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# Constructive effects of environmental noise in an excitable prey–predator plankton system with infected prey

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ABSTRACT

An excitable model of fast phytoplankton and slow zooplankton dynamics is considered for the case of lysogenic viral infection of the phytoplankton population. The phytoplankton population is split into a susceptible (S) and an infected (I) part. Both parts grow logistically, limited by a common carrying capacity. Zooplankton (Z) is grazing on susceptibles and infected, following a Holling-type III functional response. The local analysis of the S–I–Z differential equations yields a number of stationary and/or oscillatory regimes and their combinations. Correspondingly interesting is the behaviour under multiplicative noise, modelled by stochastic differential equations. The external noise can enhance the survival of susceptibles and infected, respectively, that would go extinct in a deterministic environment. In the parameter range of excitability, noise can induce prey–predator oscillations and coherence resonance (CR). In the spatially extended case, synchronized global oscillations can be observed for medium noise intensities. Higher values of noise give rise to the formation of stationary spatial patterns.

## 1. Introduction

Excitability is found in many natural systems. Examples include chemical reactions, neural systems and cardiovascular tissues, cf. Lindner et al. (2004) for a review. One important application in aquatic ecology is the modelling of recurrent phytoplankton blooms that might be generated through external excitations as temporary temperature or nutrient peaks (Truscott and Brindley, 1994; Beltrami, 1996; Freund et al., 2006) and that might have adverse effects on fisheries and aquaculture (Cosper et al., 1989; Okaichi, 2004). Biological control is one of the desirable countermeasures. There is some evidence that viral infections might accelerate the termination of phytoplankton blooms (Suttle and Chan, 1993; Bratbak et al., 1995; Jacquet et al., 2002; Gastrich et al., 2004). However, there is much less known about marine viruses and their role in aquatic ecosystems and the species that they infect, than about plankton patchiness and blooming, for reviews, cf. Fuhrman (1999) and Suttle (2005). Despite the increasing number of reports, the role of viral infection in the phytoplankton population is still far from understood.

Viral infections of phytoplankton cells can be lysogenic or lytic. The understanding of the importance of lysogeny is just at the beginning (McDaniel et al., 2002; Ortmann et al., 2002;

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Wilcox and Fuhrman, 1994; Jiang and Paul, 1998). There is some evidence that many environmentally important pollutants may be inducing agents for natural lysogenic viral production in the marine environment (Cochran et al., 1998). Contrary to lytic infections with destruction and without reproduction of the host cell, lysogenic infections are a strategy whereby viruses integrate their genome into the host's genome. As the host reproduces and duplicates its genome, the viral genome reproduces, too.

Mathematical models of the dynamics of virally infected phytoplankton populations are rare as well, the already classical publication is by Beltrami and Carroll (1994). More recent work is of Chattopadhyay et al. (2002, 2003). The latter deals with lytic infections and mass action incidence functions. Hilker and Malchow et al. have observed oscillations and waves in a phytoplankton–zooplankton system with Holling-type II (Malchow et al., 2004; Hilker and Malchow, 2006; Hilker et al., 2006) and III (Malchow et al., 2005) grazing under lysogenic viral infection and proportionate mixing incidence function (frequency-dependent transmission) (Nold, 1980; Hethcote, 2000; McCallum et al., 2001).

In this paper, we continue considering the latter case but focus on modelling the impact of multiplicative noise (Spagnolo et al., 2002, 2004; Allen, 2003; Anishchenko et al., 2003; Valenti et al., 2004, 2006) on the excitable local dynamics, i.e., noise-induced effects on interacting phytoplankton and zooplankton with Holling-type III grazing, in the sub-excitable parameter range in time and space.

## 2. The mathematical model

The Truscott–Brindley model (1994) for the prey–predator dynamics of phytoplankton $P$ and zooplankton $Z$ at time $t$ reads in dimensionless quantities:

$$\epsilon\frac{dP}{dt} = rP(1-P) - \frac{a^2P^2}{1+b^2P^2}Z, \tag{1}$$

$$\frac{dZ}{dt} = \frac{a^2P^2}{1+b^2P^2}Z - m_3Z. \tag{2}$$

There is logistic growth of the phytoplankton with intrinsic rate $r$ and Holling-type III grazing with maximum rate $a^2/b^2$ as well as natural mortality of zooplankton with rate $m_3$. The growth rate $r$ is scaled as the ratio of the current rate $r_{\text{cur}}$ and a fictive long-term mean $\langle r\rangle$.

