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

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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 μ m, nanoplankton 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

(Michaelis and Menten 1913; Monod and Jacob 1961) are just as much in use (Steele and Henderson 1981; 1992a, b; Scheffer 1991a, 1998; Malchow 1993; Truscott and Brindley 1994a, b). Observed temporal patterns include the well-known stable prey-predator oscillations as well as the oscillatory or monotonic relaxation to one of the possibly multiple steady states. Excitable systems are of special interest because their long-lasting relaxation to the steady state after a supercritical external perturbation like a sudden temperature increase and nutrient inflow is very suitable to model red or brown tides (Beltrami 1989, 1996; Truscott and Brindley 1994a, b).

Concerning the temporal variability of plankton species abundance, an issue of particular interest concerns the limits of its predictability. At early stages, development of mathematical models of marine ecosystems was driven by the idea that the larger the number of species that were explicitly included into the model, the higher would be its predictive ability. As a result, a number of many-species models appeared allowing for a detailed structure of the food web of the community (De Angelis 1992; Jörgensen 1994; Yodzis 1994). However, the real predictive ability of this class of models is not very high and rarely exceeds a few weeks. Moreover, the increase of the number of the model agents may sometimes make the properties of the model even worse. This apparent paradox can be explained in terms of dynamical chaos (May 1974; see also § 2.3). It should be noted that although strict evidence of chaotic behaviour in natural populations is still absent, there are more and more strong indications in favour of its existence (Scheffer 1991b, 1998; Godfray and Hassell 1997; Huisman and Weissing 1999). Chaotic population dynamics changes essentially the very approach to system predictability (Scheffer 1991b), and makes conceptual few-species models of as much use as manyspecies ones. Moreover, few-species models can sometimes be even more instructive since they take into account only principal features of community functioning (Pascual 1993; Petrovskii and Malchow 1999, 2000b).

Another interesting problem is the dynamics of externally forced systems. Ideally periodic forcing appears rather naturally due to daily, seasonal or annual cycles, photosynthetically active radiation, temperature, nutrient availability etc. (Evans and Parslow 1985; Truscott 1995; Popova *et al* 1997; Ryabchenko *et al* 1997). Natural forcing is of course superposed by a certain environmental noise. A number of forcing models for parts of or the complete food chain from nutrients, phytoplankton and zooplankton to planktivorous fish have been investigated and many different routes to chaotic dynamics have been demonstrated (Kuznetsov *et al* 1992; Ascioti *et al* 1993; Doveri *et al* 1993; Rinaldi and Muratori 1993; Steffen and Malchow 1996a, b; Steffen *et al* 1997; Scheffer *et al* 1997; Scheffer 1998).

The abundance of plankton species is not only subject to temporal changes but also depends on space. Distinct spatial heterogeneity of plankton distribution (also known as patchiness) is found in many field observations (Fasham 1978; Steele 1978; Mackas and Boyd 1979; Greene et al 1992; Abbott 1993). This phenomenon takes place on all scales, from centimetres to kilometres. A number of explanations has been suggested, particularly, relating the spatial structure of a plankton system to marine turbulence (Platt 1972) or to the inhomogeneity of the temperature field in the ocean (Denmann 1976). A well-studied stripy plankton pattern is due to trapping of populations of sinking microorganisms in Langmuir circulation cells (Stommel 1948; Leibovich 1993). Other physically determined plankton distributions like steep density gradients due to local temperature differences, nutrient upwelling, turbulent mixing or internal waves have been reported too (Yoder et al 1994; Franks 1997; Abraham 1998).

On a small spatial scale of some tens of centimetres and under relative physical uniformity also differences in diffusive mobility of individuals and the ability of locomotion might create finer spatial structures, e.g. due to bioconvection and gyrotaxis (Platt 1961; Winet and Jahn 1972; Pedley and Kessler 1992; Timm and Okubo 1994). Till now, not for plankton but for certain bacteria, the mechanism of diffusion-limited aggregation (Witten and Sander 1981) has been proposed and experimentally proven to lead to the spatial fingering of colonies (Matsushita and Fujikawa 1990; Ben-Jacob *et al* 1992).

Thus, mathematical models of plankton population dynamics have not only to account for growth and interactions but also for spatial processes like random or directed and joint or relative motion of species as well as the variability of the environment. According to a widely accepted point of view, it is the interplay of phytoplankton and zooplankton, interactions and transport that yields the whole variety of spatio-temporal plankton structures, in particular the phenomenon of plankton patchiness (Fasham 1978; Okubo 1980). Mathematical modelling requires the use of reaction-diffusion and perhaps advection equations. A good introduction to the latter field is provided by Holmes *et al* (1994).

Since the classic paper by Turing (1952) on the role of nonequilibrium reaction-diffusion patterns in biomorphogenesis, dissipative mechanisms of spontaneous spatial and spatio-temporal pattern formation in a homogeneous environment have been of continuing interest in theoretical biology and ecology. Turing showed that the nonlinear interaction of at least two agent with considerably different diffusion coefficients can give rise to spatial structure. Segel and Jackson (1972) were the first to apply Turing's idea to a problem in population dynamics: the dissipative instability in the prey-predator interaction of phytoplankton and herbivorous copepods with higher herbivore motility. Levin and Segel (1976) suggested this scenario of spatial pattern formation for a possible origin of planktonic patchiness. Recently, local bistability, predator–prey limit-cycle oscillations, plankton front propagation and the generation and drift of planktonic Turing patches were found in a minimal phytoplankton–zooplankton interaction model (Malchow 1993, 1994) that was originally formulated by Scheffer (1991a), accounting for the effects of nutrients and planktivorous fish on alternative local equilibria of the plankton community.

Kierstead and Slobodkin (1953) and also Skellam (1951) were perhaps the first to think of the critical size problem for plankton patches, presenting what is known as the KISS model with the coupling of exponential growth and diffusion of a single population. Of course, their patches are unstable because this coupling leads to an explosive spatial spread of the initial patch of species with, surprisingly, the same diffusive front speed as the asymptotic speed of a logistically growing population (Luther 1906; Fisher 1937; Kolmogorov *et al* 1937).

Populations with an Allee effect (Allee 1931; Allee *et al* 1949), i.e. when the existence of a minimum viable number of species of a population yields two stable population states: extinction and survival at its carrying capacity, show a spatial critical size as well (Schlögl 1972; Nitzan *et al* 1974; Ebeling and Schimansky-Geier 1980; Malchow and Schimansky-Geier 1985; Lewis and Kareiva 1993; Petrovskii 1994). Population patches greater than the critical size will survive, the others will go extinct. However, bistability and the emergence of a critical spatial size do not necessarily require an Allee effect. Logistically growing prey with a parameterized predator of type II and type III functional response can exhibit two stable states and related hysteresis loops (Ludwig *et al* 1978; Wissel 1989).

