frac{dg}{dx} f, \quad (3.1 c)$$

with initial conditions taken as†

$$s = 0: \quad t = p, \quad x = r, \quad y = q. \quad (3.2)$$

† This notation is equivalent to equation (I.2.13) but simpler.

The set (3.1) can be solved by two exact integrals and a quadrature. Integrating (3.1 *a*) directly, and after equating ds from (3.1 *b, c*), we obtain

$$t = s + p, \quad (3.3 a)$$

$$yg(x) = qg(r), \quad (3.3 b)$$

and after equating ds from (3.1 *a, b*)

$$\mathcal{G}(x, r) = \alpha \mathcal{F}(t, p), \quad \mathcal{G}(x, r) \equiv \int_r^x \frac{dx'}{g(x')}, \quad \mathcal{F}(t, p) \equiv \int_p^t f(t') dt'. \quad (3.3 c)$$

The function $f(t)$ is chosen so as to represent either (i) a steady-state flow (S), or (ii) a time-periodic flow with non-dimensional frequency ω , which over a half-period may be taken to represent an advective event (E). Thus

$$\text{S:} \quad f = 1, \quad \mathcal{F}_S = t - p, \quad (3.4 a)$$

$$\text{E:} \quad f = \sin \omega t, \quad \mathcal{F}_E = \frac{1}{\omega} [\cos \omega p - \cos \omega t]. \quad (3.4 b)$$

Three flow forms are evaluated for the function $g(x)$: (i) a simple stretching deformation (D) as in Part I of this study; (ii) a localized (exponentially decaying) deformation (L); (iii) a simply periodic wave form (W). Whence

$$\text{D:} \quad g = x, \quad xy = qr, \quad \mathcal{G}_D = \ln \frac{x}{r} \quad (3.4 c)$$

$$\text{L:} \quad g = 1 - e^{-x} (x > 0), \quad y(1 - e^{-x}) = q(1 - e^{-r}), \quad \mathcal{G}_L = \ln \left[\frac{(e^x - 1)}{(e^r - 1)} \right] \quad (3.4 d)$$

$$\text{W:} \quad g = \sin x, \quad y \sin x = q \sin r, \quad \mathcal{G}_W = \ln \left[\frac{\tan x/2}{\tan r/2} \right]. \quad (3.4 e)$$

Consider the half-plane $x > 0$; then (3.4 *d*) provides a simple kinematic model for coastal upwelling. To study an open ocean isolated and localized upwelling the flow may be completed by $g = -1 + e^x$ ($x < 0$). Similarly, (3.4 *e*) represents a periodic pattern of upwelling and downwelling cells. The upwelling region $-\pi/2 \leq x \leq \pi/2$ can serve as a simple two-dimensional kinematic model of a cyclonic (cold core) eddy.

Two initial value problems in s are necessary to carry out the dynamical studies of the next sections. We assume that light penetrates, and biological activity occurs, only to the base of the euphotic zone located at $y = 1$. The first problem is the time initial value problem (T) as in Part I. The second problem is the boundary value problem (B), which specifies the values of the state variables as they are advected across the base of the euphotic zone from the deeper aphotic zone, where $\lambda = 0$. As will be seen below, the T problem is relevant to the deep pure advection (TA), and to the biological dynamics in the water located initially in the upper euphotic zone (TE). Most interestingly, the B problem describes the biological activity, in the euphotic zone, of water located initially below the euphotic zone. Under equations (I.2.13) and (3.2)

$$\text{T:} \quad \text{when } s = 0, t = 0; \text{ thus } p = 0 \text{ and } \phi_i(x, y, 0) \equiv \phi_{i0}(x, y) \Rightarrow \phi_{i0}(r, q), \quad (3.5 a)$$

$$\text{B:} \quad \text{when } s = 0, y = 1; \text{ thus } q = 1 \text{ and } \phi_i(x, 1, t) \equiv \phi_{i0}(x, t) \Rightarrow \phi_{i0}(r, p). \quad (3.5 b)$$

The functions following the arrows indicate the forms (see equations (I.2.13)–(I.2.15)) in which the initial conditions will appear in the solutions to the dynamical equations

Table 1. Kinematic flows

designation	structure
DS	steady upwelling
DE	upwelling event
LS	steady coastal upwelling
LE	coastal upwelling event
WS	steady wave or eddy field
WE	wave or eddy event

of the next section. The domain of interest is restricted to positive y and t . Thus $\phi_{z0}(r, p)$ is defined only for $p \geq 0$. This implies a boundary (or front) located at $y = \hat{y}(\hat{x}, \hat{t})$, separating water initially ($t = 0$) above or below the euphotic zone, which is advected upward towards the sea surface in time. Thus the domain of the B problem is defined by

$$\hat{y} < y < 1, \quad \text{where} \quad p(\hat{x}, \hat{y}, \hat{t}) \equiv 0. \quad (3.5c)$$

The domain of the TA problem is $y > 1$ and that of TE is $0 < y < \hat{y}$.

Combining the space-time kinematics, i.e. solving equations (3.3) with the structures of (3.4), yields six flow fields summarized in table 1. The 12 sets of characteristic curves corresponding to the T and B problems for each flow are presented in table 2. To study light limitation effects, it is necessary to evaluate the light attenuation coefficient and its integral in s , i.e. $\lambda(y)$ of equation (2.3d) in terms of $y(s; p, r, q)$, which is given in table 3. The $\mathcal{F}(s, p)$ are obtained from equations (3.4a, b) evaluated with $t = s + p$ for the S and E flows; $p = 0$ and $q = 1$, respectively, for the T and B problems.

