



## Original Research Article

# Plankton blooms and patchiness generated by heterogeneous physical environments



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## ABSTRACT

Microscopic turbulent motions of water have been shown to influence the dynamics of microscopic species living in that habitat. The number, stability, and excitability of stationary states in a predator–prey model of plankton species can therefore change when the strength of turbulent motions varies. In a spatial system these microscopic turbulent motions are naturally of different strength and form a heterogeneous physical environment. Spatially neighboring plankton communities with different physical conditions can impact each other due to diffusive coupling. We show that local variations in the physical conditions can influence the global system in form of propagating pulses of high population densities. For this we consider three different local predator–prey models with different local responses to variations in the physical environment. The degree of spatial heterogeneity can, depending on the model, promote or reduce the number of propagating pulses, which can be interpreted as patchy plankton distributions and recurrent blooms.

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## 1. Introduction

Organisms in the ocean crucially depend on their physical environment. Therefore, biological–physical interactions have a great impact on the spatial distribution, growth, and dominance of species. Of particular interest are flow patterns in the ocean which influence marine organisms on all spatial scales (Mann and Lazier, 1996). Large-scale flow patterns across the equatorial Pacific which are related to the El Niño phenomenon considerably diminish the plankton and subsequently the fish production at the South American coast (Marzeion et al., 2005; Heinemann et al., 2011). Mesoscale hydrodynamic flow patterns like jets and vortices are responsible for the emergence of filamental plankton patterns (Tél et al., 2005; Hernández-García et al., 2002; Sandulescu et al., 2007) which in turn have a large impact on growth, coexistence, and dominance of species (Hernández-García and López, 2004; Neufeld and Hernández-García, 2010; Scheuring et al., 2003; Bastine and Feudel, 2010). Abraham (1998), McKiver and Neufeld (2011), Hernández-García et al. (2002) and Tzella and Haynes (2007) used a carrying capacity

which can be transported by the flow, but has a fixed spatial distribution of its source, to explain the generation of plankton patchiness. Since the seminal paper by Abraham (1998), the influence of stirring and mixing in the ocean on plankton patchiness and blooms has become an important topic of current research.

In addition to the already mentioned large and mesoscale hydrodynamic flows, small-scale turbulence contributes to the redistribution of nutrients as well as the behavior of plankton, and has therefore been considered in various models.

There are many studies, showing that turbulence can affect the behavior and health of plankton species themselves. Visser and Stips (2002) and Kiørboe and Saiz (1995) analyzed the effect of microscopic turbulence on encounter rates, feeding currents, signal detection, behavior, and prey selection of copepods. Visser et al. (2009) studied the optimal behavior of zooplankton in a turbulent environment. MacKenzie and Leggett (1991) quantified the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey. Metcalfe et al. (2004) modeled a plankton foodweb in environments with different turbulent levels and therefore different values of nutrient uptake rates (half-saturation coefficients) and predator–prey capture rates. Peters and Marrasé (2000) gave an overview of some experimental data from different laboratory

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studies and made some theoretical considerations. Peters et al. (2006) studied the effects of small-scale turbulence on the growth of two diatoms of different size in a phosphorus-limited medium. However, these studies have investigated the effect of turbulence on plankton species or communities from a “local” point of view. They have not taken into account systems of species which live in regions of different strength of turbulence and may be spatially connected.

Our aim is therefore to develop a model which couples plankton population dynamics to hydrodynamic motion, including the effect of the heterogeneous environment on biological growth. We further investigate if these effects can be a mechanism for plankton patchiness or plankton blooms.

In the following section, we point out some possible effects of turbulent environments on plankton systems and develop different models which take into account these impacts. We begin with “local” models consisting of ordinary differential equations that ignore spatial fluxes. Nevertheless, we show that the effects of turbulence included in those models can influence the number and stability of stationary states of the system.

We then extend the models by incorporating spatial dynamics. Our simulations show that a spatially inhomogeneous distribution of turbulence strength has varied impacts on the whole excitable system and is able to trigger or to suppress propagating pulses of high population concentrations, corresponding to plankton blooms and patchiness.

## 2. General biological model

Since our main focus is on plankton dynamics in aquatic environments, we consider phytoplankton  $P$  and zooplankton  $Z$  as the major components of the biological system.