The consideration of dynamic predation leads to the full spectrum of spatial and spatio-temporal patterns like regular and irregular oscillations, propagating fronts, target patterns and spiral waves, pulses as well as stationary spatial patterns. Many of these structures were first known from oscillating chemical reactions (Field and Burger 1985), but have never been observed in natural plankton populations. However, spirals have been seen in the ocean as rotary motions of plankton patches on a kilometre scale (Wyatt 1973). Furthermore, they have been found important in parasitoid-host systems (Boerlijst et al 1993). For other motile microorganisms, stationary structures and traveling waves like targets or spirals have been found in various bacteria and in the cellular slime mould Dictyostelium discoideum (Platt 1961; Adler 1966; Adler and Templeton 1967; Gerisch 1968, 1971; Keller and Segel 1970, 1971a, b; Segel and Stoeckly 1972; Nanjundiah 1973, 1985, 1998; Segel

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1977; Newell 1983; Alt and Hoffman 1990; Ivanitsky *et al* 1991, 1994; Medvinsky *et al* 1991, 1993a, b; 1994a, b; Siegert and Weijer 1991; Steinbock *et al* 1991; Reshetilov *et al* 1992; Vasiev *et al* 1994; Höfer *et al* 1995). These cells are chemotactic species, i.e. they move actively up the gradient of a chemical attractant. Chemotaxis is a kind of density-dependent cross-diffusion and it is an interesting open question whether there is prey taxis in plankton or not.

An important point is that allowing for spatial dimensions of the plankton community functioning provides also new routes to chaotic dynamics. The emergence of diffusion-induced spatio-temporal chaos has been found by Pascual (1993) along a linear nutrient gradient. Chaotic oscillations behind propagating diffusion fronts are found in a prey-predator model (Sherratt *et al* 1995, 1997); a similar phenomenon is observed in a mathematically similar model of chemical reactor (Merkin *et al* 1996; Davidson 1998). Recently, it has been shown that the appearance of chaotic spatio-temporal oscillations in a prey-predator system is a somewhat more general phenomenon and must not be attributed to front propagation or to inhomogeneity of environmental parameters (Petrovskii and Malchow 1999, 2000b).

Conditions for the emergence of three-dimensional spatial and spatio-temporal patterns after differential-flowinduced instabilities (Rovinsky and Menzinger 1992) of spatially uniform populations were derived by Malchow (1996, 1998) and illustrated by patterns in Scheffer's model. Instabilities of the spatially uniform distribution can appear if phytoplankton and zooplankton move with different velocities but regardless of which one is faster. This mechanism of generating patchy patterns is more general than the Turing mechanism which depends on strong conditions on the diffusion coefficients; thus, one can expect a wide range of its applications in population dynamics.

Thus, the dynamics of the plankton communities, particularly, processes of pattern formation, have been under intensive investigations during the last decades. As a result, considerable progress in understanding the principal features of plankton system functioning has been achieved. Still, many mechanisms of the spatio-temporal variability of natural plankton populations are not known yet. Pronounced physical patterns like thermoclines, upwelling, fronts and eddies often set the frame for the biological processes (see Medvinsky et al 2001 for a more detailed account). However, under conditions of relative physical uniformity, the temporal and spatio-temporal variability can be a consequence of the coupled nonlinear biological and physico-chemical dynamics (Levin and Segel 1976; Steele and Henderson 1992a, b). Daly and Smith (1993) concluded that biological processes may be more important at smaller scales where behaviour such as

vertical migration and predation may control the plankton production, whereas physical processes may be more important at larger scales in structuring biological communities. O'Brien and Wroblewski (1973) introduced a dimensionless parameter containing the characteristic water speed and the maximum specific biological growth rate, to distinguish parameter regions of biological and physical dominance (Wroblewski *et al* 1975; Wroblewski and O'Brien 1976).

Physical and biological processes may differ significantly not only in spatial but also in temporal scale. Particularly, the effect of external hydrodynamical forcing on the appearance and stability of nonequilibrium spatiotemporal patterns has been studied in Scheffer's model (Malchow and Shigesada 1994), making use of the separation of the different time scales of biological and physical processes. A channel under tidal forcing served as a hydrodynamical model system with a relatively high detention time of matter. Examples were provided on different time scales: the simple physical transport and deformation of a spatially nonuniform initial plankton distribution as well as the biologically determined formation of a localized spatial maximum of phytoplankton biomass.

Plankton pattern formation is essentially dependent on the interference of various physical (light, temperature, hydrodynamics) and biological (nutrient supply, predation) factors. (Platt 1972; Denmann 1976; Fasham 1978). In nature, it has been observed that the direction of motion of plankton patches does not always coincide with the direction of the water flow (Wyatt 1971, 1973), and as the spatial scale increases above approximately 100 meters, phytoplankton behaves successively less like a simple passive quantity distributed by turbulence (Nakata and Ishikawa 1975; Powell et al 1975). Similarly, the spatial variability of zooplankton abundance differs essentially from the environmental variability on scales less than a few dozen kilometres (Weber et al 1986). This indicates that biological factors play an essential role in the emergence of plankton patchiness (Steele and Henderson 1981). The question arises: may biological factors, such as predationprey growth and interactions, be a cause of plankton pattern formation without any hydrodynamic forcing?

In the present work, we apply conceptual few-species models to demonstrate that prey-predation interactions can give rise to complex spatio-temporal dynamics of both plankton and plankton-fish communities.

2. Complex patterns in a simple minimal model of plankton dynamics

2.1 Mathematical model

In this section, the spatio-temporal dynamics of an aquatic community is considered in terms of a two-species prey-

predator (i.e. phytoplankton–zooplankton) system. We show that the formation of patchy spatial distribution of species can be described by this simple model.

According to a widely accepted approach (Murray 1989; Levin *et al* 1993), the functioning of a preypredator community can be described by the following reaction-diffusion equations:

$$\frac{\partial u}{\partial t} = D\Delta u + f(u, v), \tag{1}$$

$$\frac{\partial v}{\partial t} = D\Delta v + g(u, v).$$
⁽²⁾

Here, $u(\mathbf{r}, t)$ and $v(\mathbf{r}, t)$ are the abundance of prey and predator, respectively, \mathbf{r} is the position, t is the time and Dis the diffusion coefficient, Δ is the Laplace operator. We assume that the diffusivities are equal for both the species, this is the usual case in natural plankton communities where the mixing is mainly caused by marine turbulence. The form of the functions f(u, v) and g(u, v) is determined by local biological processes in the community and, for biological reasons, can be described in the following way:

$$f(u,v) = P(u) - E(u,v),$$
$$g(u,v) = k^* E(u,v) - \mathbf{m}v.$$

The function P(u) describes the local growth and natural mortality of the prey whereas E(u, v) describes trophical interaction between the species, i.e. predation. The term **m** is the mortality rate and k^* is the coefficient of food utilization.

The particular choice of the functions P(u) and E(u, v)in eqs (1)–(2) can be different, depending on the type of the prey population and on the type of functional response of the predator. Allowing for the results of field and laboratory observations on plankton system functioning (Fasham 1978; Raymont 1980), we assume that the local growth of the prey is logistic and the predator shows a Holling type II functional response (Holling 1959, 1978). Then, having chosen the simplest mathematical expressions for P(u)and E(u, v) (Murray 1989) we arrive at the following equations:

$$\frac{\partial u}{\partial t} = D\Delta u + \frac{a}{b}u(b-u) - g\frac{u}{u+H}v,$$
(3)

$$\frac{\partial v}{\partial t} = D\Delta v + k^* \, \boldsymbol{g} \, \frac{u}{u+H} \, v - \boldsymbol{m} v, \tag{4}$$

where a, b, H and g are certain constants, a stands for the maximum growth rate of the prey, b is the carrying capacity for the prey population, H is the half-saturation abundance of prey. Let us note here that in such a schematic, few-species model (1)–(2) it hardly makes sense to

look for a more detailed parameterization. Let us also note that all the variables and parameters in eqs (3), (4) are non-negative due to their physical or biological sense. Thus, under the phase space of the system (3)–(4) we will actually mean the domain ($u \ge 0, v \ge 0$).