4. Biological dynamics

The s -domain biological dynamics for the *NPZ* system to be studied here satisfies the non-dimensional equations,

$$\frac{dP}{ds} = \frac{\lambda(y)NP}{1 + \delta N} - \beta PZ, \quad (4.1a)$$

$$\frac{dZ}{ds} = \beta PZ, \quad (4.1b)$$

$$\frac{dN}{ds} = \frac{-\lambda NP}{1 + \delta N}, \quad (4.1c)$$

with first integral

$$N + P + Z \equiv \mathcal{B} = N_0 + P_0 + Z_0, \quad (4.1d)$$

since mortality has been neglected.

The presence of the light attenuation (λ) and nutrient saturation (δ) parameters in addition to the grazing parameter (β) generalize the *NPZ* system of equations (I.4.11). To elucidate basic processes we shall consider the dynamics of systems of one-, two- and three-state variables.

Table 2. *Characteristics*

flow	s	p
DST	t	0
DSB	$t - p$	$t - \frac{1}{\alpha} \ln \left[\frac{1}{y} \right]$
DET	t	$0; \mathcal{F}_{E0} = \frac{1}{\omega} [1 - \cos \omega t]$
DEB	$t - p$	$\frac{1}{\omega} \cos^{-1} \{ \cos \omega t - \ln [y^{\omega/\alpha}] \}$
LST	t	0
LSB	$t - p$	$t - \frac{1}{\alpha} \ln \left[e^x \left(\frac{1}{y} - 1 \right) + 1 \right]$
LET	t	$0; \mathcal{F}_{E0} = \frac{1}{\omega} [1 - \cos \omega t]$
LEB	$t - p$	$\frac{1}{\omega} \cos^{-1} \left\{ \cos \omega t + \frac{\omega}{\alpha} \ln \left[e^x \left(\frac{1}{y} - 1 \right) + 1 \right] \right\}$
WST	t	0
WSB	$t - p$	$t - \frac{1}{\alpha} \ln \left[\frac{1 + (1 - y^2 \sin^2 x)^{1/2}}{y(1 + \cos x)} \right]$
WET	t	$p = 0; \mathcal{F}_{E0} = \frac{1}{\omega} [1 - \cos \omega t]$
WEB	$t - p$	$\frac{1}{\omega} \cos^{-1} \left\{ \cos \omega t + \frac{\omega}{\alpha} \ln \left[\frac{1 + (1 - y^2 \sin^2 x)^{1/2}}{y(1 + \cos x)} \right] \right\}$
flow	r	q
DST	$x e^{-\alpha t}$	$y e^{\alpha t}$
DSB	xy	1
DET	$x e^{-\alpha \mathcal{F}_{E0}}$	$y e^{\alpha \mathcal{F}_{E0}}$
DEB	xy	1
LST	$\ln [1 + e^{-\alpha t} (e^x - 1)]$	$y [1 + e^{-x} (e^{\alpha t} - 1)]$
LSB	$-\ln [1 - y(1 - e^{-x})]$	1
LET	$\ln [1 + e^{-\alpha \mathcal{F}_{E0}} (e^x - 1)]$	$y [1 + e^{-x} (e^{\alpha \mathcal{F}_{E0}} - 1)]$
LEB	$-\ln [1 - y(1 - e^{-x})]$	1
WST	$2 \tan^{-1} [e^{-\alpha t} \tan x/2]$	$\frac{1}{2} y [e^{\alpha t} (1 + \cos x) + e^{-\alpha t} (1 - \cos x)]$
WSB	$\sin^{-1} (y \sin x)$	1
WET	$2 \tan^{-1} [e^{-\alpha \mathcal{F}_{E0}} \tan x/2]$	$\frac{1}{2} y [e^{\alpha \mathcal{F}_{E0}} (1 + \cos x) + e^{-\alpha \mathcal{F}_{E0}} (1 - \cos x)]$
WEB	$\sin^{-1} (y \sin x)$	1

Table 3. *Light attenuation*

flow	$y(s; p, r, q)$
D	$qe^{-\alpha\mathcal{F}} \quad \mathcal{F} = \mathcal{F}(s, p)$
L	$q[e^{-\alpha\mathcal{F}}e^{-r} + (1 - e^{-r})]$
W	$\frac{1}{2}q \sin r [e^{-\alpha\mathcal{F}} \tan(r/2) + e^{\alpha\mathcal{F}} \tan(r/2)]$

(a) *P model*

The Malthusian growth of phytoplankton with unlimited nutrient and no predation ($Z = 0$) satisfies (4.1 a) with $\delta \gg 1$

$$P = P_0 e^{\sigma/\delta}, \quad \sigma \equiv \int_0^s \lambda(y(s'; p, r, q)), \quad (4.2)$$

with reference to table 3.

