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Spatially implicit plankton population models: Transient spatial variability

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ABSTRACT

Ocean plankton models are useful tools for understanding and predicting the behaviour of planktonic ecosystems. However, when the regions represented by the model grid cells are not well mixed, the population dynamics of grid cell averages may differ from those of smaller scales (such as the laboratory scale). Here, the 'mean field approximation' fails due to 'biological Reynolds fluxes' arising from nonlinearity in the fine-scale biological interactions and unresolved spatial variability. We investigate the domain-scale behaviour of two-component, 2D reaction–diffusion plankton models producing transient dynamics, with spatial variability resulting only from the initial conditions. Failure of the mean field approximation can be quite significant for sub grid-scale mixing rates applicable to practical ocean models. To improve the approximation of domain-scale dynamics, we investigate implicit spatial resolution methods such as spatial moment closure. For weak and moderate strengths of biological nonlinearity, spatial moment closure models generally yield significant improvements on the mean field approximation, especially at low mixing rates. However, they are less accurate given weaker transience and stronger nonlinearity. In the latter case, an alternative 'two-spike' approximation is accurate at low mixing rates. We argue that, after suitable extension, these methods may be useful for understanding and skillfully predicting the large-scale behaviour of marine ecosystems.

1. Introduction

Plankton population models have had a degree of success in explaining the dynamics of laboratory cultures (Fussman et al., 2000; McCauley et al., 1999). In such experiments, the plankton are kept *well mixed* by stirring and zooplankton swimming. This means that they move, or are moved, around the experimental volume sufficiently swiftly and randomly that they experience volumetric average concentrations over their generation time-scales (Dieckmann et al., 2000). Consequently, spatial variability within the laboratory experiment has by-design a negligible influence on the population dynamics.

At slightly larger scales (tens of metres or less) in the ocean surface mixed layer, turbulent currents might be expected to do a good job of creating well-mixed conditions. Tracer experiments (Okubo, 1971) suggest an order-of-magnitude turbulent 'eddy-mixing' timescale of between 0.01 and 1 day for mixed layer volumes of scale 10 m. Plankton populations with typical generation timescales of 1 day are therefore likely to be well mixed on these scales.

A crucially important feature of the oceans, however, is that they mix material slower over larger spatial scales (Okubo and Levin, 1980). In fact, Okubo (1976) proposes a mixing rate $\lambda_a \approx 120L^{-0.85}$ day^{-1}, plus or minus an order of magnitude, for an ocean scale of L m (obtained from the Okubo, 1976 relation: $K(L) = 0.068L^{1.15}$ cm^2 s^{-1} for L cm, by dividing by L^2 and converting the units). Consequently, at scales larger than $L = 10$ m it is not generally safe to assume well-mixed plankton populations. A plankton population that is not well mixed may not obey the same dynamics as a well mixed one, because of dynamical *nonlinearity*: laboratory population growth rates usually do not depend just on population size but also on (population size)^2 and perhaps higher powers. Dynamical nonlinearity acting on spatial variability can distort the coarse-scale (mean-field) population dynamics. This may lead to failure of the *mean field approximation* (MFA), whereby the population dynamics are extrapolated from the fine to the coarse scale. For plankton populations, this failure could be very serious, as demonstrated for a simplified plankton model by Brentnall et al. (2003) (hereafter B03). Failure of the MFA could be endemic in plankton modelling, where well-mixed laboratory population dynamics are often assumed to hold true over ocean model grid cells ranging in scale from 100 m in regional models to 100 km in global ocean models.

The most obvious, and currently prevalent, method of accounting for fine-scale variability in plankton ecosystems is to increase the explicit spatial resolution of the model (i.e., the

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number of grid cells). However, this places heavier demands on data and model inputs (forcings, initial/boundary conditions) to accurately constrain extra degrees of model freedom when fitting the model and making predictions. Moreover, the added computational burden may impose practical restrictions e.g., on the spatio-temporal range of the model run, or the number of times it may be re-run with different parameter values, which in turn may limit our ability to make, and assess the robustness of, model predictions for different scenarios e.g., changes in climate.

An alternative, long-familiar to the turbulence modelling community, is to model higher moments of the unresolved variability as well as the mean fields (Reynolds, 1895). Hence, fine scales are resolved 'implicitly' in terms of their effect on larger scales. Over recent decades, a host of 'turbulence closure' models, themselves derived from models used in engineering, have been applied to model the physics of the ocean mixed layer and horizontal boundary layers (see Sander, 1998; Umlauf and Burchard, 2005 for general reviews, or Carniel et al., 2007 for an oceanographic summary). These account for the effect of advective nonlinearity acting on unresolved variability in physical/biological fields to produce mean turbulent fluxes, also known as the 'transport Reynolds terms' (Lévy, 2006). Similar techniques have also been applied to coarse-resolution large-scale ocean models to parameterise the effects of unresolved mesoscale eddies (e.g., Gent and McWilliams, 1990; Gent et al., 1995). Modification of the standard eddy-diffusivity approach to parameterising turbulent fluxes to allow for the finite lifetime of reactive scalars such as plankton has been suggested by Pasquero (2005).