The next step is to introduce dimensionless variables. Considering

$$\widetilde{u} = u/b, \ \widetilde{v} = v g/(a b), \ \widetilde{t} = a t, \ \widetilde{\mathbf{r}} = \mathbf{r}(a/D)^{1/2}$$
 (5)

and new dimensionless parameters h = H/b, m = m/a and k = k*g/a, from (3)–(4) we arrive at the following equations containing only dimensionless quantities:

$$\frac{\partial u}{\partial t} = \Delta u + u(1-u) - \frac{u}{u+h}v,$$
(6)

$$\frac{\partial v}{\partial t} = \Delta v + k \frac{u}{u+h} v - mv.$$
⁽⁷⁾

(tildes are omitted here and farther on).

Before proceeding to the study of spatio-temporal pattern formation, it seems reasonable to consider first the local dynamics of the system, i.e. the properties of eqs (6)-(7) without diffusion terms. One finds by linear stability analysis that the system

$$\frac{\partial u}{\partial t} = u(1-u) - \frac{u}{u+h}v,$$
(8a)

$$\frac{\partial v}{\partial t} = k \frac{u}{u+h} v - mv, \tag{8b}$$

possesses three stationary states: (0, 0), total extinction; (1, 0), extinction of predator; (u_*, v_*) , coexistence of prey and predator, where

$$u_* = \frac{rh}{1-r}$$
, and $v_* = (1-u_*)(h+u_*)$, (9)

where r = m/k. It is readily seen that for all non-negative values of k, m and h, (0, 0) is a saddle-point. The stationary point (1, 0) is a saddle-point if the nontrivial point (u_*, v_*) lies in the biologically meaningful region u > 0, v > 0, or a stable node otherwise. The stationary point (u_*, v_*) can be of any type.

Let us note here that the coexistence state (u_*, v_*) moves to the biologically meaningful region u > 0, v > 0when

$$h < \frac{1-r}{r},\tag{10}$$

and becomes unstable when the parameter value

$$h < \frac{1-r}{1+r}.\tag{11}$$

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In the latter case, the steady state is surrounded by a stable limit cycle and the kinetic of the system is oscillatory.

We consider the following zero-flux boundary conditions:

$$\frac{\partial u(x=0,t)}{\partial x} = \frac{\partial u(x=L,t)}{\partial x} = \frac{\partial v(x=0,t)}{\partial x} = \frac{\partial v(x=L,t)}{\partial x} = 0.$$

(in a two-dimensional case, it means that derivatives along the direction perpendicular to the boundary of the domain must be equal to zero). This type of boundary condition is typical for modelling the dynamics of spatially-bounded aquatic ecosystems (Scheffer 1998). However, we want to mention that the principal result obtained in this section (the formation of *irregular* spatial patterns) stays qualitatively the same for periodical boundary conditions which are also often used for ecological modelling, see § 3.

Eqs (6)–(7) are solved numerically by the semi-implicit finite-difference method. The steps Δx and Δt of the numerical grid are chosen sufficiently small so that the results do not depend on the value of the steps. Besides, the results of the calculations are tested by their comparison with known analytical predictions (Fisher 1937; Dunbar 1986; Murray 1989).

These results provide helpful information to choose the parameter value for numerical simulations of the full problem (6)–(7). In case of existence of a stable stationary point in the phase space of the system [i.e. when condition (10) is held and condition (11) is broken], the dynamics of the system is typically reduced to the relaxation to the stable spatially homogeneous state (u_*, v_*) . The details of the process depend on the type of the initial conditions, e.g. for a finite initial distribution of species the relaxation usually takes place after propagation of diffusive fronts (Dunbar 1986; Murray 1989; Petrovskii et al 1998; Petrovskii and Malchow 2000a). Since here we are more concerned with the formation of transient spatio-temporal patterns, it is the parameter values satisfying condition (11) that are of primary interest (Koppel and Howard 1973; Sherratt et al 1995; Petrovskii and Malchow 1999).

2.2 1D computer simulations

The spatio-temporal dynamics of a diffusion-reaction system depends to a large extent on the choice of initial conditions. In a real community, the details of the initial spatial distribution of the species can be caused by specific reasons. The simplest form of the allocated initial distribution would be spatially homogeneous initial conditions. However, in this case the distribution of the species stays homogeneous for any time and no spatial pattern can emerge. To get a non-trivial spatio-temporal dynamics, one has to perturb the homogeneous distribution.

In this subsection we focus on the 1D dynamics of the system (6)-(7). A few different forms of the disturbed initial conditions will be considered. We begin with the constant-gradient distribution:

$$u(x, 0) = u_*$$
 (12)

$$v(x, 0) = f_1(x) = v_* + e_x + d_y, \qquad (13)$$

where **e** and **d** are certain parameters.

The results of our computer simulations show that the type of the system dynamics is determined by the values e and d. In case e is small, the initial conditions (12)-(13) evolve to a smooth heterogeneous spatial distribution of species (Petrovskii and Malchow 1999). The spatial distributions gradually vary in time, the local temporal behaviour of the dynamical variables u and vfollows the limit cycle of the homogeneous system. This regime is not self-contained, and the smooth spatial pattern arising in this case slowly relaxates to the spatially homogeneous distribution of species (Petrovskii and Malchow 2000b).

However, for another set of parameters (e.g. if the value of the gradient exceeds a certain critical value, $e \ge e_{cr}$ where e_{cr} depends on **d**), the features of the species spatial distribution become essentially different (Petrovskii and Malchow 1999). Figure 1 shows the spatial distribution at the moment t = 640 and t = 2640 calculated for $k = 2, r = 0.4, h = 0.3, e = 10^{-6}$ and $d = -1.5 \times 10^{-3}$. In this case, the initial distribution (12)-(13) leads to the formation of strongly irregular sharp transient patterns

(a)

1.0

0.8

0.6

0.4

inside a sub-domain of the system (figure 1a). The size of the region occupied by this pattern steadily grows with time and finally irregular spatio-temporal oscillations prevail over the whole domain (figure 1b). An important note is that this regime is persistent. Long-time numerical simulations show that, after irregular spatio-temporal oscillations occupy the whole domain, the dynamics of the system does not undergo any farther changes.

Also the temporal behaviour of the concentrations uand v becomes completely different. Figure 2 exhibits the local phase plane of the system obtained in a fixed point $\overline{x} = 480$ inside the region invaded by the irregular spatiotemporal oscillations. Instead of following the limit cycle as it happens in case of smooth pattern formation, the trajectory now fills nearly the whole domain inside the limit cycle. Below we will show that this regime of the system dynamics corresponds to spatio-temporal chaos (Petrovskii and Malchow 1999).

A remarkable property of the system dynamics is that, until the irregular pattern spreads over the whole domain, there exist distinct boundaries at every moment separating the regions with different dynamical regimes, i.e. the formation of sharp irregular patterns and smooth regular patterns. Our numerical results show that these interfaces propagate with an approximately constant speed in opposite directions, so that the size of the region with chaotic dynamics is always growing. The phenomenon is essentially spatio-temporal: the chaos prevails as a result of the displacement of the regular regime by the chaotic regime. The dynamics of the system looks similar to a phase transition between regular and chaotic phases.



