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Some physical factors affecting ecosystems

by Patrice Klein^{1,2} and John H. Steele¹

ABSTRACT

The response of a simple pelagic ecosystem is investigated in a domain with zero, one- and two-dimensional descriptions of the physical processes. Assuming complete mixing, internal recycling and external exchange of nutrients and their biological products are not additive in terms of the rate of primary production. In a one-dimensional system, advection without diffusion leads to low values of primary production. With two horizontal dimensions, cross diffusion at the boundary gives higher values of production. The consequences for higher trophic levels are described.

1. Introduction

There is considerable interest in the processes, physical and biological, by which nutrients are made available for the photosynthetic production of organic matter in the sea. The concept of “new” versus recycled nutrients corresponds to the separation of physical input from biological cycling (Dugdale and Goering, 1967; Eppley and Peterson, 1979). Areas with high production rates are usually associated with large physical input of new nutrients (Sambrotto *et al.*, 1984). It is not always clear, however, what exactly are the physical mechanisms. Some aspects of this problem will be explored here using simple models.

A second reason for interest in this dichotomy (new/recycled) concerns production at higher trophic levels. By definition, recycling predominantly by herbivores, does not provide food (as nutrients) for predators, whereas “new” production can be passed upward and then taken out of the system (Walsh *et al.*, 1981). This is of particular interest for shelf systems subject to commercial fishing.

Comparing the North Sea and Georges Bank, the former has a primary production of 100–200 $\mu\text{C}/\text{m}^2/\text{year}$ or greater (Steele, 1974; Gieskes and Kraay, 1984) while estimates for Georges Bank are about 300–400 $\mu\text{C}/\text{m}^2/\text{year}$ (Cohen *et al.*, 1982). The average residence time of water in the North Sea is of the order of a year. Magnell *et al.* (1981) consider that the vertically homogeneous area on Georges Bank is surrounded by a leaky eddy and their calculations suggest a residence time within this eddy of about one month. Georges Bank and the North Sea are very different in area

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(about a factor of ten) but the combination of greater exchange as well as greater primary production would suggest that fish production per unit area on Georges Bank be in proportion to, if not greater than, the ratio of the primary production. Yet, the exploitable fish production on Georges Bank is only slightly greater than the North Sea (Cohen *et al.*, 1982).

Zooplankton lifetimes of 20–50 days (Frost, 1980; Davis, 1984) are of the same order as the residence times in areas of the size of Georges Bank and thus likely to be significantly affected by this physical exchange. Since excretion by these herbivores is the predominant process in nutrient recycling, their interaction with the phytoplankton must be included in any model of the physical and biological interactions. To accommodate the physics, the model for nutrients (N), phytoplankton (P) and zooplankton (Z) is kept as simple as possible. Correspondingly, three simple physical situations are considered; zero-dimension (chemostat) mixing; one-dimensional (channel) flow with diffusion; and a two-dimensional (disc) model with dispersion along and across streamlines. The purpose is to explore the roles of advection and diffusion on nutrient utilization within this simple food chain system.

In this study, numerical simulations are made for the different dimensional systems. For these calculations, the domain is considered to be at the spatial scale of Georges Bank, 0(100 km), but the conclusions should apply to other areas at the same scale. The particular case of seasonal change on Georges Bank is considered elsewhere (Klein, 1985).

2. The biological model

A very simple nutrient cycle through plants and herbivores is used. The equations are

$$\begin{aligned} dZ/dt &= b_2PZ - dZ \\ dP/dt &= aNP - bPZ \\ dN/dt &= -aNP + b_1PZ + d_1Z \end{aligned} \quad (1)$$

where the units for N , Z , P are nitrogen in mgat/m³ and time is in days. For a purely recycling mode with no physical change

$$b = b_1 + b_2, d = d_1$$

then

$$d(N + P + Z)/dt = 0, N + P + Z = N_0.$$

Assume a maximum nitrate concentration, $N_0 = 5$; maximum phytoplankton growth rate is 1 (day⁻¹); then $a = 0.2$. Assume ratio of 1:100 for nitrogen content of eggs: adult herbivores; then $b = 0.15$. Assume a growth efficiency for herbivores of 20%; then $b_1 = 0.12$, $b_2 = 0.03$ (see Steele, 1974).