(b) *NP model*

We retain $Z = 0$, insert P from (4.1 d) into (4.1 c) and integrate, whence

$$(\mathcal{B} - N)^{1+\delta\mathcal{B}} = \mathcal{A}N, \quad \mathcal{A} \equiv \frac{P_0^{1+\delta\mathcal{B}}}{N_0} e^{\mathcal{B}\sigma} \quad (4.3 a)$$

with σ as in (4.2). For $\delta = 0$ the solutions are as in equation (I.4.12 i)

$$P = \frac{P_0\mathcal{B}}{N_0 e^{-\mathcal{B}\sigma} + P_0}, \quad N = \frac{N_0\mathcal{B}e^{-\mathcal{B}\sigma}}{N_0 e^{-\mathcal{B}\sigma} + P_0}. \quad (4.3 b)$$

(c) *NPZ model*

To continue analytically following the procedure of equations (I.4.12 a–c), it is necessary to restrict consideration to a uniformly illuminated euphotic zone overlying a deep completely aphotic ocean, i.e.

$$\lambda = \lambda_0, \quad 0 < y < 1; \quad \lambda = 0, \quad 1 < y. \quad (4.4)$$

Without loss of generality, we may set $\lambda_0 = 1$ by rescaling the parameters of (2.4 g), i.e. by replacing a_{13} by $\lambda_0 a_{13}$. Then equating ds from (4.1 b, c) yields another first integral, which together with (4.1 d) reduces (4.1 c) to quadrature, i.e.

$$ZN^\beta e^{\beta\delta N} \equiv \mathcal{C}, \quad (4.5 a)$$

$$\int \frac{(1 + \delta N) dN}{-N^2 + \mathcal{B}N - \mathcal{C}N^{(1-\beta)} e^{-\delta\beta N}} = -s. \quad (4.5 b)$$

For the case of $\beta = 1$, we can generalize the results of (I.4.12 d, e) for $\delta N \leq 1$. Keeping three terms in the Taylor series expansion of the exponential, the denominator of (4.5 b) becomes

$$-(1 + \frac{1}{2}\mathcal{C}\delta^2)N^2 + (\mathcal{B} + \mathcal{C}\delta)N - \mathcal{C}, \quad (4.5 c)$$

and integration is straightforward.

The case of $\delta = 0$ reduces to (I.4.12 *d, e*)

$$\left. \begin{aligned} N &= \frac{\mathcal{E}(\mathcal{B} - \mathcal{D}) + (\mathcal{B} + \mathcal{D})e^{-Ds}}{2(\mathcal{E} + e^{-Ds})}, & \mathcal{D} &= (\mathcal{B}^2 - 4\mathcal{C})^{1/2} \\ \mathcal{B} &= N_0 + P_0 + Z_0, & \mathcal{C} &= N_0 Z_0, & \mathcal{E} &= \frac{\mathcal{B} + \mathcal{D} - 2N_0}{2N_0 - (\mathcal{B} - \mathcal{D})}. \end{aligned} \right\} \quad (4.5 d)$$

5. General solution

For the n -state variables of equation (2.1), there are n -dynamical equations,

$$\frac{d\phi_i}{ds} = B_i(\phi_j), \quad i, j = 1, \dots, n \quad 0 < y < 1, \quad (5.1 a)$$

$$\frac{d\phi_i}{ds} = 0, \quad 1 < y, \quad (5.1 b)$$

to be solved together with the characteristics (3.1). Recall the three regions introduced preceding equation (3.5). The TE problem is an independent time initial value problem, but the B problem is coupled to the TA problem. For the characteristic solutions (table 2) we introduce both for the (s, r, p, q) and ϕ_i variables a subscript a for the advective aphotic zone ($1 < y$) and e for the dynamically active euphotic zone ($\hat{y} < y < 1$). Let

$$\phi_{ia}(x, y, 0) \equiv \phi_{iao}(x, y). \quad (5.2 a)$$

Then by (5.1 *b*)

$$\phi_{ia}(x, y, t) = \phi_{iao}(r_a(x, y, t), q_a(x, y, t)), \quad (5.2 b)$$

and at the base of the euphotic zone

$$\phi_{ia}(x, 1, t) = \phi_{iao}(r_a(x, 1, t), q_a(x, 1, t)) \equiv \phi_{ieo}(x, t) = \phi_{ie}(x, 1, t). \quad (5.2 c)$$

Thus the initial condition functions for the solution of (5.1 *a*) in $\hat{y} < y < 1$ are given by

$$\phi_{ieo}(r_e, p_e) = \phi_{iao}(r_a(r_e, 1, p_e), q_a(r_e, 1, p_e)). \quad (5.2 d)$$

The general solution to (5.1 *a*) is expressed as

$$\phi_{ie}(x, y, t) = \phi_{ie}(s_e; \phi_{jeo}(r_e, p_e)), \quad j = 1, \dots, n, \quad (5.3 a)$$

with the ϕ_{jeo} as given by (5.2 *d*).

Consider now the case of pure advection everywhere, i.e. set $B_i = 0$ in (5.1 *a*). Then the advective solution (5.2 *b*) is valid also in $\hat{y} < y < 1$. Also, however, for pure advection the state variables are uncoupled and the general solution (5.3 *a*) reduces to

$$\phi_{ie}(x, y, t) = \phi_{ieo}(r_e, p_e), \quad (5.3 b)$$

i.e. to (5.2 *d*). Since the advective solutions (5.2 *b*) and (5.2 *d*) must be the same, the identities

$$r_a(r_e, 1, p_e) = r_a(x, y, t), \quad q_a(r_e, 1, p_e) = q_a(x, y, t) \quad (5.3 c)$$

must hold.