(b)

0.8

 $0.\epsilon$

0.4

Figure 1. Spatial distribution of the populations (solid lines for prey, dashed for predator) calculated for the case when the regular phase is gradually displaced, leading to the onset of a chaotic phase. (a) t = 640 and (b) t = 2640.

Since the spatial distribution of the species abundance is essentially inhomogeneous, it seems that more information can be obtained from consideration of values specially designed to take into account both temporal dynamics and the spatial dimension of the system. The simplest example of such a value is given by the spatially averaged concentration of species (another examples will be considered below). Figure 3 shows a sketch of the phase plane $(\langle u \rangle, \langle v \rangle)$ drawn for the parameters k = 2.0, r =0.33, h = 0.43. While in case of the smooth pattern the trajectory (not shown in the sketch) slowly approaches the limit cycle (dashed curve), for the regime of sharp pattern the trajectory is retained in a close vicinity of the steady state $\langle u \rangle = u_*, \langle v \rangle = v_*$, filling the space inside a certain domain. The diameter of the domain is notably smaller than the diameter of the limit cycle. Thus it means that the amplitude of the temporal changes in the spatially averaged species abundance is much smaller in case of the formation of sharp chaotic pattern than in case of smooth regular pattern.

We want to note that the two-phase dynamics of the system (6)–(7) described above should not be attributed to the specific choice of the initial conditions in the form (12)–(13). Particularly, for the following initial conditions

$$u(x,0) = u_*,$$
 (14)

$$v(x, 0) = v_*$$
 for $x \le x_0$ or $x \ge x_0 + S$, and



Figure 2. Phase plane of the system obtained in a fixed point inside the domain occupied by irregular spatio-temporal oscillations.

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$$v(x, 0) = v_* + A \sin\left(\frac{2\mathbf{p} \ (x - x_0)}{S}\right) \text{for } x_0 \le x \le x_0 + S,$$
(15)

spatially homogeneous distribution (with the periodical temporal behaviour according the limit cycle) survives only for very small values of amplitude A and/or magnitude S of the perturbation, cf. Petrovskii and Malchow (2000b) for more details. For somewhat larger, but still small values of A and S, initial distribution (14)–(15) evolves to formation of sharp irregular spatio-temporal pattern. The embryo of the chaotic phase first appears in vicinity of the initial finite perturbation of the homogeneous steady state. The moving interface now separates the domain occupied by irregular spatio-temporal oscillations from the region of homogeneous spatial distribution, the speed of the interface in this case can be found analytically (Petrovskii and Malchow 2000b).

Let us note that, if started with somewhat more complex, e.g. non-monotonic initial conditions, the dynamics of the system can be even more complicated showing a phenomenon which may be called intermittency: the domains occupied by regular and chaotic phases alternate in space, cf. figure 4. As a particular example, we consider the following form of the initial conditions:

$$u(x,0) = u_* + e(x - x_1)(x - x_2),$$
(16)



Figure 3. Phase plane of spatially averaged densities of prey and predator calculated for the case of irregular dynamics of the system; parameters are given in the text. Dashed line shows the limit cycle of the spatially homogeneous system, short-dashed straight lines indicate the position of the steady state.

$$v(x, 0) = v_*.$$
 (17)

In this case, slightly disturbed initial conditions evolve to a complex spatial structure where two domains occupied by sharp patterns are separated by regions with smooth patterns, cf. figure 4 showing a snapshot of the species distribution at t = 600 calculated for $e = 10^{-8}$, $x_1 = 1200$, $x_2 = 2800$, other parameters as in figure 1. As in the previous case, the size of the chaotic domains steadily grows so that finally they displace the regular phase and occupy the whole region.

The results of our numerical experiments fulfilled for different types of initial conditions and different parameter values indicate that formation of sharp pattern typically takes place first in vicinity of a point/points x_{cr} where $u(x_{cr}, 0) = u_*, v(x_{cr}, 0) = v_*$. In case the initial conditions do not contain such a critical point, the factors determining the position of the embryos are not clear.

The scenario of pattern formation described above appears to be essentially different from those already known for two-component reaction-diffusion systems (Turing 1952; Segel and Jackson 1972; Rovinsky and Menzinger 1992; Pascual 1993; Malchow and Shigesada 1994; Malchow 1994; Sherratt *et al* 1995). Note that mathematical model (6)–(7) describing formation of the sharp irregular spatial structure is, in a certain sense, minimal because it does not contain commonly encountered assumptions and restraints, e.g. about different mobility of interacting species or any type of environmental heterogeneity. In the rest of this section, we give an extensive consideration of



Figure 4. An intermittent spatial structure appearing from nonmonotonic initial conditions (16)–(17); parameters are given in the text. Solid line for prey and dashed line for predator.

this new mechanism of pattern formation. Firstly, we will produce clear evidence of the chaotic nature of the irregular spatio-temporal oscillations observed above. And secondly, to estimate applicability of this mechanism to the dynamics of ecological communities, the extension of the results on the case of two spatial dimensions will be made.

2.3 Spatio-temporal chaos

In this subsection we show that the formation of sharp non-stationary patchy structure in the distribution of the species corresponds to spatio-temporal chaos. It should be noted that the term chaos has a specific meaning and a visible irregularity of the system behaviour, whatever complex it may be, does not necessary means chaotic dynamics. According to its definition, chaos means sensitivity to the initial conditions when small variations of the initial distribution of species lead to large discrepancy between species distribution hereafter. Particularly, it means that the initial perturbation with a small amplitude d(0)grows with time as $d(t) \cong d(0) \exp(\mathbf{l}t)$ where $\mathbf{l} > 0$ is the dominant Lyapunov exponent (Kantz and Schreiber 1997). This exponential growth has been proved to be equivalent to some other properties of the system dynamics, e.g. to a specific flat form of the power spectra for the dynamical variables of the system and to exponential decreasing of the autocorrelation function (Nayfeh and Balachandran 1995). Thus, to reveal chaos in the dynamics of the system a variety of methods can be used.

We want to note that the concept of chaos appeared originally in connection with the temporal dynamics of a spatially homogeneous system. Meanwhile, accounting for the spatial dimensions of the system can make its dynamics much more complex and provide a possibility for chaos to arise in those cases where it would be impossible otherwise. Particularly, the appearance of chaos in the two-species system is a crucial consequence of the formation of spatial patterns. The phenomenon is essentially spatio-temporal; thus, to distinguish it from a purely temporal chaotic dynamics of a homogeneous system, the term spatio-temporal chaos (Pande and Pandit 2000) seems to be more adequate.

In order to show that the formation of sharp transient patterns corresponds to chaotic dynamics, we test sensitivity of the species distribution to variations of the initial conditions. Figures 5–8 present the results of our computer investigation of the problem. Firstly, eqs (6)–(7) are solved for the parameter values corresponding to oscillatory local kinetics of the system, cf. (11), to provide the formation of sharp irregular patterns. The initial conditions are taken in the form (12)–(13). Then, eqs (6)–(7) have been solved for the same but slightly perturbed initial conditions, $u(x, 0) = u_*$, $v(x, 0) = f_1(x) + \Delta v$,

the perturbation Δv being chosen in the following form:

$$\Delta v = \boldsymbol{e}_{pert} \sin\left(\frac{2\boldsymbol{p}(x-x_0)}{L_{pert}}\right) \text{for } x_0 \le x \le x_0 + L_{pert},$$
otherwise $\Delta v = 0.$ (18)

After that, the spatial distributions of species calculated in each case are compared. Figure 5 shows the prey abundance (the comparison made for the predator leads to similar results) obtained at t = 600 and t = 800 for perturbed (with $x_0 = 150$, $L_{pert} = 5$ and $e_{pert} = 0.01$) and unperturbed initial conditions (12)-(13) for parameter values k = 2.0, r = 0.4, h = 0.3, $e = 2 \times 10^{-4}$, $d = -3 \times 10^{-2}$, solid and dashed lines correspond to the solutions obtained for unperturbed and perturbed initial conditions, respectively. Thus, until $t \approx 600$ there is a very small difference between the solutions. However, for t > 600 the visible discrepancy begins growing promptly and already for t = 800 the difference between the solutions is of the same order as the solutions themselves. We want to mention that qualitatively similar behaviour is also observed for other values of L_{pert} and \boldsymbol{e}_{pert} , and for other values of the parameters corresponding to the formation of irregular structures.