The solution to (1) at steady state is:

$$\begin{aligned} P_s &= d/b_2, \\ N_s &= (N_0 - d/b_2)/(1 + a/b), \\ Z_s &= (N_0 - d/b_2)/(1 + b/a). \end{aligned}$$

Primary production rate, P_p , is:

$$P_p = aN_sP_s = ad(N_0 - d/b_2)/[b_2(1 + a/b)],$$

and zooplankton production rate, S_p , is:

$$S_p = b_2P_sZ_s = d(N_0 - d/b_2)/(1 + b/a).$$

Both production rates are zero for $d = b_2N_0$ and are maximal for $d = b_2N_0/2 = 0.075$ when primary production is approximately 1.6 gC/m²/day (using a C/N ratio of 7 and a mean depth of 30 m). This is comparable with observed values for Georges Bank during the productive season (Cohen *et al.*, 1982). Recycling (rate d) occurs through some unspecified mortality of the herbivores which returns herbivore nitrogen to the inorganic state. This undefined component indicates the significance of the rest of the "ecosystem" which is not included in this simple model. Figure 1 displays the temporal sequence from initial conditions $N = 4.8$, $P = 0.1$, $Z = 0.1$ with two values of d .

For highly productive areas, however, it is thought that a combination of recycling and of nutrient introduction by water exchange should maximize production (Sambrotto *et al.*, 1984). The exchange can take place by advection and diffusion. Will these processes increase production? What is the relative importance of each process? How dependent are they on the physical conditions within the area considered? These questions will be explored by considering zero, one- and two-dimensional physical models added to the "biology."

3. Models with different physical dimensions

The set of equations (1) can be written as

$$d\phi/dt = A(\phi) \cdot \phi \quad (2)$$

where

$$\phi = \begin{bmatrix} Z \\ P \\ N \end{bmatrix}, \quad A(\phi) = \begin{bmatrix} b_2P - d & 0 & 0 \\ -bP & aN & 0 \\ b_1P + d_1 & -aN & 0 \end{bmatrix}$$

For the well mixed, chemostat case, there is an exchange rate k_0 (day⁻¹). The equations for the average conditions, $\bar{\phi}$, within the domain are

$$\begin{aligned} d\bar{\phi}/dt + k_0 \cdot (\bar{\phi} - \phi_0) &= \overline{A(\phi) \cdot \phi} \\ &= A(\bar{\phi}) \cdot \bar{\phi} \end{aligned}$$

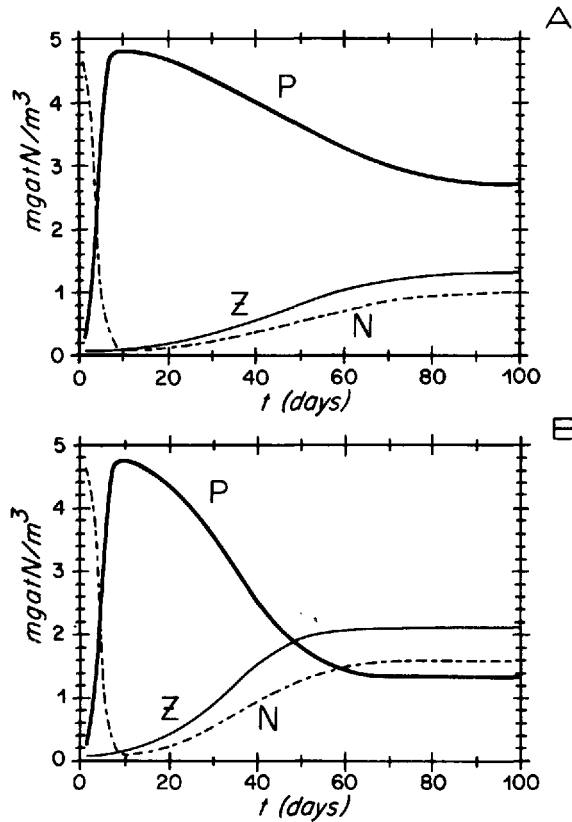


Figure 1. Time evolution of Z, P, N (from Eq. 1) with $d = 0.08$ (a) and $d = 0.04$ (b).

