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Plankton cycles disguised by turbulent advection
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Summary
Mathematical models used to represent plankton dynamics often display limit cycle behavior in a range of realistic parameter values. However, experimental data do not show evidence of plankton oscillations besides externally-driven seasonal blooms, casting doubts on the validity of the models themselves. In this work we show that spatial-temporal variability, coupled with advection by mesoscale turbulence, can disguise limit cycle behaviour to the point that it cannot be detected in fixed-point measurements of plankton abundance. The results presented here have more general implications as they indicate that the behaviour of ecosystem models in the presence of advection can be very different from that occurring for homogeneous conditions. Care should thus be exercised in drawing general conclusions from the analysis of homogeneous ecosystem models.

Keywords:
Aquatic Ecosystems, Plankton Dynamics, Mesoscale Turbulence, Advection of Biological Tracers, Spatial Ecology.
1 Introduction

Theoretical studies of population biology in aquatic ecosystems are often based on the use of spatially-homogeneous descriptions, that are formalized in terms of ordinary differential equations. This type of approach led to the discovery that some of the standard models used to represent plankton dynamics in the marine ecosystem display limit-cycle behavior for standard functional representations of biological processes and for realistic parameter values, see e.g. Steele and Henderson (1992); Truscott and Brindley (1994); Fasham (1995); Edwards and Brindley (1996); Ryabchenko et al. (1997); Edwards and Brindley (1999); Edwards and Yool (2000); Gibson et al. (2005). However, field observations do not support the presence of self-sustained oscillations in plankton abundance, besides the seasonal blooms driven by variations in the control parameters (light and nutrient availability and mixed-layer depth).

The discrepancy between theoretical predictions and experimental evidence can be reconciled by observing that plankton distributions are spatially inhomogeneous and population dynamics takes place in a turbulent ocean. Horizontal and vertical turbulent diffusion can significantly affect plankton dynamics, see e.g. Okubo (1980); Medvinsky et al. (2001); Martin (2003); Hillary and Bees (2004); Huisman et al. (2006). Mesoscale features such as vortices, fronts and jets advect plankton and nutrient concentrations on space scales of several tens of km and time scales of a few days, comparable with the time scales of biological reactions (Abraham, 1998; Flierl and McGillicuddy, 2002; Martin et al., 2002; Levy et al., 2001; Pasquero et al., 2005). The interplay of advection and diffusion can also change the dynamics of reactive tracers, see e.g. Richards and Brentnall (2006) and references therein for a recent study of plankton relaxation oscillations. One can thus wonder whether the conclusions drawn from the analysis of homogeneous conditions still hold in a turbulent, heterogeneous environment.

In this work we address this issue from a different perspective and numerically investigate the detectability of limit-cycle behavior in spatially-extended plankton systems characterized by the simultaneous presence of spatially-inhomogeneous nutrient input and turbulent advection at the mesoscales. We show that the coupling of inhomogeneity and advection can lead to the practical undetectability of limit-cycle behavior in plankton time series, even though it is present in the corresponding homogeneous system. The results presented in this work can have general implications on the study of population biology in spatially-extended systems: Turbulent advection and spatial inhomogeneity can significantly alter the conclusions drawn from the analysis of homogeneous ecosystem models.

2 Ecosystem model

We adopt a standard three-compartment (Nutrient-Phytoplankton-Zooplankton, NPZ) model of the lower trophic levels in the marine ecosystem that displays self-sustained oscillations (Edwards and Yool, 2000). The precise form of the system is not crucial, as we simply need an ecosystem model capable of displaying self-sustained oscillations in homogeneous conditions. In the following, we consider the effect of spatial inhomogeneities on the system dynamics and study the effect of turbulent advection on spatial scales larger than a few km, where the motion is predominantly horizontal (Abraham, 1998; Flierl and McGillicuddy,
2002; Martin et al., 2002; Pasquero et al., 2005). Consistently, we focus on the vertically-integrated nutrient and plankton concentrations and discard explicit vertical motions.