Thus, the sensitivity of the species density to small variations of the initial conditions is demonstrated, based on the discrepancy between perturbed $u_{pert}(x, t)$ and unper-

turbed $u_{unpt}(x,t)$ solutions of eqs (6)–(7). To make it more quantitative, figure 6 shows the absolute value b(t) of the local difference between the prey density in a fixed point $\bar{x} = 150$ obtained for the two cases, i.e.

$$b(t) = \left| u_{pert}(\bar{x}, t) - u_{unpt}(\bar{x}, t) \right|.$$
(19)

The behaviour of b(t) is in agreement with the results shown in figure 5: the difference between the solutions is negligible for t < 500 and starts growing fast for larger times.

The results presented in figure 6 would be probably exhaustive if obtained for a system without a spatial structure. This is not so in our case. The existence of the prominent spatial patterns makes it somewhat doubtful whether the dynamics of the system can be adequately represented by the results obtained in a single point \bar{x} . To make it more convincing, we also calculate the distance d(t) between the perturbed and unperturbed solutions allowing for the spatial dimension of the system. Specifically, the difference between the solution is now determined not in a fixed point but as a maximum discrepancy found throughout the domain, i.e.

$$d(t) = \max \left| u_{pert}(x, t) - u_{unpt}(x, t) \right|, 0 \le x \le L,$$
(20)

where L is the overall length of the domain. The values of d calculated for different moments of time are shown in figure 7 (parameters are the same as above). Thus, the behaviour of the distance d(t) also confirms sensitivity of



Figure 5. The spatial distribution of the prey abundance at (a) t = 600 and (b) t = 800 calculated for perturbed (dashed line) and unperturbed (solid line) initial conditions.

the species spatial distribution to small variation of the initial conditions.

Another way to take into account the spatial dimension of the system is to consider the difference between the spatially averaged solutions. Note that, generally speaking, this approach is not equivalent to the one based on (20). Indeed, one can imagine a situation when two spatial distributions differ significantly only in a few points but appear quite close in terms of averaged values. To break these last doubts, we use the following expression for the distance-in-average:

$$n(t) = |\langle u_{pert} \rangle(t) - \langle u_{unpt} \rangle(t)|, \qquad (21)$$

where

 $0.\epsilon$

0.

0.2

0.0

Discrepancy

$$\langle u \rangle(t) = \frac{1}{L} \int_{0}^{L} u(x, t) dx.$$

The results of the calculations of n(t) shown in figure 8 (parameters are the same as in figures 5–7) are in good agreement with the results obtained in course other approaches.

Thus, the results shown in figures 5–8 clearly indicate that small variations of the initial conditions lead, after a certain time *T*, to the formation of completely different spatial distribution of species. This result is robust with respect to the way of quantification of the difference between the perturbed and unperturbed solutions, cf. eqs (19)–(21). To quantify the rate of the exponential growth of the difference d(t) between the solutions becomes significant is $T \cong 600$. This leads to an estimate for the dominant Lyapunov exponent as $I = 1/T \cong 0.001$. Our



1000

numerical experiments show that this value stays approximately the same for the values of initial perturbations at least in the range from $\boldsymbol{e}_{pert} = 0.005$ to $\boldsymbol{e}_{pert} = 0.001$ [see eq. (18)]. The observed sensitivity of the solutions to small variations of the initial conditions provides a conclusive argument for the existence of chaos (Nayfeh and Balachandran 1995; Kaplan and Glass 1995; Katz and Schreiber 1997).

Another way to demonstrate chaotic nature of the irregular spatio-temporal oscillations of the species abundance is to calculate the autocorrelation functions. The state of a prey-predator community is naturally described by the two dynamical variables u and v, i.e. the densities of prey and predator, respectively. Thus, for a general case, one has to consider two autocorrelation functions as well as the cross-correlations. Here, we restrict ourselves to the results obtained for the prey abundance, the autocorrelation function for predator shows qualitatively similar behaviour.

It should be noted that an immediate application of the standard definition leads to certain problems. According to the usual approach, in case a dynamical variable y is a function of a variable t which may have the meaning of time or position or anything else, the autocorrelation function is defined by the following expression:

$$F(\mathbf{x}) = \lim_{Z \to \infty} \frac{1}{Z} \int_{0}^{Z} \mathbf{y} (\mathbf{t} + \mathbf{x}) \mathbf{y} (\mathbf{t}) d\mathbf{t}.$$
 (22)

In the problem under consideration, the prey density depends on two variables, position and time. Thus, trying



Figure 6. The local difference b(t) between perturbed and unperturbed solutions calculated at a fixed point $\overline{x} = 150$.

500

Time

250

Figure 7. The distance d(t) between perturbed and unperturbed solutions calculated according to eq. (20).

to apply the definition (22) to characterize the spatial structure of the system, we arrive at

$$\overline{F}(\mathbf{x},t) = \lim_{Z \to \infty} \frac{1}{Z} \int_{0}^{Z} u(x+\mathbf{x},t)u(x,t) \, dx.$$
(23)

Eq. (23) has a few evident drawbacks. First, the autocorrelation function calculated according to (23) depends not only on the distance \mathbf{x} but also on time. The situation when the properties of \overline{F} , considered as a function of \mathbf{x} , are explicitly time-dependent appears rather exotic and makes the interpretation of the results highly difficult. On the other hand, since the problem is essentially transient it seems reasonable that a proper definition of the autocorrelation function should take into account both spatial and temporal behaviour of the system. Another problem is that, in order to obtain reliable results during computer simulations, the value of Z in eq. (23) must be chosen sufficiently large. Practically, it means that the numerical grid must consist of, at least, a few dozen thousands of nodes which is hardly possible.

To overcome these difficulties, we consider a modified definition of the autocorrelation function where the averaging over space is changed to the averaging over time:

$$K(\mathbf{x}) = \lim_{T \to \infty} \frac{1}{T} \int_{0}^{T} u(x_0 + \mathbf{x}, t) u(x_0, t) dt.$$
(24)

Note that eq. (24) includes the usual definition as a particle case if the system exhibits ergodic behaviour. Let us also mention here that, although the value of *K* formally depends on the parameter x_0 , the results of the numerical simulations implemented for different values of x_0 do not show any dependence on x_0 .

The autocorrelation function $K(\mathbf{x})$ calculated according to (24) is shown in figure 9 (for parameter values $k = 2 \cdot 0$, $r = 0 \cdot 2$, $H = 0 \cdot 3$, $x_0 = 100$, averaging is done over the time interval from t = 4000 to t = 12000), the solid line corresponds to the case of irregular dynamics (formation of sharp patterns), the dashed line corresponds to the regular dynamics (smooth patterns).