Thus the general solution (5.3 *a*) with biological dynamics has the final form

$$\phi_{ie}(x, y, t) = \phi_{ie}(s_e; \phi_{jao}(r_a(x, y, t), q_a(x, y, t))), \quad j = 1, \dots, n, \quad (5.3 d)$$

or omitting subscripts

$$= \phi_i(s; \phi_{jo}(r, q)), \quad \hat{y} < y < 1. \quad (5.3 e)$$

At the base of the euphotic zone $y = 1$ and $s = 0$. At the shoaling front $y = \hat{y}$ and $s = \hat{t}$ by (3.5 *c*) and (3.3 *a*).

6. Examples

The general results derived here are intended to provide the basis for a number of theoretical studies relevant to real ocean processes. Here we will simply illustrate effects in terms of a few idealized simple examples.

(a) Light limitation

We will first consider the localization effects arising from biological activity being restricted to the euphotic zone, in terms of the time initial value problem and deformation field flow of Part I, i.e. the DSB and DST flows of table 2. We assume initially no nutrient in the euphotic zone but a reservoir of nutrient and seed populations of plankton below the euphotic zone. The TE problem is trivially advective. For $y \geq 1$ (5.2 *b*) takes the form, e.g.

$$P(x, y, t) = P_0(r, q) = P_0(xe^{-\alpha t}, ye^{\alpha t}) \quad (6.1 a)$$

and equations (5.2 *c, d*) become at $y = 1$

$$P(x, 1, t) = P_0(xe^{-\alpha t}, e^{\alpha t}), \quad P_0(r, p) = P_0(re^{\alpha p}, e^{\alpha p}). \quad (6.1 b)$$

From table 2,

$$re^{\alpha p} = xy e^{-\alpha[t-1/\alpha \ln 1/y]} = xe^{-\alpha t}, \quad e^{\alpha p} = ye^{\alpha t}, \quad (6.1 c)$$

consistently with (5.3 *c*); thus

$$P_0(r, p) = P_0(xe^{-\alpha t}, ye^{\alpha t}), \quad (6.1 d)$$

and similarly for N_0, Z_0 . From (3.5 *c*) the advancing front is given by

$$\hat{t} = \frac{1}{\alpha} \ln \frac{1}{\hat{y}} \quad \text{or} \quad \hat{y} = e^{-\alpha \hat{t}}, \quad P_0(x, \hat{y}, \hat{t}) = P_0(xe^{-\alpha \hat{t}}, 1). \quad (6.1 e)$$

The simplest example is the Malthusian growth of equation (4.2). Without loss of generality we can set $\delta = 1$, i.e. by replacing a_{13} in (2.4 *g*) by $\delta^{-1}a_{13}$. We consider two cases: (i) uniform light;† (ii) linearly decreasing light. Then

$$\left. \begin{aligned} \text{(i)} \quad \lambda = \lambda_0, \quad \sigma = \lambda_0 s = \frac{\lambda_0}{\alpha} \ln \frac{1}{y}, \quad e^\sigma = \left(\frac{1}{y}\right)^{\lambda_0/\alpha}, \\ \text{(ii)} \quad \lambda = 1 - y, \quad \sigma = \frac{1}{\alpha} \left[\ln \frac{1}{y} + (y - 1) \right], \quad e^\sigma = \left[\frac{1}{y} e^{(y-1)} \right]^{1/\alpha}. \end{aligned} \right\} \quad (6.2 a)$$

† These idealized dependencies yield simpler analytical solutions than the more accurate exponential decay which can be treated later.

For the case of no x -dependence, the solutions (4.2) are

$$\left. \begin{aligned} \text{(i)} \quad & P(y, t) = P_0(ye^{\alpha t}) \left(\frac{1}{y}\right)^{\lambda_0/\alpha}, & P(1, t) = P_0(e^{\alpha t}), \\ & P(\hat{y}, t) = P_0(1)e^{\lambda_0 t}, \\ \text{(ii)} \quad & P(y, t) = P_0(ye^{\alpha t}) \left[\frac{1}{y}e^{(y-1)}\right]^{1/\alpha}, & P(1, t) = P_0(e^{\alpha t}), \\ & P(\hat{y}, t) = P_0(1)e^{t+(e^{-\alpha t}-1)/\alpha}. \end{aligned} \right\} \quad (6.2b)$$

Consider first the case of a deep reservoir of seed plankton which is independent of depth, $P_0 = 1$. Then for $\hat{y} < y < 1$ there is a steady-state solution, since water parcels reaching a given depth at any time have spent the same amount of time in the euphotic zone. The shallowest parcels have spent the longest time under illumination, resulting in the simple exponential growth at \hat{y} , independent of α , for case (i). For short times and depths near unity, the two solutions are dominated by advection. If the time-interval of interest is $t < \hat{t}$ and $\alpha \hat{t} \gg 1$, then the choice of an effective uniform illumination $\lambda_0 = 1 - (\alpha \hat{t})^{-1}$ equates $P(\hat{y}, \hat{t})$ for the two cases. Any criteria to determine an effective λ_0 , e.g. integrated net production, must take into account the flow (α) and duration (\hat{t}).