We focus on excitable predator–prey models based on the model introduced by Truscott and Brindley (1994) to explain the emergence of large plankton blooms such as red tides:

$$\begin{cases} \frac{dZ}{dt} = \frac{aP^n}{h^n + P^n}Z - m_z Z^q, \\ \xi \frac{dP}{dt} = rP \left(1 - \frac{P}{K}\right) - \frac{aP^n}{h^n + P^n}Z, \end{cases} \quad (1)$$

where  $P$  denotes the phytoplankton density as the prey and  $Z$  is the zooplankton density corresponding to the predators. In the absence of predators,  $P$  grows logistically with the maximum per capita growth rate  $r$  until it reaches the carrying capacity  $K$ .  $P$  is grazed upon by  $Z$  with the maximal grazing rate  $a$ .  $h$  is the half-saturation density of prey, so that the factor  $(P^n)/(h^n + P^n) = 0.5$  for  $P = h$ . The type of functional response is defined by  $n$ . If  $n = 1$ , the predator grazes with a Holling-type II functional response. If  $n = 2$ , grazing is of Holling-type III.  $q$  gives the order of the predator mortality (Edwards and Yool, 2000). We analyze models with a linear predator mortality ( $q = 1$ ) and a model with quadratic mortality ( $q = 2$ ). A quadratic predator mortality is motivated by possible intraspecific competition or the existence of a top predator, which is not explicitly modeled.  $m_z$  is the predator’s per capita mortality rate.  $\xi$  is a factor describing the different timescales of the dynamics of the two different species (Sieber et al., 2007).

All quantities are non-dimensional in this paper (see Appendix A).

The predator–prey models have a trivial stationary state  $(P^{(1)}, Z^{(1)}) = (0, 0)$ , a semi-trivial stationary state  $(P^{(2)}, Z^{(2)}) = (K, 0)$ , and, depending on the set of parameters, one or more non-trivial stationary states in the positive quadrant of the phase-plane.

### 2.1. Possible effects of turbulent flows on the vital parameters and feeding behavior

In this section we point out how turbulent motion on the length scale of the diameter of plankton cells can influence the parameters of the system (1).

Experimental results show that in a low turbulent regime only insignificant effects on plankton organism can be observed (Peters and Marrasé, 2000). In an intermediate turbulent environment, positive effects on growth rates of phytoplankton and capture rates of zooplankton were measured; in highly turbulent environments insignificant or negative effects were found. However, negative effects were observed for unrealistically strong turbulence, which cannot be observed in oceans but only in cultures with artificial turbulence.

According to our aim to investigate the influence of small-scale turbulence on plankton growth, we consider two possible mechanisms of how turbulence can change the growth rates of phyto- and zooplankton. On the one hand, we assume that a higher turbulence level increases the zooplankton capture rate of phytoplankton. On the other hand, we incorporate a turbulence-dependent growth of phytoplankton in our model. For the latter, we suppose that turbulent mixing leads to a homogenization of the nutrient distribution reflected by a turbulence-dependent carrying capacity.

Regarding turbulence-dependent zooplankton growth, we base our model on some experimental results. Peters et al. (2006) observed more *Coscinodiscus* sp. (a species of diatoms) cells in a turbulent environment than under still water conditions with low nutrient concentrations. They explained this observation by comparing these experimental results to a model using the Michaelis–Menten nutrient uptake model with a turbulence-dependent half-saturation constant. Metcalfe et al. (2004) used the same ansatz and provided values for the half-saturation constant for copepods and ciliates between  $71 \text{ nmol P l}^{-1}$  in a non-turbulent environment and  $44 \text{ nmol P l}^{-1}$  in a turbulent environment with a high turbulent kinetic energy dissipation.

To study the impact of turbulence on the growth of zooplankton we adopt the ideas of Peters et al. (2006) and introduce a turbulence-dependent half-saturation constant  $h \equiv h(\text{turb})$  in the predator functional response. For an example, we illustrate this for the Holling-type III functional response  $g_{H3}$ :

$$g_{H3}(P, \text{turb}) := \frac{aP^2}{h^2(\text{turb}) + P^2}, \quad (2)$$

where  $P$  is the density of prey, and  $a$  the maximal ingestion rate of the predator. The normalized parameter  $\text{turb}$ , with  $0 \leq \text{turb} \leq 1$ , describes the relative strength of turbulence.

We define

$$h(\text{turb}) = \frac{h_0}{1 + \text{turb} \cdot c_h} \quad (3)$$

as the turbulence-dependent half-saturation density, where  $h_0$  is the maximal half-saturation density. The explicit dependence of  $h$  on  $\text{turb}$  can be influenced by the parameter  $c_h$ . We use this simple dependence on turbulence, but in a more complex model  $c_h$  can be a function of  $\text{turb}$  as well.

Regarding the turbulence-dependent phytoplankton growth in an environment with high nutrient concentration, we use a logistic model for the growth of phytoplankton. In a static environment, the cell depletes the nutrients in its near surrounding. New nutrients can enter this zone by molecular diffusion from the nutrient rich environment. If the population of the phytoplankton cells is very high, it might be that other cells deplete the near surrounding as well. Light can be diminished because of self-shading. In a turbulent environment clusters of cells will be segregated, the nutrient

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