since $\phi = \bar{\phi}$ within the domain. ϕ_0 is the value of ϕ outside the domain and $1/k_0$ can be considered as a residence time.

For the one-dimensional case advection and diffusion along streamlines are considered. Velocity, U , and diffusion K are constant. The boundary conditions are $\phi(0, t) = \phi(L, t) = \phi_0$ where L is a length scale, with a value of 200 km used in the calculations (corresponding to about half the circumference of Georges Bank). The full equations are given in the Appendix. For comparison with the other cases, the equations for the mean values are written as

$$\begin{aligned} \frac{d\bar{\phi}}{dt} + k_1 \cdot (\bar{\phi} - \phi_0) &= \overline{A(\phi) \cdot \phi} \\ \frac{d\bar{\phi}}{dt} + k_1 \cdot (\bar{\phi} - \phi_0) &= A(\bar{\phi}) \cdot \bar{\phi} + \Delta_1. \end{aligned} \tag{3}$$

Since ϕ is not uniform within the domain, there is an extra term, Δ_1 , resulting from the nonlinear biological interactions, expressed as cross-correlations of the spatial fluctuations. The overall exchange rate, k_1 , is an explicit function of the advective and

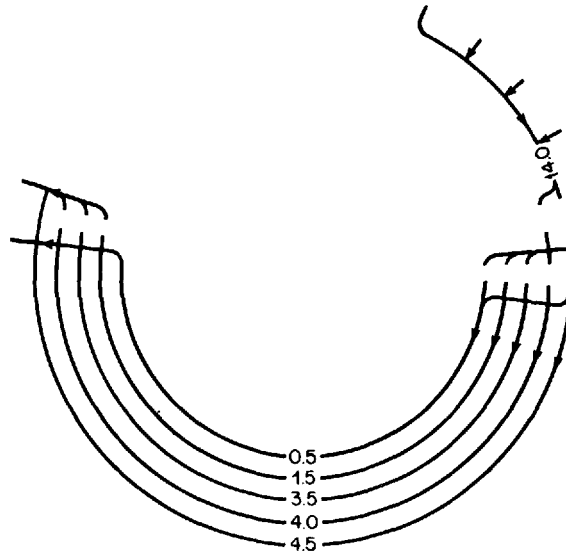


Figure 2. Flow lines and velocities (m/sec) for the two-dimensional model (see text).

diffusive exchanges across the boundaries (A4, A5) and can have different values for each variable Z , P , N .

The main feature of the two-dimensional case is the introduction of diffusion across, as well as along, the streamlines representative of the velocity field and shear dispersion encountered on Georges Bank (Butman *et al.*, 1982). The domain is taken to be a disc with radius R_{\max} . Cylindrical coordinates (r, θ) are used with velocity components U_r , U_θ , and diffusion K_r , K_θ . Boundary conditions are $\phi(R_{\max}, \theta, t) = \phi_0$. Streamlines are constrained as portions of circles between intake and output regions (Fig. 2). A shear across the streamlines is introduced by a velocity gradient from 4.5 cm/sec at the boundary to 0.5 cm/sec at about $r = R_{\max}/2$. In the region between input and output, the flow is confined to a 5 km band just inside the boundary.