(b) *Uniform deep reservoirs*

We extend the case of uniform deep reservoirs with DS flow to biological systems with two- (2) and three- (3) state variables, and consider essentially a unit source of nutrient together with very small amount(s) of background plankton(s). The solutions retain the character of establishing a steady state below a shoaling front. The analytical solutions to equations (4.3a) and (4.5d) are particularly simple with (2) $\mathcal{B} = 1$, and (3) $\mathcal{D} = 1$, respectively, which is achieved by choosing

$$\left. \begin{aligned} \text{(2):} \quad & N_0 = 1 - \epsilon, \quad P_0 = \epsilon \ll 1, \quad \mathcal{B} = 1, \\ \text{(3):} \quad & N_0 = 1, \quad P_0 = \epsilon(1 - \epsilon), \quad Z_0 = \epsilon(1 + \epsilon) \\ & \mathcal{B} = 1 + 2\epsilon, \quad \mathcal{C} = \epsilon(1 + \epsilon), \quad \mathcal{D} = 1 \quad \mathcal{E} = \epsilon(1 - \epsilon)^{-1}. \end{aligned} \right\} \quad (6.3)$$

For the NP model, (4.3a) now becomes

$$\eta(1 - \epsilon)(1 - N)^{1+\delta} = \epsilon^{1+\delta} N, \quad \eta \equiv e^{-\sigma}, \quad (6.4a)$$

with σ given by (6.2a). Simple exact analytical solutions exist for $\delta = (0, 1)$, namely

$$\left. \begin{aligned} \delta = 0, \quad & P = \frac{\epsilon}{\epsilon + (1 - \epsilon)\eta}; \\ \delta = 1, \quad & P = \frac{\epsilon^2}{2(1 - \epsilon)\eta} \left[\left(1 + \frac{4}{\epsilon^2(1 - \epsilon)} \eta \right)^{1/2} - 1 \right]. \end{aligned} \right\} \quad (6.4b)$$

When $\eta = 0$, $N = 0$ and $P = 1$, all of the biomass is in the phytoplankton. The maximum of P is always located at the front.

For the NPZ model, the solutions (4.5d) reduce to

$$N = \frac{f}{g}, \quad P = \frac{\epsilon(1 - \epsilon)\eta}{fg}, \quad Z = \epsilon(1 + \epsilon)\frac{g}{f}, \quad (6.5a)$$

