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Stirring and mixing of biologically reactive tracers

K. J. Richards, S. J. Brentnall, P. McLeod, and A. P. Martin

Southampton Oceanography Centre, Southampton, UK

Abstract. We examine the effect of stirring and mixing on the marine planktonic ecosystem. We present a number of models investigating the impact of patchiness in the population, diffusion, and fluid stirring on the spatial structure of the population and the overall production rates of the system. It is found that the heterogeneity of the system significantly affects the way the system behaves. The response of the ecosystem to the action of the fluid flow is a function of not only the topology of the flow but also the dynamics of the ecological model itself.

1. Introduction

The marine ecosystem plays an important role in the cycling of carbon. In particular it acts as a 'carbon pump,' utilising atmospheric CO_2 through photosynthesis, a proportion of the carbon being exported to the deep ocean, and thus moderating levels of CO_2 in the atmosphere. Ecological models are now incorporated into models of climate change to predict global warming scenarios (see, e.g., it Cox et al., 2000). A physical/ecological model used in climate studies needs to incorporate both the appropriate ecological dynamics and the right physics impacting on the biological production.

Primary production in the ocean is dominated by phytoplankton. A feature of the distribution of phytoplankton distributions is that it is very heterogeneous or 'patchy' (*Bainbridge*, 1957). Structure is observed on scales ranging from metres to the basin scale (*Mann and Lazier*, 1996) with this structure often observed to be associated with physical features such as eddies and fronts (e.g., (*The Ring Group*, 1981; *Falkowski et al.*, 1991; *Strass*, 1992). A number of important questions arise:

- Does the patchiness affect the dynamics of the ecological system?
- Does the heterogeneity of the system impact on the overall production rates and/or community structure?
- Does the structure affect the way the biological system responds to changes to the environment?

Here we will use a number of relatively simple models of both the ecological dynamics and the fluid flow in order to try and understand some of the more fundamental issues related to the problem of marine biological patchiness. The models should be thought of as caricatures of the more complex system, but we hope they will provide the building blocks for understanding of that system. The work is very much 'in progress' and so this not a presentation of a 'complete theory' but rather some initial attempts and their results.

2. Biological reactions and fluid flow

Fluid flow can impact on the marine ecological system in two distinct ways: (a) through the vertical movement of nutrients and biological species in or out of the euphotic zone, and (b) the stirring and mixing of components of the system. A good example of when both are important is baroclinic instability (*Spall and Richards*, 2000). Associated with the instability process is a permanent vertical displacement carrying nutrient rich waters into the sunlit surface layers. These nutrients are then stirred and mixed with the surrounding water and are utilised by the biota. Here we will concentrate on this second process, the stirring and mixing by lateral fluid flow.

2.1. General advection–diffusion–reaction equation

We shall model the ecological system using the advection–diffusion–reaction equation

$$\frac{\partial \mathbf{E}}{\partial t} + (\mathbf{u} \cdot \nabla)\,\mathbf{E} = \mathbf{f}(\mathbf{E}) + \nabla \cdot (D \nabla \mathbf{E})$$

where, for example, the state vector may take the form

$$\mathbf{E} = \begin{bmatrix} N \\ P \\ Z \end{bmatrix}$$

with the elements representing the concentration of nutrients (N), phytoplankton (P) and zooplankton (Z) expressed in terms of a currency, such as nitrogen.

The elements are advected by the flow $\mathbf{u}$ and diffused. The reaction between elements is represented by $\mathbf{f}(\mathbf{E})$.(How well the field equation approach models the marine ecological system is a matter of debate. There is some evidence that it fails if behavioural aspects of the zooplankton are important (*Flierl et al.*, 1999).

A measure of the relative 'strength' of the reaction terms to either diffusion or advection can be gauged by considering the ratio of timescales, i.e.

$$\beta_\kappa = \frac{\mu L^2}{\kappa}$$

and

$$\beta_u = \frac{\mu L}{U}$$

respectively, where U and L are typical velocity and length scales, κ a diffusion coefficient, and μ the reaction rate. The nondimensional parameters β_κ and β_u are equivalent to diffusive and advective inverse Damköhler numbers. Large values imply that the reaction dominates.

We present three models using (2.1). The first looks at the case of no flow and the structure that evolves simply through the combination of reaction and diffusion. The second considers simple biology in a simple flow, a pure strain, and examines the structure of filaments of biological material. The third takes a 2D geostrophic turbulent flow and investigates the impact the stirring has on biological production. The underlying message is that the response of the ecology to the action of the fluid flow is a function of not only the topology of the flow but also the dynamics of the ecological model itself.