A similar equation exists for $\bar{\phi}$ (see Appendix)

$$d\bar{\phi}/dt + k_2 \cdot (\bar{\phi} - \phi_0) = A(\bar{\phi}) \cdot \bar{\phi} + \Delta_2. \quad (4)$$

In all three cases, the same biological parameters are used. These imply 100% efficiency in recycling and maintain the condition that $\bar{N} + \bar{P} + \bar{Z} = N_0$. This is unlikely to be true in any particular area, but it is the simplest assumption for this approach which concentrates on physical variations.

Numerical simulations performed using Eqs. 3 and 4 have a duration of 100 days and a steady state is attained at this time. At the end of each simulation, the mean primary and secondary production were calculated using the relations derived in the Appendix.

4. Well-mixed case

The steady state solutions are

$$\begin{aligned} P_s &= (d + k_0)/b_2 \\ N_s &= [N_0 - (d + k_0)/b_2 + k_0/b]/(1 + a/b) \\ Z_s &= [N_0 - (d + k_0)/b_2 - k_0/a]/(1 + b/a). \end{aligned} \quad (5)$$

Since $b = 5b_2$ and $a = 30b_2$, the last terms in the square brackets can be neglected to a first approximation. Then, by comparison with pure recycling case, the results are the same with $(d + k_0)$ replacing d .

The major implication is that, in this well-mixed case, a combination of recycling and exchange does not significantly increase the primary productivity of the system. The physical and biological processes are not additive in terms of basic production. This conclusion is independent of the actual numbers but, using the previous calculation, we have maximum production for $k_0 + d$.

If we assume that exchange and recycling are equally important (Loder *et al.*, 1982) then $k_0 = 0.04$ corresponding to a residence time of 25 days which is low but not impossible for the inner, mixed area on Georges Bank. The effect of this physical removal of water from the domain can be considered by assessing the ratio

$$\begin{aligned} \text{rate of loss/rate of growth} &= k_0/(P_p/P_s), \text{ for phytoplankton} \\ &= k_0/(S_p/Z_s), \text{ for zooplankton.} \end{aligned}$$

For phytoplankton the ratio is only 15% but is 50% for zooplankton indicating there are major effects on the herbivore populations if physical exchange is a significant factor.

In Figure 3, values of P_s and P_p are given for a range of exchange rates keeping $d = 0.04$ and this value of d is used for the one- and two-dimensional cases.

5. One-dimensional case

When diffusion is taken to be zero and only advection is considered, then changes along the one spatial dimension will correspond to the temporal evolution in Figure 1b where $d = 0.04$. Thus, a range of velocities from 0.01 to 0.10 m/sec corresponds to travel times along a 200 km channel of 200 to 20 days covering the probable residence times (defined as the inverse of the exchange rate) for an area such as Georges Bank. This range of velocities will cause different quantities and relative proportions of P and Z to be removed from the domain (as indicated by Fig. 1). The consequences can be seen in Figure 3, where the phytoplankton is well above the well-mixed case, but the average production is well below and decreases with increased advection.

A major conclusion is that in the context of this simplified model, advection without diffusion does not enhance production, in fact, the opposite is true.

The introduction of diffusion with a low (or zero) advection does have a stimulatory effect on production, Figure 3. A range of values from $K = 0-600$ m²/sec was used