The model equations used in this work are written as:

\[
\frac{\partial N}{\partial t} + \mathbf{u} \cdot \nabla N = s(N_0 - N) - \beta \frac{N}{k + N} P \left(1 - \frac{P}{\gamma}\right) + (1 - \alpha) \frac{\lambda P^2}{\mu^2 + P^2} Z,
\]

\[
\frac{\partial P}{\partial t} + \mathbf{u} \cdot \nabla P = \beta \frac{N}{k + N} P \left(1 - \frac{P}{\gamma}\right) - \frac{P^2}{\mu^2 + P^2} Z,
\]

\[
\frac{\partial Z}{\partial t} + \mathbf{u} \cdot \nabla Z = \alpha \frac{\mu^2 P^2}{\mu^2 + P^2} Z - \omega Z^2,
\]

where \( t \) is time in days, \( N, P, Z \) are the concentrations of nutrient, phytoplankton and zooplankton averaged over the depth of the mixed layer and expressed in terms of a common currency (grams of carbon per cubic meter, \( g \text{C m}^{-3} \)), \( \nabla \) is the horizontal gradient and \( \mathbf{u} \) is the horizontal velocity field. \( N_0 \) is the deep-water nutrient concentration below the mixed layer, \( s \) is the vertical exchange rate of water at the base of the mixed layer and \( k \) is the half-saturation constant for nutrient uptake. The parameters \( \beta \) and \( \gamma \) are the maximum growth rate and the carrying capacity of phytoplankton, \( \alpha \) is zooplankton efficiency in transforming phytoplankton into zooplankton biomass, \( \lambda \) is the maximum zooplankton grazing rate, \( \mu \) is the half-saturation coefficient for zooplankton grazing and \( \omega \) gives the rate of zooplankton mortality. This specific model adopts a Holling type II form for phytoplankton growth and a Holling type III form for zooplankton grazing. The last term of the equation for the nutrient concentration is a regeneration term where the part of phytoplankton biomass that is not transformed into zooplankton is regenerated as nutrient. The model has a net source term in the nutrient input, \( s(N_0 - N) \), and a net biomass loss in the zooplankton mortality term, \(-\omega Z^2\). Quadratic mortality is used to close the system and parameterise the effect of predation by higher trophic levels (Steele and Henderson, 1992). The relaxation form of the nutrient input chosen here provides a simplified representation of turbulent vertical exchanges between the mixed layer and the deeper ocean, and it can be used to describe nutrient input due to turbulent upwelling. As discussed in Pasquero et al. (2005), explicit export of nutrient and plankton in downwelling regions can usually be discarded in a simplified model such as the one adopted here, owing to the fact that downwelling takes place in nutrient-poor areas.

Without advection (\( \mathbf{u} = 0 \)) and for spatially homogeneous conditions, model (1) displays limit cycle behavior in an extended parameter range. Figure 1a shows an example of self-sustained oscillations for the parameter values \( N_0 = 0.6 \text{ gC m}^{-3} \), \( s = 0.05 \text{ d}^{-1} \), \( k = 0.03 \text{ gC m}^{-3} \), \( \beta = 1 \text{ d}^{-1} \), \( \gamma = 1 \text{ gC m}^{-3} \), \( \mu = 0.035 \text{ gC m}^{-3} \), \( \alpha = 0.25 \), \( \omega = 0.25 \text{ (gC)}^{-1} \text{ m}^3 \text{ d}^{-1} \), and \( \lambda = 0.6 \text{ d}^{-1} \). In this case, the period of the self-sustained oscillations is \( T \approx 41 \) days. Further details on this particular model are given in Steele and Henderson (1992) and Edwards and Yool (2000). Figure 1b shows the amplitude and period of the self-sustained oscillations as a function of \( \beta \), and figure 1c shows a region of the \( \beta - s \) parameter plane where limit-cycle behaviour is present. To elucidate the system’s behaviour more clearly, here we do not explicitly include seasonal variability of the growth rate, \( \beta \) (associated with light availability), and of the relaxation rate, \( s \) (associated with variations in the mixed-layer depth). We shall return to this point in Section 4.