2.2. Model 1: Intrinsic structure

Consider the case of no flow ($\mathbf{u} \equiv 0$). We shall consider a two compartment model:

$$\mathbf{E} = \begin{bmatrix} P \\ Z \end{bmatrix}$$

where $P \in [0, 1]$, and the reaction terms are

$$\mathbf{f} = \begin{bmatrix} \mu P(1-P) - \frac{ZP^2}{\nu^2+P^2} \\ \gamma\left(\frac{ZP^2}{\nu^2+P^2}\right) - \omega h(Z) \end{bmatrix}$$

The reaction terms for the phytoplankton, P, include limited growth (known as logistic growth) and grazing by zooplankton (the functional form used here is known as Holling type III). The zooplankton, Z, grow at a reduced rate $\gamma \ll 1$. The mortality term $h(Z)$ is taken to be either a linear or quadratic function of Z, corresponding to the zooplankton dying of old age or being consumed by a higher predator, respectively.

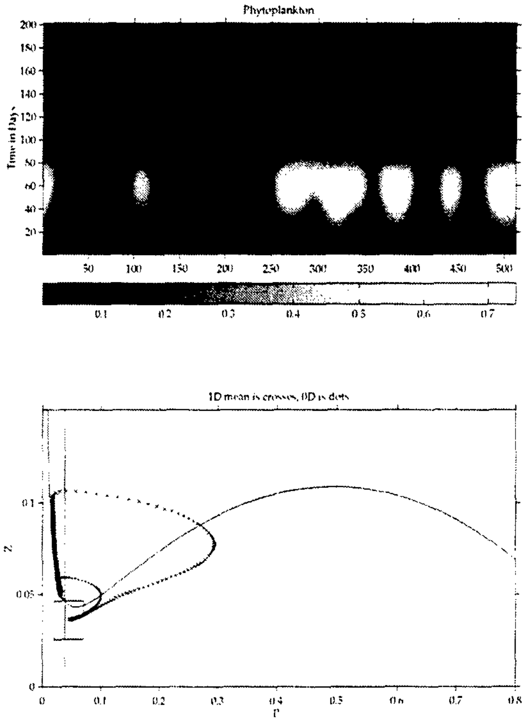

Figure 1. Model 1 with linear mortality. Upper panel, plot of phytoplankton concentration as a function of distance (given in tens of metres) and time. Lower panel, trajectories of the mean values of P and Z for the randomly perturbed (crosses) and unperturbed (dots) cases. Also shown are the null–clines of the reaction equations (i.e., $\partial P/\partial t = 0$ and $\partial Z/\partial t = 0$. The null–clines intersect giving a single stable equilibrium point

The model for the reaction terms is that of *Truscott and Brindley* (1994). It is chosen because of its simplicity and because the mathematical structure of the ecological dynamics is known. In particular the system becomes excitable (i.e., small but finite perturbations from an equilibrium point can lead to large excursions in model phase space) if both γ and ν are small enough.

The diffusion tensor is taken to be

$$D = \begin{bmatrix} \kappa & 0 \\ 0 & r\kappa \end{bmatrix}$$

so that zooplankton may diffuse at a different rate to phytoplankton (allowing cross diffusion, i.e., zooplankton diffusing up the phytoplankton gradient, has also been investigated).

Here we present two examples to illustrate the different behaviour of the system for linear (Figure 1) and quadratic (Figure 2) mortality (further details of the behaviour of the system are given in *Brentnall et al.* (2001). We take a one–dimensional case, i.e., variables only vary in one horizontal direction. The system is initialised on a grid with random values of P and Z about some mean value. The size of the rectangular box in the lower panel of each figure gives an indication of the spread of values. In both the linear and quadratic mortality cases a structure appears. The difference is that this structure persists for a longer time for the quadratic mortality case. The length scale of the structure scales with $\sqrt{\mu/\kappa}$ (i.e., the diffusive inverse Damköhler number, β_κ is the relevant parameter). With a growth rate of 1 day^{-1} and diffusion coefficient of 10^{-2} m^{2}s^{-1} the emergent scale is of order $\simeq$ 500 m.