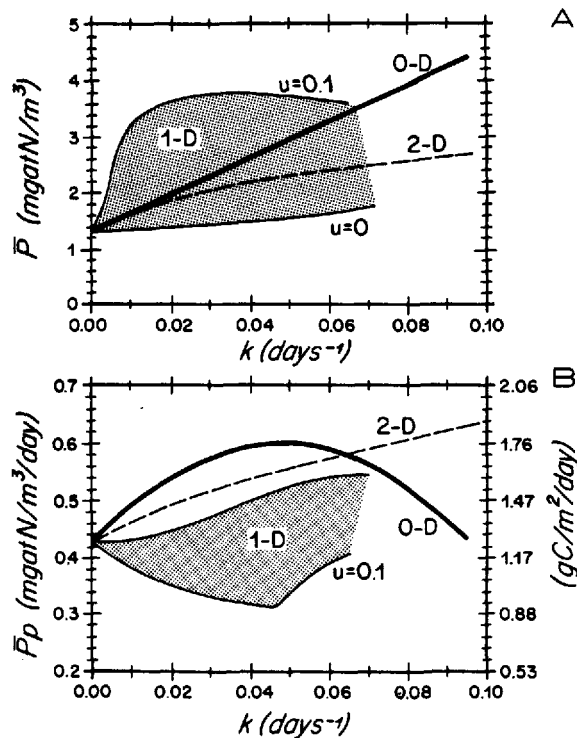


Figure 3. Steady state values of (a) P and (b) P_p as functions of exchange rate, k . Heavy line, well-mixed case. Stippled area; one-dimensional case for U between 0 and 0.1 m/sec. and for a range of diffusion. Dashed line is for two-dimensions with fixed advection and variable diffusion.

which, again, covers the likely diffusivities for an area such as Georges Bank (Loder *et al.*, 1982). The shaded areas between these lines on Figure 3 indicate the intermediate range of velocity and diffusivity. As a result, any combination of these parameters in a one-dimensional model still has the primary production significantly below the maximum for the well-mixed case.

6. Two-dimensional case

Initially, a simulation was made with zero cross diffusion. The ecosystem response, Figure 4, is similar to the one-dimensional case with $u = 0.03$ m/sec, $K = 0$. Figure 4 shows the strong spatial separation between phytoplankton and zooplankton maxima induced by an advective flow field without cross diffusion, and emphasizes the need for addition of these diffusive effects.

Diffusion within the domain is taken to be homogeneous with $K_x = K_y = 350$ m²/sec, within the range estimated by Loder *et al.* (1982) and typical of areas such as Georges

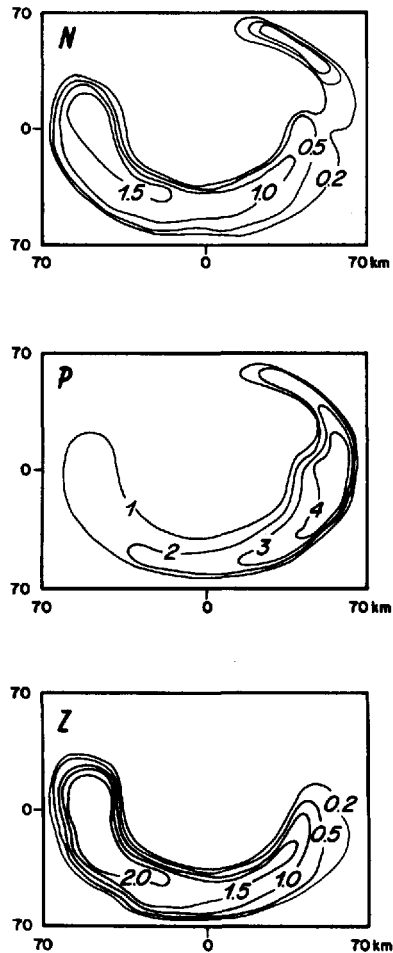


Figure 4. N , P , Z distribution at $t = 100$ days when cross-diffusion is zero and diffusion along the streamlines is $50 \text{ m}^2/\text{s}$. Stretched horizontal axis is due to the plotting program.

Bank (Klein, 1985a). The remaining parameter is diffusion across the boundary (K_R). Because such regions usually have defined hydrographic boundaries in the form of fronts, the effective exchange should correspond to a lower diffusion coefficient. A range of coefficients was used, $30\text{--}300 \text{ m}^2/\text{sec}$ with the same advection. The calculated average exchange rates for phytoplankton then range from 0.018 (55 days) to 0.100 (10 days). The corresponding variations in phytoplankton and primary production, Figure 3, show that increased boundary diffusion increases the primary production and keeps it above the values for the one-dimensional case, and closer to, although lower than, the well-mixed case for exchange rates less than 0.07. From Table 1, while the phytoplankton standing crop increases, the zooplankton decrease. Also, the secondary

Table 1. Mean values of Z , P , N (Mg at nitrogen/m³); primary (P_p) and secondary (S_p) production and their ratio for different values of K_R . The nitrate exchange rate k_N is used to calculate the ratio N/T = new/total production (see text).