Thus, one can see that, in case of regular dynamics, the spatio-temporal behaviour of the system is highly correlated over the whole domain. Moreover, since the regime of smooth patterns is a process of slow relaxation to the homogeneous spatial distribution, the autocorrelation function gradually changes with time so that the correlativity of the temporal behaviour between different point increases. In the infinite time limit temporal oscillations throughout the system become synchronized and $K(\mathbf{x}) \equiv 1$.

On the contrary, the behaviour of the autocorrelation function for the case of sharp pattern shown in figure 9 is typical for chaotic dynamics (Nayfeh and Balachandran 1995). It should be mentioned here that the irregular oscillations of finite (non-zero) amplitude in $K(\mathbf{x})$ is the consequence of the finiteness of the averaging interval T; the results of our numerical simulations show that their amplitude tends to zero as T is increasing. Since our modified definition (24) of the autocorrelation function



Figure 8. The distance n(t) between perturbed and unperturbed solutions calculated on the basis of spatially averaged values, cf. eq. (21).



Figure 9. Autocorrelation function $K(\mathbf{x})$ calculated for the regimes of sharp patterns (solid line) and smooth patterns (dashed line).

takes into account both spatial and temporal aspects, the regime of the system dynamics corresponding to the formation of sharp patterns can be classified as spatiotemporal chaos; this is in agreement with the comments made at the beginning of the subsection. This conclusion is also in agreement with recent results of Petrovskii and Malchow (1999) where spatio-temporal chaos in a prey– predator system is described in terms of the temporal behaviour of spatially averaged densities.

2.4 Pattern formation in 2D case

Now we are concerned with the extension of the results above to the case of two spatial dimensions. In this case, eqs (6)–(7) take the following form:

$$\frac{\partial u(x, y, t)}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + u(1-u) - \frac{u}{u+h}v, \qquad (25)$$

$$\frac{\partial v(x, y, t)}{\partial t} = \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} + k \frac{u}{u+h} v - mv.$$
(26)

In eqs (25)–(26) $0 < x < L_x$, $0 < y < L_y$. Eqs (25)–(26) describe the dynamics of an aquatic community in a horizontal layer, vertical distribution of species inside the layer is assumed homogeneous.

Eqs (25)-(26) are solved numerically. The choice of the length L_x and the width L_y of the domain may be different in different computer experiments; in the results shown below, $L_x = 900$, $L_y = 300$. At the domain boundary, the zero-flux conditions are imposed. As above, the type of the system dynamics to a certain extent depends on the choice of the initial conditions. For a purely homogeneous initial distribution of species, the system stays homogeneous for every moment of time and no spatial pattern emerges. In case of only a very slightly perturbed initial conditions [the shape of perturbation can be different, e.g. cf. eqs (12)-(13) and (14)-(15)] a smooth spatial pattern arises which is not persistent and gradually evolves to the homogeneous species distribution. However, for somewhat stronger disturbed initial conditions, the system evolves to formation of sharp irregular spatial patterns which is persistent in time.

Here we present the results of two computer experiments differing in the form of the initial conditions. In the first case, the initial distribution of species provides a 2D generalization of eqs (16)-(17). Specifically,

$$u(x, y, 0) = u_* - \boldsymbol{e}_1(x - 0.1y - 225)(x - 0.1y - 675),$$
(27)

$$v(x, y, 0) = v_* - \boldsymbol{e}_2(x - 450) - \boldsymbol{e}_3(y - 150)$$
(28)

where $\mathbf{e}_1 = 2 \times 10^{-1}$, $\mathbf{e}_2 = 3 \times 10^{-3}$ and $\mathbf{e}_3 = 1.2 \times 10^{-4}$ (note that the initial conditions are deliberately chosen not to be symmetrical in order to make more explicit possible impact of the corners of the domain). The values of parameters in eqs (25)–(26) are chosen as k = 2.0, r = 0.3, h = 0.4. Snapshots of the species spatial distribution arising from (27)–(28) are shown in figure 10 for t = 0, t = 150, t = 200, t = 300, t = 400, and t = 1000. Since both species exhibit qualitatively similar behaviour except for early stages of the process when the influence of the initial conditions is essential, only the prey (phytoplankton) abundance is shown.

Thus, for a 2D system (25)-(26), the formation of irregular patchy structure (cf. figure 10f) can be preceded by the evolution of a regular spiral spatial pattern. Note that the appearance of the spirals is not induced by the initial conditions. The centre of each spiral is situated at a critical point, i.e. at the point (x_{cr}, y_{cr}) where $u(x_{cr}, y_{cr}) = u_*$, $v(x_{cr}, y_{cr}) = v_*$ (cf. with the results obtained for the 1D case). It is readily seen that distribution (27)-(28) contains exactly two such points, for another initial conditions the number of spirals can be different. After they are formed (figure 10b), the spirals slightly grow in size during a certain time, their spatial structure becoming more distinct (figure 10b, c). The destruction of the spirals begins in their centres (figure 10d). Once appearing, the embryos of the patchy structure steadily grow (figure 10d, e), and finally an irregular patchy spatial pattern prevails over the whole domain.

In the second case, the initial conditions describe a phytoplankton (prey) patch placed into a domain with a constant-gradient zooplankton (predator) distribution:

$$u(x, y, 0) = u_* - \mathbf{e}_1(x - 180)(x - 720) - \mathbf{e}_2(y - 90)(y - 210),$$
(29)

$$v(x, y, 0) = v_* - \boldsymbol{e}_3(x - 450) - \boldsymbol{e}_4(y - 135)$$
(30)

where $\mathbf{e}_1 = 2 \times 10^{-7}$, $\mathbf{e}_2 = 6 \times 10^{-7}$, $\mathbf{e}_3 = 3 \times 10^{-5}$, $\mathbf{e}_4 = 6 \times 10^{-5}$. Figure 11 shows the snapshots of phytoplankton spatial distribution obtained at t = 0, t = 120, t = 160, t = 300, t = 400 and t = 1200 for parameter values $k = 2 \cdot 0$, $r = 0 \cdot 3$, $h = 0 \cdot 4$. Although for these initial conditions the dynamics of the system preceding the formation of patchy spatial structure is somewhat less regular, it seems to follow a similar scenario. First, again, the spirals appear with their centres being disposed in vicinity of critical points (figure 11b, c), the form of the spirals is not so perfect as it was in the previous case. The destruction of the spirals leads to the formation of two growing embryos of the patchy spatial pattern (figure 11d, e), and finally to the formation of irregular patchy species distribution in the whole domain.



Figure 10. Spatial distribution of prey (phytoplankton) for (a) t = 0, (b) t = 150, (c) t = 200, (d) t = 300, (e) t = 400, and (f) t = 1000, parameters are given in the text. Irregular patchy structure arises as a result of destruction of spirals.

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Figure 11. Spatial distribution of prey (phytoplankton) for (a) t = 0, (b) t = 120, (c) t = 160, (d) t = 300, (e) t = 400, and (f) t = 1200, parameters are given in the text.

We want to note that the formation of a spiral structure in the spatial distribution of plankton may shed a new light on some well-known problems. The existence of a dipole-like structure in the plankton distribution in the ocean is widely known, usually it is associated with socalled mushroom-like structure of the field of advective currents (Fedorov and Ginzburg 1988). Here we have shown that a structure of that type may appear due to trophical prey-predator interactions in the aquatic community and must not be necessarily associated with the ocean hydrodynamics.