Excitability is found for parameter ranges where the straight predator nullcline intersects the S-shaped prey nullcline to the left of its minimum at the only stable stationary solution. Intersections at the minimum or maximum of the predator nullcline lead to Hopf bifurcations, i.e., one finds limit cycles to the right of the minimum, etc.

The phenomenon of slow–fast predator–prey cycles in this model has been specified by Fernández et al. (2002). However, slow–fast cycles or processes with longer and shorter turnover times are well known in ecosystem dynamics. Prominent examples are forest–pest interactions with periodic massive outbreaks of insect pests (Ludwig et al., 1978; Rinaldi and Muratori, 1992a, b) or cyclic grazing systems with periodic collapses and recoveries of the vegetation (Noy-Meir, 1975; Rietkerk, 1998). Other sudden catastrophic regime shifts in ecosystems with long return times have been reviewed by Scheffer et al. (2001), Scheffer and Carpenter (2003) and Rietkerk et al. (2004), cf. also Carpenter and Turner (2000) and the whole *Ecosystems* issue including the work by Rinaldi and Scheffer (2000) on prey–predator food chain models.

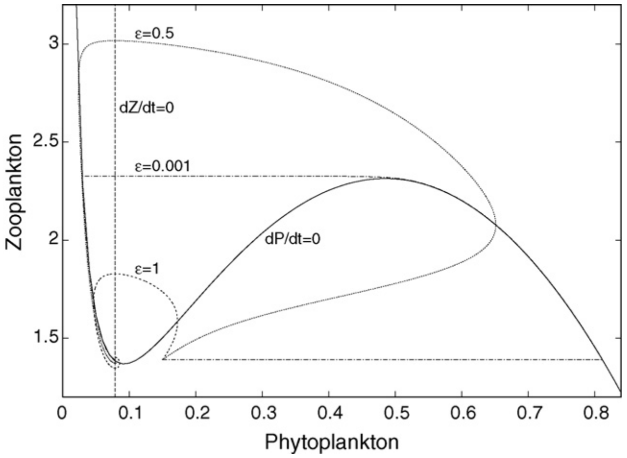

**Fig. 1 – Nullclines of the Truscott–Brindley model. Trajectories are given for $\epsilon = 1$, $\epsilon = 0.5$ and $\epsilon = 10^{-3}$. Other parameters: $r = 1.0$, $a = 4.0$, $b = 12.0$, $m_3 = 0.0525$.**

The parameter $\epsilon \ll 1$ even boosts the fast prey dynamics describing the high sensitivity and much faster response of the phytoplankton population to environmental changes like variations of temperature or nutrient supply. An example for nullclines and trajectories for decreasing $\epsilon$ after initial perturbation of the system is shown in Fig. 1.

For $\epsilon = 1$, the system almost immediately returns to the stationary state. For $\epsilon = 0.5$, the excitation of the system is already seen. However, for $\epsilon = 10^{-3}$, the trajectory is shot parallel to the abscissa to the temporary maximum of phytoplankton density at the right branch of stable solutions on the prey nullcline. Then, it slowly moves to the maximum of the nullcline, speedily falls back to the left stable branch and slowly approaches the stationary point again. The corresponding dynamics of the phytoplankton population can be seen in Fig. 2.

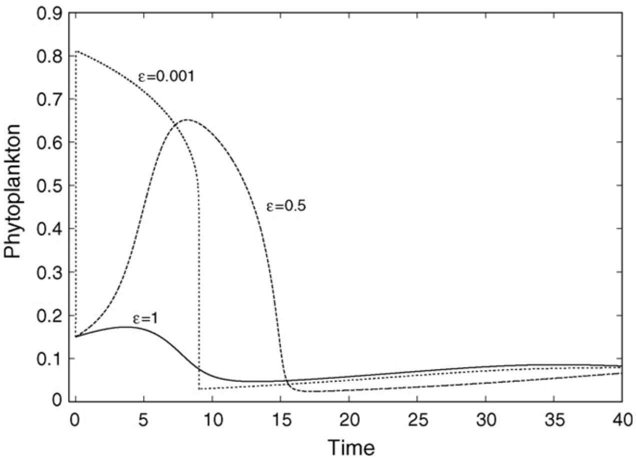

**Fig. 2 – Corresponding phytoplankton dynamics.**