K_R (m ² /s)	\bar{Z}	\bar{P}	\bar{N}	\bar{P}_p	\bar{S}_p	\bar{P}_p/\bar{P}	k_N	N/T
30.	1.75	1.87	1.37	0.48	0.09	0.19	0.017	0.13
100.	1.45	2.28	1.27	0.55	0.09	0.16	0.038	0.26
200.	1.19	2.58	1.23	0.60	0.08	0.13	0.064	0.40
300.	1.02	2.72	1.26	0.64	0.08	0.12	0.086	0.50

production does not increase with increased exchange so that the ratio of secondary to primary production decreases significantly.

As an example of the spatial patterns with diffusion, Figure 5, shows the relative uniformity within the domain except for strong gradients near the boundary. High diffusion across the boundaries gives distributions very different from the pure advective case and closer to the observed uniformity in areas such as Georges Bank. These results emphasize the role of diffusion on the ecosystem response. More significantly, this response in a two-dimensional model associates an increase of primary production with a high physical export unlike the well-mixed case where production decreases at high exchange rates, Figure 3. When $K_r = 300$ m²/sec, the ratio (export/growth) is 40% for phytoplankton and 54% for zooplankton, yet production (at 1.9 gC/m²/day) is higher than the maximum for the well-mixed case at half the exchange rate.

One test of this model is to examine the ratio of new to total primary production (Eppley and Peterson, 1979) where "new" is defined here as rate of nutrient introduction $k_n(N_0 - N)$. This ratio, Table 1, increases from 0.13 to 0.50 as exchange increases and this range is close to that deduced from observation (excluding upwelling) by Eppley and Peterson (1979). However, as seen from the S_p/P_p ratio, there is a decrease rather than an increase in transfer to higher trophic levels within the domain.

7. Conclusions

An ecological system in a complicated physical environment will display patchiness and temporal variability on many scales (Steele, 1978). This makes it impossible to model all the interactions. For regions of intermediate scale, 0(100 km), the fine structure associated with phytoplankton, 0(1 km), and the largest ambits of migratory fish, 0(1000 km), may be less relevant than those of the herbivorous zooplankton whose lifetimes, 0(50 days), are comparable to the dispersion times at these intermediate spatial scales (Davis, 1984). Here, a very simple model incorporating zooplankton dynamics is used to explore the consequences of different representations of physical processes. The zooplankton/food relation is itself simplified to a form which may apply to some, but not all species (Davis, 1984).

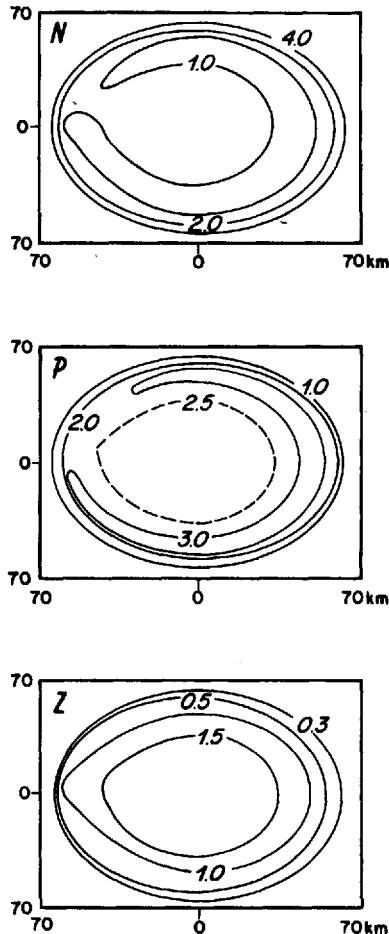


Figure 5. N , P , Z distribution at $t = 100$ days when $K_R = 300 \text{ m}^2/\text{s}$.