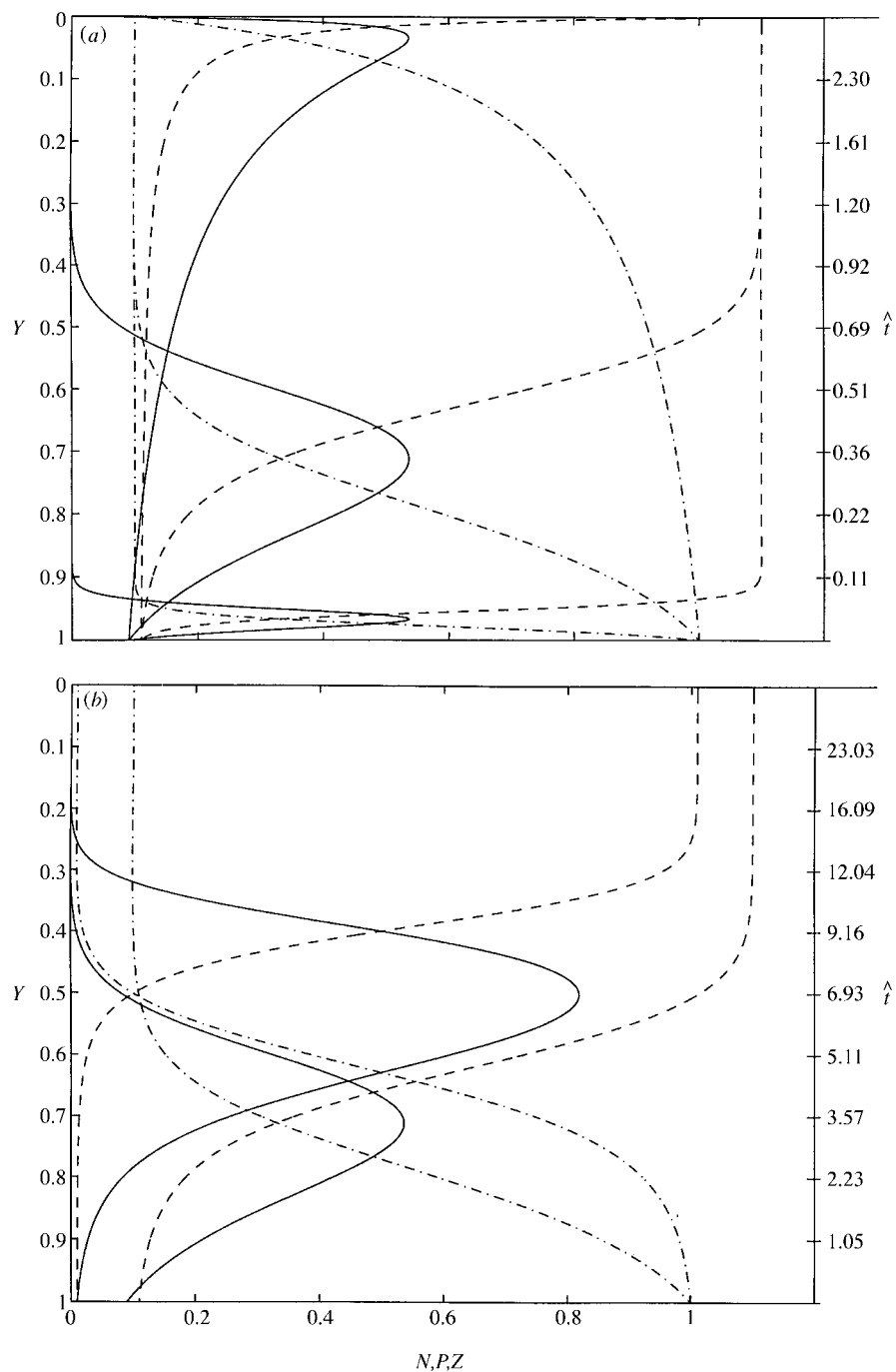


Figure 1. Profiles of N (dot-dash line), P (solid line), Z (dashed line) versus depth. Dependencies upon (a) advection for fixed $\epsilon = 0.1$, ($\alpha = 1$: upper P_m , $\alpha = 0.1$; middle P_m , $\alpha = 0.01$; lower P_m); (b) seed plankton for fixed $\alpha = 0.1$ ($\epsilon = 0.1$: larger P_m , $\epsilon = 0.01$; smaller P_m). $N_m = Z_m$ at P_m identifies the associated curves. The \hat{t} scale to the right of (a) is for $\alpha = 1$; for $\alpha = 0.1(0.01)$ multiply by 10 (10^2).

where

$$f(\eta) \equiv \epsilon^2 + (1 - \epsilon^2)\eta, \quad g(\eta) \equiv \epsilon + (1 - \epsilon)\eta, \quad \eta = e^{-s} = (y^{1/\alpha}).$$

At the advancing front $\hat{y} = e^{-\alpha t}$, $\hat{\eta} = e^{-t}$ and asymptotically in time

$$\eta = 0, \quad N_\infty = \epsilon, \quad P_\infty = 0, \quad Z_\infty = 1 + \epsilon, \quad (6.5b)$$

a result consistent with (I.4.12*h*). The solutions and their dependencies upon (α, ϵ) are illustrated on figure 1. As time progresses P grows, eventually achieving a maximum (P_m at y_m , where $N_m = Z_m$). Subsequently, as the front advances P decreases, as Z increases towards the sea surface. The time \hat{t} at which the front arrives at a given level is shown on the scale on the right. An interesting result is that the shapes and subsurface locations of the nutricline and of the phytoplankton maximum depend sensitively on the parameter α . For rapid advection ($\alpha = 1$, figure 1*a*) $y_m = 0.3$, whereas for slow advection ($\alpha = 0.01$) $y_m = 0.97$. The magnitude of P_m depends solely upon the fractional biomass of seed plankton ϵ . Note (e.g. $\epsilon = 0.1$, figure 1*b*) a P_m considerably less than B can mediate the conversion of almost the entire biomass to Z . Analytically,

$$\left. \begin{aligned} \eta_m &= \left[\frac{\epsilon^3}{(1 - \epsilon)(1 - \epsilon^2)} \right]^{1/2}, & y_m &= \eta_m^\alpha, \\ N_m = Z_m &= [\epsilon(1 + \epsilon)]^{1/2}, & P_m &= 1 + 2\{\epsilon - [\epsilon(1 + \epsilon)]^{1/2}\}. \end{aligned} \right\} \quad (6.5c)$$

In general, for uniform deep reservoirs with $\beta = 1$, it can be shown that

$$N_m = Z_m = (N_0 Z_0)^{1/2}, \quad P_m = N_0 + P_0 + Z_0 - 2(N_0 Z_0)^{1/2}. \quad (6.6)$$

Thus the sensitivity is primarily related to the amount of seed zooplankton. Although this is a very simple example, the results indicate the potential applicability of the theory to important phenomena, including deep chlorophyll maxima (Parsons *et al.* 1984) and zooplankton control of blooms (Steele & Henderson 1995). This mid-depth phytoplankton bloom P_m is of course dynamically analogous to the temporal bloom, e.g. the solution given by equation (I.4.12).

(c) Deep nutricline

Now consider the case that at $t = 0$ nutrient increases linearly with depth from zero at the base of the euphotic zone to unity at a non-dimensional depth (H) in the aphotic zone. We retain the assumptions of no x -dependence, no nutrient in the euphotic zone initially in time, and a uniform deep reservoir of seed phytoplankton. Thus

$$y < 1, \quad N(y, 0) = 0; \quad y > 1, \quad N(y, 0) = \left[\frac{(y - 1)}{H - 1} \right], \quad (6.7a)$$

and

$$y \leq 1, \quad N_0 = \left[\frac{ye^{\alpha t} - 1}{H - 1} \right], \quad P_0 = \epsilon, \quad (6.7b)$$

for solution to equation (4.3) following the arguments of equation (6.1). The dependencies upon the parameters α, ϵ, δ has been studied numerically with $\lambda = 1 - y$. The results are summarized on figure 2 for the case $H = 2$ such that $N_0(y = 2, t = 0) = 1$.