The presence of spatial dependence in nutrient and plankton distributions calls for considering the effects of diffusion and advection. Some of past studies focused on the smooth-
Figure 1: (a) \( N, P \) and \( Z \) time series from the ecosystem model (1) for the set of parameter values leading to self-sustained oscillations as given in the text. (b) Amplitude and period of the self-sustained oscillations in phytoplankton concentration as a function of phytoplankton growth-rate, \( \beta \). All other parameters are as in panel a. (c) Classification of the model solutions as obtained from linear stability analysis. The shaded area indicates the region in parameter space where the system settles on a stable limit cycle, while the white region corresponds to the presence of one stable steady state. The two crosses indicate the parameter values used in the simulations described in section 4.
ing and/or destabilising role of horizontal and vertical turbulent diffusion (Okubo, 1980; Matthews and Brindley, 1997; Huisman et al., 2006), on the effects of diffusion on limit-cycle dynamics (Malchow and Shigesada, 2001; Edwards and Yool, 2000; Medvinsky et al., 2001; Gibson et al., 2005), and on synchronisation of oscillations in space (Hillary and Bees, 2004). The role of advection has been studied for example by Abraham (1998); Flierl and McGillicuddy (2002); Martin et al. (2002); Levy et al. (2001); Pasquero et al. (2005), and the interplay between advection and diffusion has been explored by Neufeld et al. (1999); Hernandez-Garcia et al. (2002); Richards and Brentnall (2006), see also Martin (2003) for a review on plankton patchiness and its possible dynamical causes.

3 Advection by ocean mesoscale turbulence

We simulate horizontal advection at the ocean mesoscale by integrating the barotropic quasigeostrophic (QG) equation (Pedlosky, 1987; Salmon, 1998), which provides a simplified dynamical description of mid-latitude open-ocean motions. The horizontal turbulent velocity field in the mixed layer is determined by the equation

\[
\frac{Dq}{Dt} = F + (-1)^{p-1} D_p \nabla^{2p} q + (-1)^{r-1} D_r \nabla^{2r} q
\]

where \( q \) is vorticity, \( q = \nabla^2 \psi \), \( \psi \) is the streamfunction, \( \nabla \) is the horizontal gradient and the two-dimensional, non-divergent velocity field \( u = (u, v) \) is given by \( u = -\partial_y \psi \) and \( v = \partial_x \psi \). The forcing \( F \) is obtained by fixing the energy spectrum at a given forcing wavenumber, \( k_F \). Dissipation is provided by the sum of a hyperviscosity term acting at small scales, \((-1)^{p-1} D_p \nabla^{2p} q\) with \( p = 4 \), and by large-scale dissipation, \((-1)^{r-1} D_r \nabla^{2r} q\) with \( r = 1 \), used to dissipate energy that piles up at small wavenumbers due to the inverse energy cascade (Babiano et al., 1987; Elhmaidi et al., 1993; Pasquero et al., 2001).

The turbulent flow described by equation (1) is characterized by the presence of coherent mesoscale eddies which dominate the transport properties of the flow (McWilliams, 1984; Babiano et al., 1987; Elhmaidi et al., 1993; Provenzale, 1999). Barotropic turbulence has been used to study the effect of oceanic advection on the coexistence of competing plankton species (Bracco et al., 2000) and to assess the impact of the spatial-temporal variability of nutrient input on primary productivity (Pasquero et al., 2004, 2005). The use of stratified, baroclinic QG turbulence provides similar results, as transport and mixing in baroclinic and barotropic QG flows are very similar (Bracco et al., 2004).

Equation (1) is integrated using a pseudo-spectral method and a third-order Adams-Bashforth time integration scheme in a doubly-periodic square domain with size \( L = 256 \) km and spatial resolution \( \Delta = 0.5 \) km. The forcing scale is one tenth of the domain size. The turbulent field is characterized by an Eulerian decorrelation time \( T_E = 3.6 \) days and r.m.s. velocity fluctuation \( \sigma = 4 \) cm/s, in the appropriate range for mid-ocean conditions.