The “chemostat” assumption of complete mixing provides insight into the relative contributions of internal recycling and external exchange of nutrients and their biological products. It is concluded that the two processes are not additive in terms of the level of primary production. Further, systems with residence times of about one month may export significant fractions of zooplankton production to regions outside the system.

These conclusions for the zero-dimensional case do not differentiate between advection and diffusion as exchange processes. A one-dimensional model including both processes shows that advection alone not only produces spatial separation of plant and herbivore maxima, but decreases the primary production due to this decoupling. Thus, a second conclusion is that, at these scales, advection alone may not be an

appropriate mechanism to increase productivity. One-dimensional diffusion reverses this trend, but at a level of primary production lower than the well-mixed case.

A two-dimensional "disc" model with diffusion along and across the streamlines, and mixing by diffusion at the boundary, produces more acceptable spatial patterns, and has production rates generally similar to the well-mixed case. Thus, a third conclusion is that diffusion across the boundary may be the critical process for nutrient input rather than simple advection.

However, the particular relations between production and exchange are different for the well-mixed and the two-dimensional models. Thus, a general conclusion is that use of a simple "residence time" concept is inadequate for physical and biological interactions. A knowledge of advective and diffusive processes is required.

A general feature of the zero- and two-dimensional models is that, as exchange is increased, the primary production increases, but the secondary production does not. Thus, high primary production need not imply that this production is passed up the food chain in the area where it occurs. In consequence, yield at higher trophic levels such as fish may not increase in proportion to the primary production. Or, alternatively, the energy flow must be applied to a much larger area as in the North Sea. These factors may explain why the high primary production on Georges Bank is not reflected in fish yields from the Bank.

Lastly, we must stress the simplicity of the biological and physical components of the models used here. Loss of primary production by sinking to the bottom may be as important as grazing or physical export (Dagg *et al.*, 1982). Also, losses by export may be utilized elsewhere so that a larger domain could include these downstream aspects. The three physical "cases" considered here are still very simple, especially in excluding vertical processes such as upwelling. The aim has been to provide insight into some, but certainly not all, of physical/biological interactions at a selected range of spatial and temporal scales.

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APPENDIX

Numerical integration of Eqs. A1 and A7 are detailed in Klein (1984b). In the one-dimensional case, space increments Δx and time step Δt , chosen to ensure stability and accuracy, vary respectively from 2.5 km to 5 km and 1 hour to 3 hours. In the two dimensional case, spacing grids chosen are $\Delta r = 5$ km, $\Delta \theta = 2\pi/30$. And the time step is $\Delta t = 3$ hours. Boundary conditions in all simulations are: $N_0 = 4.8$, $P_0 = 0.1$ and $Z_0 = 0.1$. Initial conditions are $\phi = \phi_0$.

Equations for the mean values in the one- and two-dimensional cases*One-dimensional case.*

The equation for $\phi(x, t)$ is:

$$\frac{\partial \phi}{\partial t} + U \frac{\partial \phi}{\partial x} - K \frac{\partial^2 \phi}{\partial x^2} = A(\phi) \cdot \phi, \quad (\text{A1})$$

with $\phi(0, t) = \phi_0 = \phi(L, t)$.

