Biological factors underlying regularity and chaos in aquatic ecosystems: Simple models of complex dynamics

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This work is focused on the processes underlying the dynamics of spatially inhomogeneous plankton communities. We demonstrate that reaction–diffusion mathematical models are an appropriate tool for searching and understanding basic mechanisms of complex spatio-temporal plankton dynamics and fractal properties of planktivorous fish school walks.

1. Introduction

1.1 Patterns in nonlinear nonequilibrium systems

The exploration of pattern formation mechanisms in complex nonlinear systems is one of the central problems of natural, social, and technological sciences (Haken 1977; Nicolis and Prigogine 1977; Weidlich and Haag 1983). The occurrence of multiple steady states and transitions from one to another after critical fluctuations, the phenomena of excitability, oscillations, waves and, in general, the emergence of macroscopic order from microscopic interactions in various nonlinear nonequilibrium systems in nature and society has required and stimulated many theoretical and, where possible, experimental studies.

The classical approach to the solution of the problem of the origin of spatial structures was first developed by Turing (1952) and then elaborated in the works of his followers (appropriate references can be found in Medvinsky et al 1997). The results obtained in the course of these investigations indicate that the initially uniform distribution of reacting components can become unstable. As the instability develops further, a spatially nonuniform distribution (a spatial structure) of activators and inhibitors of the reaction occurs. Turing pattern formation is based on the coupling of linear diffusion and nonlinear local kinetics of the reaction under conditions when the diffusivity of the activator is less than the diffusivity of the inhibitor. Fairly recent experimental work by de Kepper et al (1991) has demonstrated Turing structures in the context of chemical reactions.

A major unsolved problem with the Turing approach is that a clear identification of activators and inhibitors which could be involved in the formation of patterns of different nature: physico-chemical, biological or social, mainly remains to be absent and even seems to be hardly achievable. Now-a-days, more realistic theoretical approaches are in progress. They are able to account for complex spatio-temporal dynamics of open spatially confined systems in terms of the interaction between the intrinsic dynamics of the system and external forcing due to the impact of the system environment. In ecology, such an interaction can include both physico-chemical and biological factors. In this work we focus on the biological factors influencing the dynamics of aquatic communities. We study the role of predator invasion, planktivorous fish cruising, and the interaction of neighbouring habitats in the formation of the complex transient spatio-temporal plankton patterns which often occur in the ocean.

Keywords. Aquatic ecosystems; chaos; modelling; order; scaling
The paper is organized as follows. In § 1.2 we give a short review of the theoretical considerations underlying plankton dynamics and conclude that biological factors can play a key role in the emergence of plankton spatial structures. In § 2, we consider the spatio-temporal dynamics of an aquatic community in terms of a prey–predator (i.e. phytoplankton–zooplankton) system and demonstrate the efficiency of the two-species minimal model for describing pattern formation in plankton communities. In § 3, we develop a minimal mathematical model describing the interplay between plankton spatio-temporal pattern formation and planktivorous fish school cruising. We show that fish school walks can give rise to rather complex plankton dynamics. In turn, fish school trajectories depending on the plankton dynamics can manifest fractal and multifractal properties.

1.2 Plankton and models of plankton dynamics

Plankton are floating organisms of many different phyla, living in the pelagic of the sea, in freshwater or in larger rivers. They are to a large extent subjected to water movements (Sommer 1994, 1996; Baretta-Bekker et al. 1998). Their functional classification is based on trophic level, size and distribution. Autotrophs, i.e. primary producers, constitute phytoplankton whereas heterotrophs, i.e. consumers, include bacterioplankton and zooplankton. A differentiation in size classes is related to the retention by different mesh sizes of plankton nets and filters. There is picoplankton less than 2 μm, nanoplanктон 0.2–2 mm, macroplankton 2–20 mm and megaplankton greater than 20 mm (Raymont 1980; Baretta-Bekker et al. 1998).

In the 17th century, the Dutch pioneer microscopist Anton van Leeuwenhoek was probably the first human being to see minute creatures, which he called animalcules, in pond water (Hallegraeff 1988). The German Victor Hensen who organized Germany’s first big oceanographic expedition in 1889 (Hensen 1892; Porep 1970) introduced the term plankton (due to the Greek planktos = made to wander).

Phytoplankton are microscopic plants that drive all marine ecological communities and the life within them. Due to their photosynthetic growth, the world’s phytoplankton generate half of the oxygen that mankind needs for maintaining life and also absorb half of the carbon dioxide that may be contributing to global warming (Duinker and Wefer 1994). It is not only oxygen and carbon dioxide but there are also other substances and gases that are recycled by phytoplankton, e.g. phosphorus, nitrogen and sulphur compounds (Bain 1968; Ritschard 1992; Malin 1997). Hence, the phytoplankton is one of the main factors controlling the further development of the world’s climate and there is a vast literature supporting such a claim (Charlson et al. 1987; Williamson and Gribbin 1991).

Zooplankton are the animals in plankton. In marine zooplankton both herbivores and predators occur, herbivores graze on phytoplankton and are eaten by zooplankton predators. Together, phyto- and zooplankton form the basis for all food chains and webs in the sea. In its turn, the abundance of the plankton species is affected by a number of environmental factors such as water temperature, salinity, sunlight intensity, biogen availability etc. (Raymont 1980; Sommer 1994). Temporal variability of the species composition is caused by seasonal changes and, according to a concept going back to the seminal papers of Lotka (1925) and Volterra (1926), due to trophical prey–predator interactions between phyto- and zooplankton.

Because of their obvious importance, the dynamics of plankton systems have been under continuous investigations for more than a hundred years. It should be noted that practically from the very beginning, regular plankton studies have combined field observations, laboratory experiments and mathematical modelling. It was in the 19th century that fisheries stimulated an interest in plankton dynamics because strong positive correlations between zooplankton and fish abundance were found. The already mentioned German plankton expedition of 1889 was mainly motivated by fisheries interests. At the same time, fishery science began to develop. In the beginning of the 20th century, the first mathematical models were developed in order to understand and to predict fish stock dynamics and its correlations with biological and physical factors and human interventions (Cushing 1975; Gulland 1977; Steele 1977).

Contemporary mathematical modelling of phytoplankton productivity has its roots in the works of Fleming (1939), Ivlev (1945), Riley (1946), Odum (1956) and others. A review of the developments has been given by Droop (1983). Recently, a collection of the most frequently used models has been presented by Behrenfeld and Falkowski (1997).

The control of phytoplankton blooming by zooplankton grazing has been modelled first by Fleming (1939), using a single ordinary differential equation for the temporal dynamics of phytoplankton biomass. Other approaches have been the construction of data fitted functions (Riley 1963) and the application of standard Lotka–Volterra equations to describe the prey–predator relations of phytoplankton and zooplankton (Segel and Jackson 1972; Dubois 1975; Levin and Segel 1976; Vinogradov and Menshutkin 1977; Mimura and Murray 1978). More realistic descriptions of zooplankton grazing with functional responses to phytoplankton abundance have been introduced by Ivlev (1945) with a certain modification by Mayzaud and Poulet (1978). Holling-type response terms (Holling 1959) which are also known from Monod or Michaelis–Menten saturation models of enzyme kinetics.