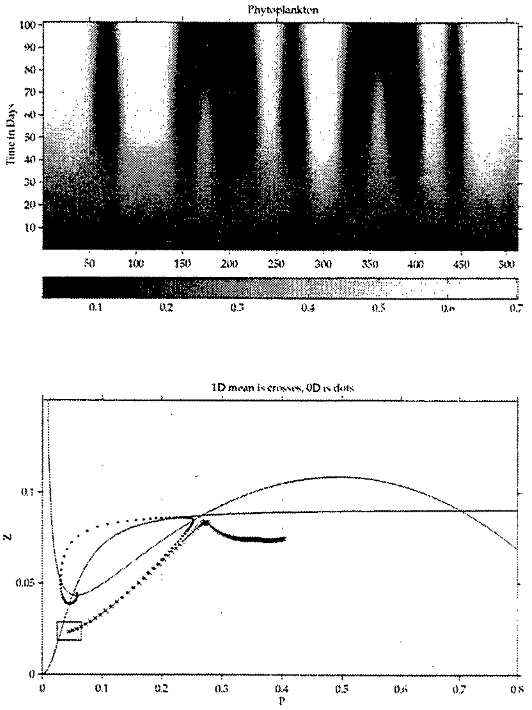

Figure 2. Model 1 with quadratic mortality. As for Figure 1, but in this case the null–clines intersect at three points, with two stable equilibria at $P = 0.05$ and 0.7 and an unstable equilibrium point at $P = 0.27$

The trajectory in P/Z phase space changes significantly when horizontal structure is introduced. The trajectories for the mean P and Z with and without the small random perturbation are shown in the lower panel of Figures 1 and 2. With linear mortality, although the two trajectories converge to the same stable equilibrium, the excursion in P is much greater when the perturbation is introduced. With quadratic mortality, the two trajectories converge to two different stable equilibria, with the perturbed case converging very slowly. Clearly the heterogeneity of the biology (with diffusion acting) is playing a significant role in the time evolution of the system. It is also clear that we need to consider what happens when there is a flow, which we do in the next section

2.3. Model 2: filaments

We now consider a pure strain flow

$$\mathbf{u} = (-\lambda x, \lambda y)$$

Such a flow will tend to pull a tracer into a thin filament.

For an **inert** tracer the filament width attains a value

$$W_i = \sqrt{\frac{\kappa}{\lambda}}$$

when the straining of the flow is balanced by diffusion. (34 (@) has shown that filaments of an exponentially growing tracer have the same width as an inert tracer)

The biology we will use is a simplified version of that used above, namely

$$\mathbf{E} = [\ P\ ]$$

with

$$\mathbf{f} = [\ \mu P(1-P)\ ]$$

A feature of this system is that the combination of logistic growth and diffusion allows the existence of reactive travelling waves (or Fisher waves) which have a minimum speed $2\sqrt{\kappa\mu}$ (c.f., *Murray*, 1993). These waves are important in transmitting 'information' and means that the biological population can advance faster than through pure diffusion. The waves are important in setting the width of filaments.

We may expect the travelling wave to be brought to rest when its speed matches that of the converging flow, such that the width of the filament

$$W_r \sim \frac{\sqrt{\kappa\mu}}{\lambda}$$

Indeed this is found to be the case for sufficiently large values of $\beta_u = \mu/\lambda$, an inverse advective Damköhler number (see the lower panel of Figure 3). The shape of the distribution of concentration changes with increasing β_u (upper panel Figure 3) from a Gaussian to a square wave as shown by the kurtosis of the distribution (lower panel Figure 3) (*McLeod et al.*, 2001).

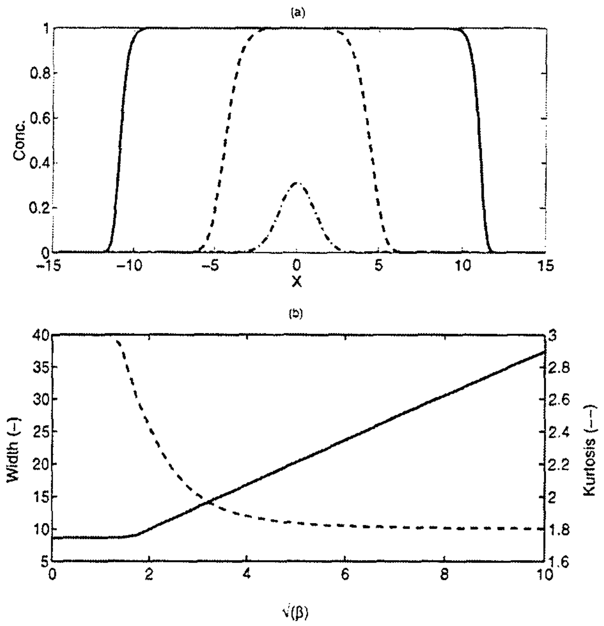

Figure 3. Model 2, filament structure. Upper panel: the distribution of phytoplankton across the filament for three values of β_u: dash-dot β_u=2, dash β_u=10 and solid β_u=50. The horizontal distance has been scaled with $\sqrt{\kappa\mu}/\lambda$. Lower panel: the filament width (scaled with $\sqrt{\kappa/\lambda}$) and kurtosis as a function of β_u.