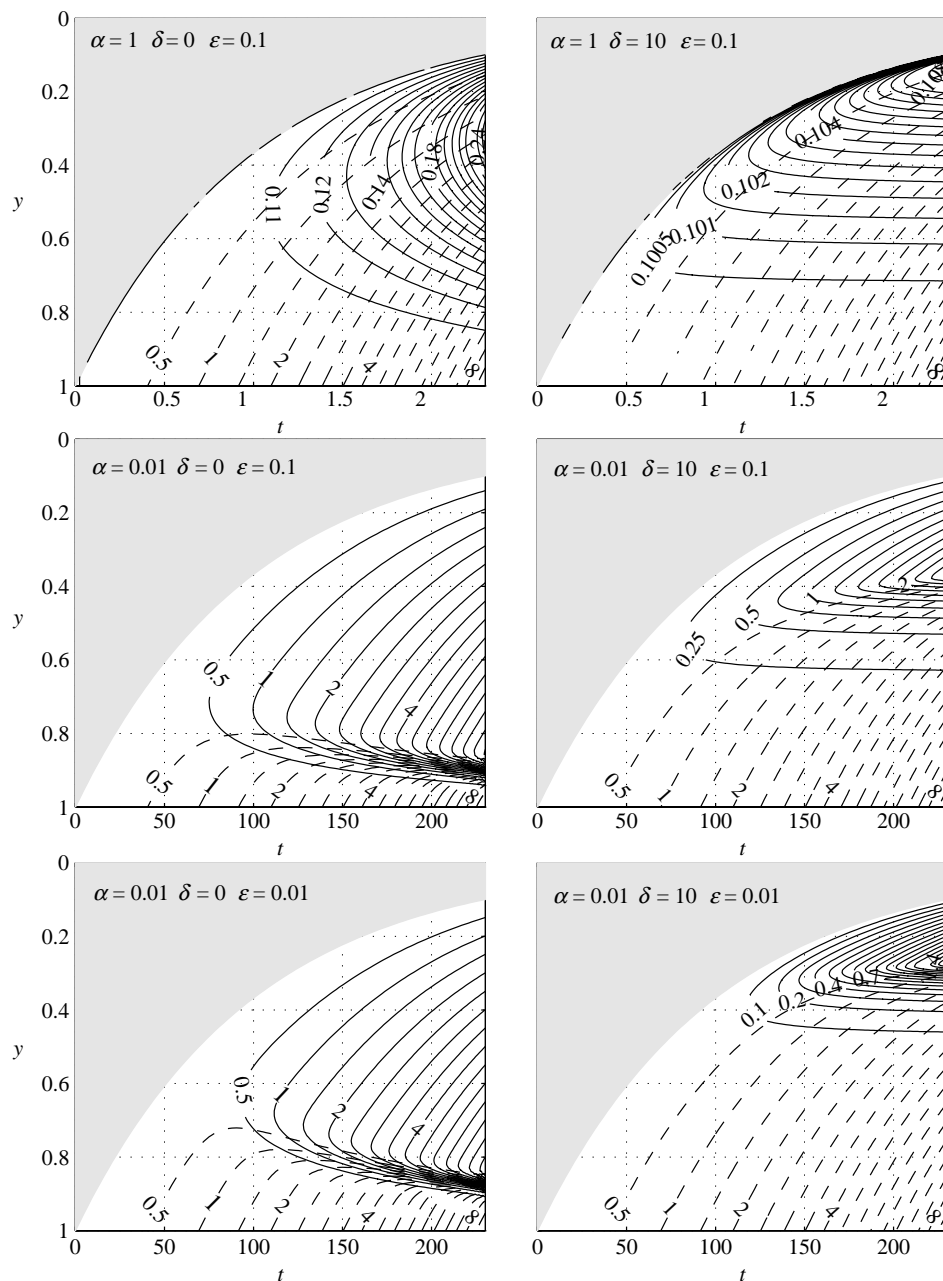


Figure 2. Isolines of N (dashed line), P (solid line) in the y - t -plane as a function of α , δ , ϵ . The dynamically inert upper euphotic zone is shaded.

The greatest sensitivity is again related to α . The important result here is the existence of a subsurface maximum of phytoplankton (P_m) in the absence of grazing loss to zooplankton. At any given time \hat{t} , the water in the vicinity of \hat{y} entered the euphotic zone with negligible nutrient. The water just above $y = 1$ has been illumi-