The turbulent flow is evolved to a statistically stationary state prior to its use in the runs with biological tracers.\(^1\) Once the flow has reached a statistically stationary state, we integrate the dynamics of biological tracers adopting the Lagrangian approach described in

\(^1\)The resolution adopted here, \( \Delta = 0.5 \) km, is below the range where QG turbulence provides an adequate description of ocean turbulence. This high resolution is adopted only for assuring the numerical convergence of the solutions, and the fluid flow is smooth below a scale of a few km. The representation of sub-mesoscale
Pasquero et al. (2004). Here, \(512 \times 512\) ecosystem-carrying fluid elements are advected in the two-dimensional turbulent flow described by eq. (1). Each parcel represents a given water volume and it is assumed to have homogeneous properties. Owing to the fact that our fluid volumes have a linear size of 0.5 km, we discard mixing of biological tracers between different fluid parcels. The concentration fields of biological tracers are then obtained from the distribution of fluid elements.

In the following, we study the fate of self-sustained oscillations when the nutrient relaxation rate, \(s\), is variable in space. In such conditions, we shall study the temporal variability of plankton abundance in time series obtained by either recording the concentrations in a single given fluid parcel (Lagrangian measurement) or at a “measurement station” at a fixed point in the domain (which we define as a mean over \(2 \times 2\) grid cells, i.e., a square with side 1 km), corresponding to an Eulerian measurement.

4 Spatial-temporal variability in model parameters

We consider the simplest configuration where spatial variability and advection are both present. All model parameters are kept constant in space and time, except for the nutrient input relaxation rate, which is allowed to vary in space. To this end, we assign the value \(s = s_f = 0.05\, \text{d}^{-1}\) inside a zonal strip of width 128 km and a slightly lower value, \(s = s_n = 0.03\, \text{d}^{-1}\), in the remaining portion of the domain. In the case of a homogeneous ecosystem, the value \(s_n\) would lead to steady-state behavior, while \(s_f\) is in the parameter range of self-sustained oscillations (see figure 1c). Figure 2 shows one snapshot of the simulated phytoplankton field. The strip of enhanced vertical exchange rate is placed in the middle of the domain and the integration starts from a homogeneous distribution of the biological tracers.

Figure 3 shows examples of Lagrangian and Eulerian time series of nutrient, phytoplankton and zooplankton abundances that illustrate the typical effect of advection on limit-cycle behaviour. For the sake of simplicity, here we have taken the control parameters to be constant in time.

In the case of Lagrangian time series, the repeated passage of the fluid parcel from regions where \(s\) is in the range of limit-cycle behaviour to regions where the value of \(s\) corresponds to a fixed point, and vice versa, leads to a modulation of the amplitude of the oscillations and to the presence of transients from one attractor type to the other. If the transitions back and forth from the stable point to the limit cycle are frequent, the oscillations do not have time to reach the asymptotic amplitude and the system can jump back to the fixed point before a full cycle is completed. For this reason, high fragmentation of upwelling areas (for example, two stripes of width 64 km instead of one strip of 128 km) can significantly challenge the detection of oscillatory behavior.

In the case of Eulerian measurements, shown in fig. 3b, one observes a complete obliteration of the self-sustained oscillations. In the course of time, different fluid parcels pass by the measurement site. Even though each particle could have a remnant of self-sustained oscillations, different particles have a different history of alternance between regions with ocean turbulence on smaller scales and of its effects on biological tracers requires the use of primitive equation models which resolve the vertical velocity field (Levy et al., 2001).
Figure 2: Snapshot of the phytoplankton concentration after 110 days of integration of model (1). Nutrient, phytoplankton and zooplankton are advected by barotropic turbulence, eq.(1). The vertical exchange rate is $s = s_f = 0.05 \, d^{-1}$ in the central zonal strip with side 128 km and $s = s_n = 0.03 \, d^{-1}$ elsewhere. The horizontal dashed lines indicate the edges of the strip. The simulation started from a homogeneous distribution of nutrient and of biological tracers.