Thus we see that, although at intermediate time the dynamics of the system can be quite regular (figure 10b, c), for larger times the evolution of the species spatial distribution leads to the formation of irregular patchy structure (figures 10f and 11f). This spatial pattern is in agreement with the data of field observations on the functioning of plankton systems (Denmann 1976; Weber et al 1986; Green et al 1992; Levin et al 1993). To estimate the relevance of the pattern formation mechanism considered here to the patchy plankton spatial distribution in marine environments, the question about the scale of the arising spatial structures is to be answered. Analysis of the results shown in figures 10f and 11f, as well as the behaviour of the autocorrelation function $K(\mathbf{x})$ (figure 9), indicates that there is a characteristic intrinsic length of the pattern, its value being estimated between 10 and 25 in dimensionless units. Referring to eq. (5), the magnitude of this value in dimensional units is determined by the maximum phytoplankton growth rate and the turbulent diffusivity. The value of the maximum growth rate *a* depends on the season, and for the period of blooming can be estimated as 4×10^{-5} to 10^{-5} (corresponding to the time of phytoplankton biomass doubling as between 6 and 48 h). The situation with turbulent diffusivity is somewhat more complicated. For open-sea regions the intensity of turbulent mixing usually shows clear dependence on the scale of the phenomenon (Ozmidov 1968; Okubo 1971, 1980). Particularly, for the diffusion of a single plankton patch it means that the diffusivity may grow with time (Petrovskii 1999). However, this property of the turbulent mixing is much less manifested in coastal regions, e.g. bights, harbours, etc. In this case of so-called small-scale turbulence, the value of the turbulent diffusivity can be estimated as $D = 10^3 \text{ cm}^2 \text{ s}^{-1}$ (Ozmidov 1968, 1998). Thus, taking the estimates for D and a together with eq. (5), we obtain that the dimensionless unit length corresponds to approximately 50 to 100 meters in original dimensional units. This gives the value of the intrinsic length of the spatial patterns on the order of 1 km which is consistent with the scale of plankton patterns obtained in field observations (Fasham 1978; Steele 1978; Abbott 1993).

3. The interplay between plankton spatio-temporal pattern formation and planktivorous fish school cruising

3.1 Introduction

In the previous section, the efficiency of applications of a classical two-species continuous model to describe pattern formation in a plankton community was demonstrated. However, the continuous approach based on ordinary or partial differential equations often fails to account for the individual intentional behaviour of modelled species in their environment as well as their mutual adaptation. The elaboration of the concept of complex adaptive systems since Holland (1975) till today together with the development of individual-based modelling strategies have partly overcome this problem. Usually, several so-called agents behave according to a generally small number of defined rules which control growth, interactions and motion of the agents as well as the mutual interactions of the agents and their environment. This set of rules for process on the microscale can create temporal, spatial, spatio-temporal, or functional structures on the macroscale.

In this section, we apply this concept to study the dynamics of a coupled fish-plankton system. The fish will be considered localized in a school, or super-individual (Scheffer *et al* 1995), cruising and feeding according to defined rules. In such an approach, the spatio-temporal continuous dynamics of two interacting and dispersing populations (phytoplankton and zooplankton) and the rulebased behaviour of a discrete agent (fish school) control each other in a hybrid model. A similar hybrid modelling technique has already been used by Savill and Hogeweg (1997) to describe morphogenetic process in cell tissues.

The process of aggregation of individual fishes and the persistence of schools under environmental or social constraints has already been studied by many other authors (Radakov 1973; Cushing 1975; Steele 1977; Blake 1983; Okubo 1986; Semovski 1989; Grünbaum and Okubo 1994; Huth and Wissel 1994; Reuter and Breckling 1994; Gueron *et al* 1996; Niwa 1996; Romey 1996; Flierl *et al* 1999; Stöcker 1999) and will not be considered here.

Let us note that prey-predator interactions are the basic dynamics of any food chain. However, Goodwin (1967) has applied it as well to model the class struggle where the employment rate serves as the prey while the wage bill share acts as the predator (Lorenz 1993). Coupling of economic and ecological systems is well known, for example, as applied to fishery (Ruth and Hannon 1997).

3.2 The model of a nutrient-plankton-fish coupled system

3.2a Continuous plankton dynamics: We consider a four-component nutrient-phytoplankton-zooplankton fish model where at any location (X, Y) and time t, the dynamics of phytoplankton P(X, Y, t) and herbivorous zooplankton H(X, Y, t) populations are given by the following reaction-diffusion equations:

$$\frac{\partial P}{\partial t} = RP\left(1 - \frac{P}{K}\right) - \frac{AC_1P}{C_2 + P}H + D_P\Delta P, \qquad (31)$$

$$\frac{\partial H}{\partial t} = \frac{C_1 P}{C_2 + P} H - MH - F \frac{H^2}{C_3^2 + H^2} + D_H \Delta H.$$
(32)

The parameters R, K, M, and 1/A denote the intrinsic growth rate and carrying capacity of phytoplankton, the death rate and yield coefficient of phytoplankton to zooplankton, respectively. The constants C_1 , C_2 and C_3 parameterize the saturating functional response, F is the fish predation rate on zooplankton. D_P and D_H are the diffusion coefficients of phytoplankton and zooplankton, respectively. Δ is the two-dimensional Laplace operator. The dependence of the zooplankton grazing rate on phytoplankton is of type II, whereas the zooplankton predation by fish follows a sigmoidal functional response of type III as it has been supposed in the Scheffer (1991a) model.

The local kinetics of the model, i.e. $D_{\rm P} = D_{\rm H} = 0$, has been investigated in detail (Steele and Henderson 1981; Scheffer 1991a). In the absence of zooplankton, phytoplankton would reach its carrying capacity K. Considering zooplankton at first as a non-dynamic predator, i.e. $\partial H/\partial \hat{\mathbf{0}} = 0$ in eq. (32), the possibility of 2 stable phytoplankton levels arises for intermediate values of zooplankton densities, whereas high zooplankton densities lead to a single stable low phytoplankton level and vice versa. Dynamic zooplankton can induce the typical preypredator limit cycle oscillations and the addition of planktivorous fish by the last kinetic term in eq. (32) restores the possibility of bistability. Without external or internal noise, the initial conditions determine which of the 2 stable states will be reached. Fluctuations which might be due to the natural noise or also 'extreme' events could induce transitions between the stable states.

The behaviour of the local model under seasonal forcing has been studied as well (Scheffer *et al* 1997; Steffen *et al* 1997; Scheffer 1998). These seasonal forcings are due to the natural variability of temperature, light, and nutrient supply. The local prey–predator cycles can be driven to quasi-periodic and chaotic oscillations. Locally stable steady states simply oscillate with the frequency of the external forcing. Accounting for diffusion, diffusion-induced stationary patchy plankton distributions have been found which appeared to be stable even under weak seasonal forcing (Malchow 1993), however, such structures require differing diffusion coefficients (Turing 1952; Segel and Jackson 1972). Moving patchy distributions for equal diffusivities can be found if the interference of growth, interactions, diffusion, and advection causes an instability of the uniform plankton distribution (Malchow 1996), or if certain parameters, e.g. the nutrient distribution, possess a spatial gradient. In the latter case, even diffusion-induced chaos might appear (Pascual 1993).