Using a mean operator defined by:

$$\bar{\zeta}(t) = \frac{1}{L} \int_0^L \zeta(x, t) dx, \quad (\text{A2})$$

where $\zeta(x, t)$ is any variable, the equation for the mean value $\bar{\phi}$ is:

$$\frac{d\bar{\phi}}{dt} + k_1 \cdot (\bar{\phi} - \phi_0) = A(\bar{\phi}) \cdot \bar{\phi} + \Delta_1, \quad (\text{A3})$$

where k_1 is an exchange rate defined by:

$$k_1 \cdot (\bar{\phi} - \phi_0) = \frac{U}{L} (\phi(L, t) - \phi_0) + \frac{K}{L} \left(\frac{\partial \phi}{\partial x} \Big|_{x=0} - \frac{\partial \phi}{\partial x} \Big|_{x=L} \right), \quad (\text{A4})$$

with:

$$k_1 = \begin{bmatrix} k_{1z} & 0 & 0 \\ 0 & k_{1p} & 0 \\ 0 & 0 & k_{1n} \end{bmatrix}, \quad (\text{A5})$$

and Δ_1 is defined as:

$$\Delta_1 = \begin{bmatrix} \Delta_{1z} \\ \Delta_{1p} \\ \Delta_{1n} \end{bmatrix} = \overline{A(\phi) \cdot (\phi)} - A(\bar{\phi}) \cdot \bar{\phi}.$$

The mean primary and secondary productions are defined by:

$$\begin{aligned} \bar{P}_p &= a \overline{NP} = \frac{a}{L} \int_0^L N(x, t) P(x, t) dx, \\ \bar{S}_p &= b_2 \overline{PZ} = \frac{b_2}{L} \int_0^L P(x, t) Z(x, t) dx. \end{aligned} \quad (\text{A6})$$

Two-dimensional case.

The equation for $\phi(r, \theta, t)$ is:

$$\frac{\partial \phi}{\partial t} + U_r \frac{\partial \phi}{\partial r} + \frac{U_\theta}{r} \frac{\partial \phi}{\partial \theta} - \frac{1}{r} \frac{\partial}{\partial r} r K_r \frac{\partial \phi}{\partial r} - \frac{1}{r^2} \frac{\partial}{\partial \theta} K_\theta \frac{\partial \phi}{\partial \theta} = A(\phi) \cdot \phi, \quad (\text{A7})$$

with $\phi(R_{\max}, \theta, t) = \phi_0, \theta \in [0, 2\pi]$.

An appropriate mean operator is defined as:

$$\bar{\zeta}(t) = \frac{1}{S} \int_0^{R_{\max}} r \int_0^{2\pi} \zeta(r, \theta, t) dr d\theta, \quad (\text{A8})$$

where S is the surface of the domain. Then the equation for $\bar{\phi}$ is:

$$\frac{d\bar{\phi}}{dt} + k_2 \cdot (\bar{\phi} - \phi_0) = A(\bar{\phi}) \cdot \bar{\phi} + \Delta_2, \quad (\text{A9})$$

where

$$k_2 \cdot (\bar{\phi} - \phi_0) = -\frac{1}{S} \int_0^{2\pi} r U_r \phi(R_{\max}, \theta, t) d\theta + \frac{1}{S} \int_0^{2\pi} r K_r \frac{\partial \phi(R_{\max}, \theta, t)}{\partial \theta} d\theta, \quad (\text{A10})$$

with:

$$k_2 = \begin{bmatrix} k_{2z} & 0 & 0 \\ 0 & k_{2p} & 0 \\ 0 & 0 & k_{2n} \end{bmatrix}, \quad (\text{A11})$$

and Δ_2 is defined as:

$$\Delta_2 = \begin{bmatrix} \Delta_{2z} \\ \Delta_{2p} \\ \Delta_{2n} \end{bmatrix} = \overline{A(\phi) \cdot \phi} - A(\bar{\phi}) \cdot \bar{\phi}.$$

The mean primary and secondary productions, using (A8) are defined by:

$$\begin{aligned} \bar{P}_p &= a\overline{NP} = \frac{a}{S} \int_0^{R_{\max}} r \int_0^{2\pi} N(r, \theta, t) P(r, \theta, t) dr d\theta, \\ \bar{S}_p &= b_2\overline{PZ} = \frac{b_2}{S} \int_0^{R_{\max}} r \int_0^{2\pi} P(r, \theta, t) Z(r, \theta, t) dr d\theta, \end{aligned} \quad (\text{A12})$$

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