Figure 3: Time series of nutrient, phytoplankton and zooplankton from a Lagrangian measurement in an individual fluid parcel moving with the flow (panel a) and from an Eulerian measurement at a fixed position in space at the edge of the strip of enhanced vertical exchange rate (panel b).
Figure 4: Average power spectra of phytoplankton abundance from Lagrangian (solid) and Eulerian (dashed) time series. The Lagrangian spectrum is the average of the spectra computed from five different trajectories and the Eulerian spectrum is the average of the spectra from five different measurement sites located at the edge of the strip with enhanced vertical diffusivity. Qualitatively analogous results are found for different choices of the positions of the Eulerian measurement sites.
high and low exchange rates and thus reach the limit-cycle behavior with a different phase. As a result, the continuous advection of different parcels recorded at the measurement site, combined with the de-phasing effect due to spatial inhomogeneity completely masks the limit-cycle behavior. Figure 4 shows the power spectra of phytoplankton abundance averaged respectively over five Lagrangian trajectories and over five Eulerian time series measured at different positions at the boundary between the two regions. While a broad peak at the limit-cycle period is still visible in the power spectrum from the Lagrangian measurements, no evidence of the self-sustained oscillations is present in the Eulerian record.

The results presented here are quite general, and they hold also when other model parameters become space-dependent (e.g., $\beta$) and for different versions of the NPZ model. We have explored a case for which the values of $s$ in the two regions are such that a limit cycle is always present but its characteristics are heterogeneous, i.e., the system undergoes oscillations with different amplitude and frequency in the two regions. Also in this case, the Eulerian time series measured in any of the two regions do not allow for clear identification of the oscillatory behavior.

The above results have been obtained by assuming spatial variability of one of the control parameters and spatially homogeneous initial conditions. The case with spatially-homogeneous control parameters and inhomogeneous initial conditions leads to a reduction of the amplitude of self-sustained oscillations in Eulerian time series, but not to their complete disappearance. This happens for both random and structured initial conditions, such as an initial distribution of $N$, $P$ and $Z$ of the form $\cos(nx)\cos(my)$ with various integer values of $m$ and $n$.

On the other hand, when inhomogeneous (random or cos-like) initial conditions are used together with a spatially-inhomogeneous distribution of the control parameters, the smearing out of the limit cycle is emphasized. In this case, limit cycles are completely disguised in Eulerian time series and strongly reduced in Lagrangian data, similarly to what is shown in previous figures. This confirms that the spatial inhomogeneity of the control parameters is the true responsible for the practical undetectability of limit cycles in Eulerian oscillations.

Self-sustained oscillations are depressed also in the case of a homogeneous ecosystem model subject to temporal variations in some of the parameters. In particular, seasonal variations leading to plankton blooms damp the amplitude of the self-sustained oscillations even in the absence of advection and spatial inhomogeneity, although they do not completely obliterate the limit-cycle behaviour. When seasonal variability is coupled with spatial variability of the parameters and turbulent advection, then self-sustained oscillations completely disappear from Eulerian time series.

5 Summary and conclusions

In this work we have shown that the interplay of horizontal advection and spatial-temporal parameter variations can lead to the undetectability of self-sustained oscillations. To this end, we have used a simple model of nutrient-phytoplankton-zooplankton dynamics that displays limit-cycle behavior under homogeneous conditions. Adopting a barotropic QG model to represent advection by mesoscale turbulence, we have shown that the plankton oscillations become undetectable in Eulerian time series whenever nutrient input displays
Similar results are obtained with other ecosystem models capable of generating self-sustained oscillations, and for variations in other control parameters (e.g., the phytoplankton growth rate). Analogously, the details of the model used to represent horizontal advection do not affect the general behaviour revealed by this study. Interestingly, the temporal variability of the control parameters leads to a similar damping of the amplitude of self-sustained oscillations, although not to their complete obliteration. On the other hand, the simultaneous presence of temporal and/or spatial variability of the control parameters and of horizontal advection further enhances the results reported here.

Clearly, the fact that limit-cycle behavior can be disguised by advection does not necessarily imply that self-sustained oscillations are a real property of plankton dynamics. Our results simply show that self-sustained oscillations, when and whether they were present in homogeneous conditions, can become undetectable in Eulerian time series. Interestingly, Lagrangian signals can keep a sign of the limit-cycle behaviour. Thus, the analysis of Lagrangian time series provided by freely floating drifters could help assessing the question of whether plankton abundance displays self-sustained oscillations in homogeneous conditions.

A general conclusion of this work is that advection drastically impacts the behaviour of homogeneous ecosystem models. Inferences drawn from the analysis of homogeneous models should thus be taken with caution. Horizontal advection and dispersion should always be regarded as important players in aquatic ecosystem dynamics.

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Figure captions

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