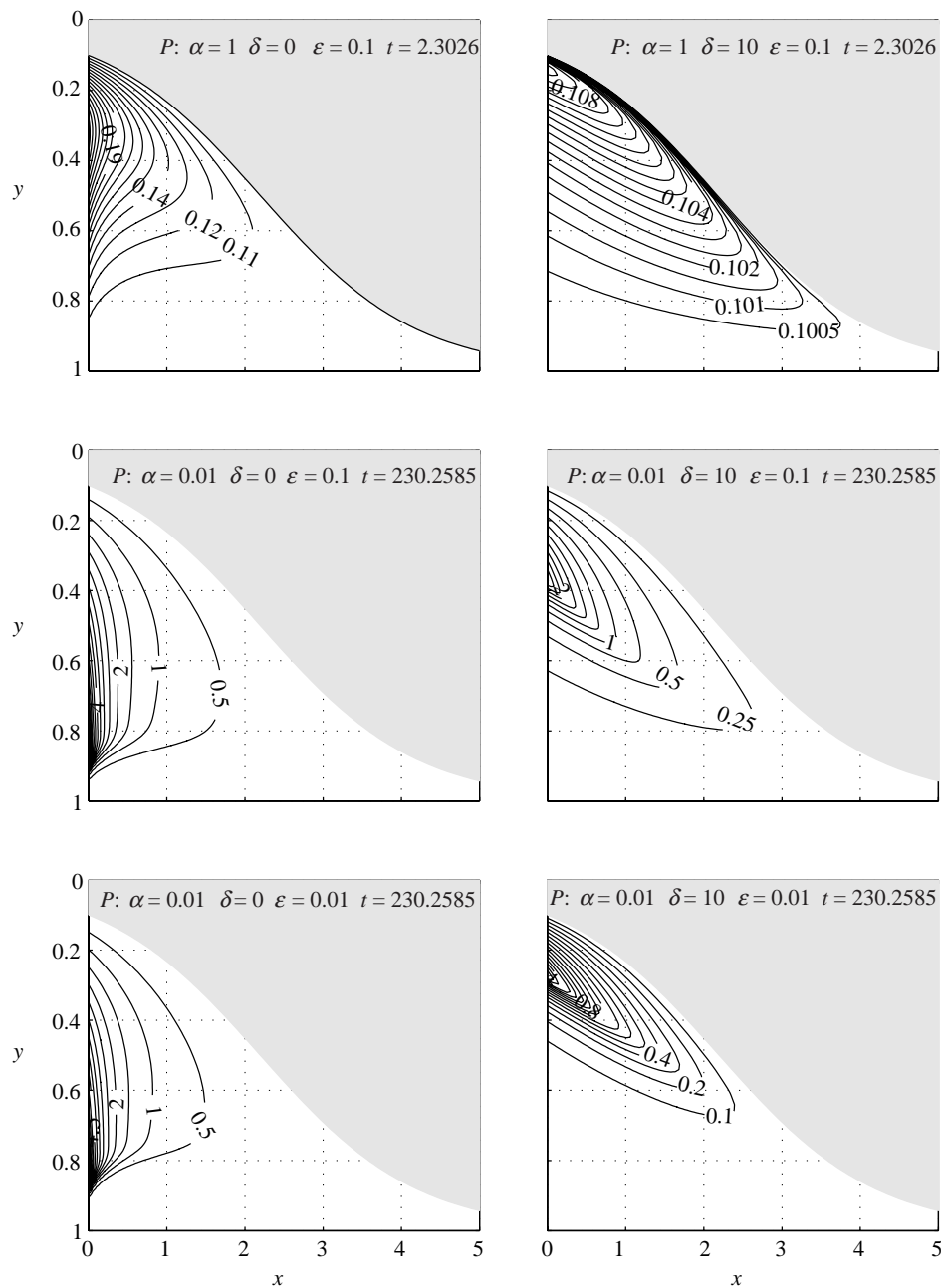


Figure 3. As in figure 2 for P , but in the y - t -plane for fixed t as indicated.

nated at a low light level and for only a short time. Thus the mid-depth P_m . The existence of subsurface phytoplankton maxima in this theory will in general be due both to this dynamical process and that of the preceding paragraph.

Finally, spatial localization is illustrated by the solution of this problem with idealized coastal upwelling kinematics (LS flow). Figure 3 shows sections (xy plots)

of phytoplankton concentration as a function of α , ϵ , δ also with $\lambda = 1 - y$ and $H = 2$. These plots are for the last time shown on the corresponding plots of figure 2. The $P(y)$ at $x = 0$ on figure 3 are thus identical to the final profiles of figure 2. The front is advancing as

$$\hat{y} = [1 + e^{-\hat{x}}(e^{\alpha \hat{t}} - 1)]^{-1}. \quad (6.8)$$

Note the development of two-dimensional subsurface phytoplankton distributions, which can be described as subsurface patches extending along the front. Subsurface patches of chlorophyll are features common to many fronts (Franks & Walstad 1997).

7. Summary and conclusions

A general theoretical solution has been obtained for a model ocean in which a dynamically active near-surface euphotic zone overlies a deeper region in which biological material is passively advected by the physical flow field. Illustrative dynamical solutions have been presented in one-to-three-state variables for an *NPZ* model in which nutrient uptake is nonlinearly modelled by Michaelis–Menten kinematics. Parametric dependencies are represented in terms of four non-dimensional parameters: (i) the ratio of the nutrient uptake rate to the advection rate (α); (ii) the ratio of the zooplankton grazing rate to the uptake rate (β); (iii) the ratio of biomass to the saturation constant (δ); and (iv) the ratio of the seed plankton biomass to nutrient mass in the aphotic zone (ϵ). A sensitivity analysis has been initiated. Interesting results are indicated for the location, shape and magnitude of phytoplankton maximum and associated nutricline in the euphotic zone, and for the dynamical mechanism by which phytoplankton mediate the conversion of nutrient to zooplankton biomass. For general biological dynamics, kinematic flow fields have been introduced representative of coastal upwelling, isolated open ocean eddies and wave fields; and upwelling events, which set-up in time over a finite time-interval. Explicit solutions for the associated family of characteristic curves have been obtained.

These results provide a theoretical framework for further studies of more realistic oceanic processes. Weak background mixing in the lower euphotic zone will merely provide some smoothing of the solutions. For the upper euphotic zone, a mixed layer model has been added to the model. Work is in progress extending the model to include zooplankton mortality (Steele & Henderson 1992). Interesting application areas include mesoscale eddy nutrient injection events (McGillicuddy *et al.* 1998), wind-driven upwelling events (Franks & Walstad 1997), equatorial upwelling (Murray *et al.* 1995) and spring blooms (Fasham 1995).

I am grateful to Dr Patrick J. Haley Jr and Dr Dennis J. McGillicuddy Jr for interesting scientific discussions and comments. It is a pleasure to acknowledge the general assistance in carrying out this research of Mr Wayne G. Leslie, who, together with Dr Haley, performed computations and prepared figures. I thank Dr Dimitri Kroujiline and Dr Pierre F. J. Lermusiaux for helpful comments on the manuscript, and Ms Gioa Sweetland and Mrs Renate D’Arcangelo for preparation of the manuscript. This research was supported in part by the Office of Naval Research under grant N00014-95-1-0371 to Harvard University.

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