It is interesting to note that

$$\frac{W_r}{W_i} = \sqrt{\beta}$$

,

i.e., the filament width for a reactive tracer will be greater than that of an inert tracer for $\beta_u > 1$. Using an observed filament width, and strain rate, to estimate κ will lead to an overestimate by a factor β if the reaction is not taken into account.

2.4. Model 3: fluid stirring

Lastly we consider the case of the ecosystem being stirred by a turbulent flow field. We use the 2D geostrophic turbulence model of *Babiano et al.* (1987) in a 512 km^2 periodic domain. The flow is forced to give a statistically steady state. An example of the potential vorticity is given in Figure 4. A characteristic of 2D turbulence is that the flow is inhabited by strong coherent vortical structures surrounded by a straining flow in the intervening regions. The coherent structures act as transport barriers inhibiting the mixing of tracers between the eddies and surrounding fluid (*Provenzale*, 1999).

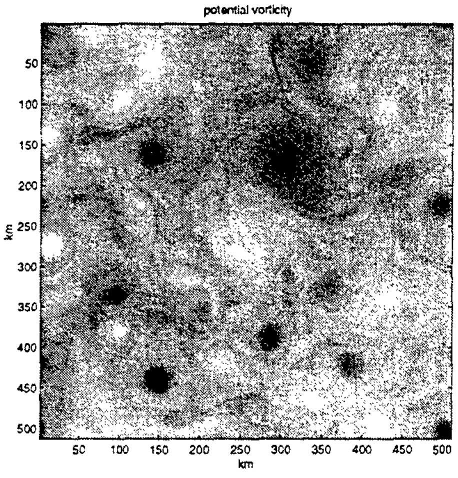

Figure 4. Model 3, fluid stirring. The potential vorticity field.

The biological model is slightly more complicated than before.

$$\mathbf{E} = \begin{bmatrix} N \\ P \\ Z \\ D \end{bmatrix}$$

with

$$\mathbf{f} = \begin{bmatrix} -\mu\left(\frac{N}{k_N+N}\right)P + \mu_D D + \gamma_2 Z \\ \mu\left(\frac{N}{k_N+N}\right)P - \left(\frac{g\epsilon P^2}{g+\epsilon P^2}\right)Z - \mu_P P \\ \gamma_1\left(\frac{g\epsilon P^2}{g+\epsilon P^2}\right)Z - \gamma_2 Z - \mu_Z Z^2 \\ (1-\gamma_1)\left(\frac{g\epsilon P^2}{g+\epsilon P^2}\right)Z + \mu_P P + \mu_Z Z^2 - \mu_D D \end{bmatrix}$$

where D represents detritus and there is an additional sinking term $-w_s D/h$ in the equation for detritus. The biological model is that of *Oschlies and Garcon* (1999) and has been chosen because it has been shown to capable of reproducing the seasonal cycle in both oligotrophic (nutrient depleted) and nonoligotrophic regions with the same set of parameter values. Details of the biological and flow model, including the parameter values, are given in *Martin et al.* (2001).

The biological system is forced by a source of nutrient

$$\Gamma_s = s(N_o - N)$$

where s is a function of position or some property of the flow, and can be thought of as modelling the input of nutrients to the euphotic zone through upwelling. *Martin et al.* (2001) investigate how the productivity depends upon the distribution of the upwelling by comparing spatially stationary sources with sources correlated or decorrelated with flow features. They conclude that the increased productivity brought about by upwelling is a function of the rate of upwelling, the distribution of the sources, and the mixing efficiency of the flow.

We consider two cases, the first with the source confined to a single patch (Figure 5) and the second with the source distributed over 64 smaller patches but such that the total area is the same as in the first case (Figure 6). The figures show the distribution of primary production at a time when the biology is in a statistical equilibrium.