However, apparently no attempt has been made to implicitly resolve the statistical effect of *biological* nonlinearity on unresolved variability in plankton ecosystems, i.e., the 'biological Reynolds term' (Lévy, 2006). This is surprising, given that the biological dynamics usually involves nonlinearity that is of higher order than the quadratic nonlinearity of advective transport, and the spatial variability in plankton concentrations seen in data is usually very high (e.g., Martin et al., 2005), suggesting that the size of these neglected biological Reynolds terms may be very significant.

In this paper, simple two-component, 2D 'reaction–diffusion' plankton models are used as high-resolution simulations (HRSs). The grid-cell scale populations react via a set of continuous-time, deterministic biological dynamics, identical in every grid cell, and interact with nearest-neighbour cells by standard linear mixing. Spatial heterogeneity is only provided by variable initial conditions, and decays due to mixing and transience of the fine-scale biological dynamics. The accuracy of extrapolating the fine-scale biological dynamics to the domain-scale mean-field dynamics (the MFA) is investigated, as well as the possibility of improving on this approximation with implicit spatial resolution (ISR) models. These include 'spatial moment closure' (SMC) models, which assume central dominance of the phase space distribution, and a '2-spike approximation' (2SA), which assumes strong bimodality. The biological models and parameter sets are chosen to explore different strengths of biological nonlinearity, and mixing rates are varied to explore a range of scales relevant to practical ocean model grid cells.

Moment closure models have been used extensively in recent years in terrestrial ecology (e.g., Bolker and Pacala, 1997; Dieckmann et al., 2000; Keeling, 2000a, b; Keeling et al., 2002; Law and Dieckmann, 2000a, b; Law et al., 2003; Lewis and Pacala, 2000; Murrell et al., 2004; Ovaskeinen and Cornell, 2006; Pascual and Levin, 1999) and terrestrial epidemiology (e.g., Ferguson et al., 2001; Filipe and Gibson, 2001; Filipe and Maule, 2003). Readers familiar with this literature should note that the problem treated here is different on several accounts.

First, as argued above, plankton populations may be considered well mixed in the ocean at the laboratory scale ($<10\,\mathrm{m}$). Therefore, rather than starting with an individual-based model (IBM), we start with a population model for the laboratory scale, which then needs to be modified somehow to work on the (much larger) ocean grid cell scale.

Second, land plants are tethered to a solid substrate and act spatially only when they reproduce, dispersing seeds or pollen broadly via air or animal movement on a timescale much shorter than that of plant growth. By contrast, phytoplankton are fully committed to their liquid environment: they are shifted around continuously by ocean currents ('plankton' deriving from the Greek for 'drifter'), and reproduce locally.

Third, in contrast to terrestrial systems, marine primary producer/consumer populations are generally large (>100 individuals) at the scale of the laboratory, at least if the consumers are microzooplankton. This suggests that *deterministic* models may be applicable to phytoplankton/zooplankton population dynamics (Renshaw, 1991). If the zooplankton are interpreted as mesozooplankton, which are only moderately numerous ($O(10–100)$) at the laboratory scale, it may be necessary to include demographic stochasticity at the level of fine-scale populations (Vainstein et al., 2007). The methods used in this paper may be generalised to account for this (e.g., Rodriguez and Tuckwell, 1996).

Hence deterministic reaction–diffusion equations are used as 'simulation' models in this study. This is not to deny that stochastic IBMs with local (Martin, 2004) and non-local interactions (Birch and Young, 2006; Flierl et al., 1999; Hernández-García and López, 2004) may be necessary for deriving population dynamics at higher trophic levels—perhaps mesozooplankton and higher. However, simulating realistic numbers of individual mesozooplankton in even a single ocean model grid cell may be computationally unfeasible. IBMs might be used to derive fine-scale, deterministic population behaviour using 'moment closure' as understood in terrestrial applications (see next paragraph). However, there remains the problem of extrapolating the fine-scale deterministic population dynamics to coarser scales for ocean models. An alternative approach might be to let simulated 'super-individuals' or 'agents' each represent large numbers of real individuals (Scheffer et al., 1995; Batchelder et al., 2002; Woods, 2005).

Consequently, the use of moment closure in this study has a more 'classical' flavour. In terrestrial ecology, it has been used to approximate the average behaviour of a stochastic IBM over a computationally expensive 'ensemble' of runs. The result is typically a closed set of partial integro-differential equations for the first moments (as functions of time) and second moments (as functions of time and spatial lag), derived using 'closure assumptions' to approximate the effects of third-order moments on the dynamics of the second moments (Murrell et al., 2004). By contrast, in the problem treated here, little is gained by just transforming from one set of finely resolved, partial differential equations (PDEs) in (time, real space) to another set of finely resolved PDEs in (time, lag space), even if the higher-order moments can be successfully approximated. However, it is shown herein that the effect of non-zero lag second moments on the zero-lag second moments can often be neglected without much loss of accuracy. The result is an SMC model of complexity comparable to the MFA.

The paper is ordered as follows. In Section 2 (and the Appendices) two ISR methods are discussed in a general context: SMC and the *n*SA. SMC is applied to a general, two-component reaction–diffusion model, and numerical methods are detailed. In Section 3 three examples are investigated with different strengths of biological nonlinearity, obtained by varying the functional