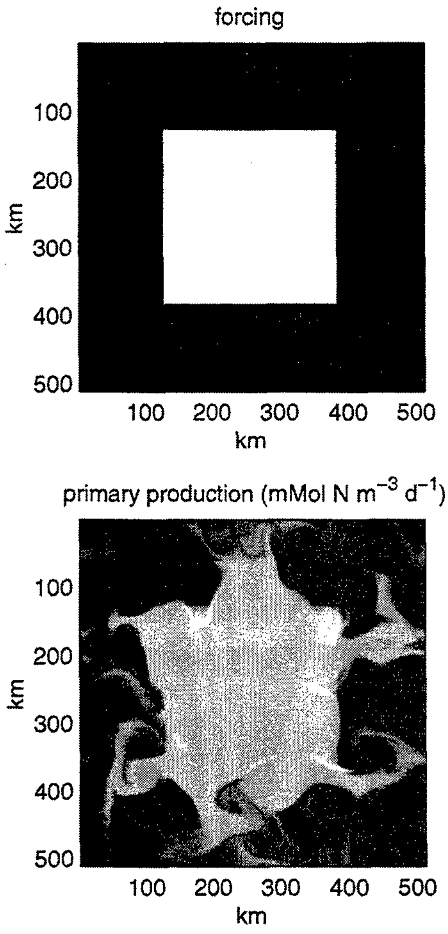

Figure 5. Model 3, fluid stirring. The forcing of nutrient and primary production resulting from stirring by a 2D turbulent field. The production ranges from 0.1 (black) to 0.45 (white) nMol N m^{-3} d^{-1}.

Referring to the single source case (Figure 5), the nutrient forcing has produced elevated rates of production above the background level of 0.1 mMol N m^{-3} d^{-1}. Compared to the case with the same forcing but no fluid stirring ($\mathbf{u} \equiv 0$) the areal average of production has increased by 36%. The fluid motion has the effect of increasing the surface area between the nutrient enriched and surrounding waters. A striking feature of the distribution of production is that it is limited to the vicinity of the forcing (an inert tracer will be spread quickly across the entire domain). The reaction limits the extent of the region of high nutrients and hence the area of contact with the surrounding waters. Reducing the reaction rate (reducing β_u) will allow greater stirring to take place before the nutrients are consumed and hence increase the area of contact, counteracting the decrease in overall production because of the decreased production rate. Experiments varying β_u show that the two effects may balance each other.

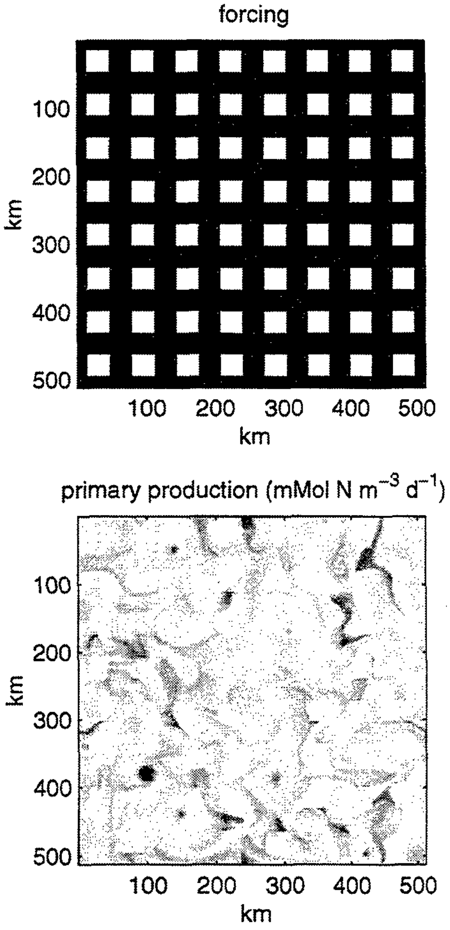

Figure 6. As for Figure 5 but for a distributed source.

As expected, distributing the source increases the mixing and hence production rate (Figure 6). In this case the overall production rate has been increased by 137% above the case with no mixing.

3. Concluding remarks

We have reported on a number of investigations into the impact of heterogeneity of the marine ecological system on the behaviour of that system as a whole. The results demonstrate that the heterogeneity cannot be ignored. Applying the results from studies such as those presented here is difficult. We freely admit that the results of our studies to date are somewhat of an anecdotal character. There are caveats on the methodology such as the exclusion of the diurnal and in particular the seasonal cycle, both of which impose a strong pacing of the system, and which need to be included in future studies.

It is disconcerting that the results are very dependent on the form of the ecological model (as an additional example, the enhancement of productivity found in model 3 was significantly reduced when a simpler [N,P] was used). Perhaps not a surprising remark but one which is often ignored. This issue needs to be explored further, but it does make the task of developing 'robust' ecological models that much more difficult.

What is clear is that viewing marine ecology as a simple 1D system (the space dimension being vertical) may well be erroneous and produce misleading results. Ecological models are often 'fitted' or rejected on the basis of the performance of a 1D version of the model compared to observations. At best the 'fitted' parameters may be dependent on the physical environment, implicitly including the effects of unresolved physical and ecological processes. At worst the functional form of the model chosen through this comparison may be wrong. In either case, in using an ecological model to predict changes to the ecological system as the physical environment changes, we need to ensure that the model captures the correct impact of those changes.

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