Hydrodynamic forces and their spatio-temporal flow patterns often govern or set the frame for the structures of drifting and swimming matter. Hydrodynamic processes are usually much faster than the plankton biology; that allows a special mathematical separation technique (Malchow and Shigesada 1994) which is beyond the scope of this paper. A physically relatively uniform period and area are considered in this chapter.

For later convenience, model (31)–(32) is simplified by introducing dimensionless variables. Following Pascual (1993), dimensionless densities p = P/K and h = AH/K are defined. Space is scaled by a characteristic length L/kwhich is the total length L of the considered area divided by an integer scale factor k which models the scale of the expected patchy patterns. Time is scaled by a characteristic value of the phytoplankton growth rate R_0 . Thus, x = kX/L, y = kY/L and $t = tR_0$. Then, eqs (31)–(32) become

$$\frac{\partial p}{\partial t} = rp(1-p) - \frac{ap}{1+bp}h + d_p\Delta p, \qquad (33)$$

$$\frac{\partial h}{\partial t} = \frac{ap}{1+bp}h - mh - f\frac{gh^2}{1+g^2h^2} + d_h\Delta h, \qquad (34)$$

where the new parameters are $r = R/R_0$, $a = C_1K/(C_2R_0)$, $b = K/C_2$, $m = M/R_0$, $f = F/(C_3R_0)$, $g = K/(C_3A)$, $d_p = k^2D_P/(L^2R_0)$, $d_h = k^2D_H/(L^2R_0)$.

The results presented here are based on numerical simulations for a set of parameters (r = 2, a = 5, b = 5, m = 0.6, g = 2.5) chosen to obtain limit cycles at each point in the absence of diffusion under f = 0. In natural waters turbulent diffusion is often supposed to dominate plankton diffusion rates. Taking this into account we consider both phytoplankton and zooplankton as passive contaminants of water turbulent motion (Malchow *et al* 2000; Medvinsky *et al* 2000; Tikhonov *et al* 2000; Tikhonova *et al* 2000). In this case, $d_p = d_h = d$. Using the relationship between turbulent diffusivity and the scale of the phenomenon in the sea (Okubo 1971, 1980) one can show that with the characteristic growth rate $R_0 = 10^{-5} \text{ s}^{-1}$ (or one division per day which is typical of phytoplankton

growth) and the characteristic length L/k = 1 km (which is typical of plankton spatial patterns) *d* is about 5×10^{-12} .

For the numerical integration of eqs (33)–(34), we used a simple difference scheme. The 2D space was divided into a rectangular grid of 64×64 quadratic finite elements with unit size length. The time step was set equal to 0.01. Repetition of the integration with smaller step size showed that the numerical results did not change, ensuring the accuracy of the chosen approximation. Periodic boundary conditions were adopted in both spatial directions in order to consider fish–plankton interactions on larger scales.

3.2b Discrete fish school dynamics: It is generally accepted that the predation rate of fish is a constant parameter of the plankton-fish interaction model (Scheffer 1991a, b; Scheffer *et al* 1997). It means that fish is always homogeneously distributed in space. But it is well known that fish can form mobile schools. For such fish schools occupying spatially confined regions, f is not a constant but is a function of zooplankton density h, time t and space (x, y), i.e. in eq. (32), f = f(h, t, x, y). The function f describes plankton density dependent motion of the fish school towards favourable habitats. This motion can be simulated in different ways (Bocharov 1990; Radakov 1973).

In this section, we suggest that the behaviour of fish schools might obey the rules introduced by Ebenhöh (1980). They are as follows:

- A localized feeding fish school moves to the neighbouring region with the highest food concentration, only if the actual local zooplankton density is grazed down to or below a certain threshold value h_{th} , resulting in a zooplankton density gradient to the surrounding higher than a defined threshold value dh_{th} , but
- not before some residence time t_{th} .

The Ebenhöh rules correspond to observations of fish school movements in natural waters (Radakov 1973; Ebenhöh 1980; Fernö *et al* 1998; Misund *et al* 1998). However, in order to keep the rules as simple as possible, the fish schools act independently of other fishes and do not change their specific characteristics as size, speed and residence time. Model (33)–(34) with the function *f* describing the fish school movement following the Ebenhöh automata rules combines features of a cellular automaton and of a model based on partial differential equations.

The calculation of the fish movement was carried out according to the Ebenhöh rules. The fish predation rate $f_{ij}^{(n)}$ is equal to a constant f_0 if at time step $n\mathbf{d}t$ the fish school is present at position (i, j) and is equal to zero otherwise. The relevant zooplankton gradients $\mathbf{x} \ \nabla h$ were numerically calculated according to

$$(\vec{\mathbf{x}} \ \vec{\nabla} h)_{ij}^{(n)} = |\mathbf{x}_x| h_{i+sign(\mathbf{x}_x),j}^{(n)} + |\mathbf{x}_y| h_{i,j+sign(\mathbf{x}_y)}^{(n)} - h_{ij}^{(n)}, \quad (35)$$

where *sign* denotes the signum function; sign(x) = +1, $x \ge 0$ and sign(x) = -1, x < 0, sign(0) = 0.

3.3 Plankton pattern formation resulting from fish school motion

Figure 12 demonstrates phytoplankton and zooplankton patterns that emerge as a result of the fish school–plankton interplay. It is seen that the phytoplankton density is lower in the regions where zooplankton density is higher and vice versa. Many early observers have reported such an inverse relationship between phytoplankton and zooplankton (cf., Fasham 1978). Obviously, this is due to consumption of phytoplankton by zooplankton. As a result, the penetration of phytoplankton into the regions occupied by zooplankton patches is blocked.

One can see spiral waves formed by phytoplankton and zooplankton (figure 12). Two- and three-dimensional spiral waves emerge in active physical, chemical and biological media (Murray 1977; Winfree 1980, 1987; Krinsky *et al* 1986; Grusa 1988). For example, they play an essential role in disturbances of the heart rhythm and in biological morphogenesis. In the ocean, they may be present as rotary motions of plankton patches on a kilometre scale (Wyatt 1973).

The formation of a plankton spiral wave is shown in figure 13. It can be seen that the fish school is a trigger of this process. First, the fish school reaches the zooplankton patch (figure 13 at t = 450). The track made by this fish school oscillates with a phase shift relative to the surrounding zooplankton density. Once the fish school has escaped from the zooplankton patch (figure 13 at t = 460), its track expands and forms a U-like structure (figure 13 at t = 490). The edges of this structure bend in opposite directions and form a pair of spiral waves (figure 13 at t = 500 and t = 540). The period of plankton pattern oscillations is equal to that of the homogeneous plankton distributions in the absence of fish. The temporal oscillations of the plankton patterns are similar to the changes in the concentration distributions initiated by rotating vortices in non-oscillating active media, e.g. chemical ones (Murray 1977). In the course of time the number of spiral waves increases, and complex spatial structures like those shown in figure 12 form. It has been checked that these spirals are stable over numerical runs of 10⁶ iterations which are equivalent to more than 50 real time years. However, it has been demonstrated that such spirals are quite sensitive against physical disturbances like shear flows (Biktashev et al 1998) or resource gradients (Malchow et al 2000).

It is interesting that at low fish predation rates f the fish school motility falls drastically, and spiral waves do

not appear for a long time. Point wave sources occur in this case (figure 14).

The formation of both spiral waves (figure 12) and point sources (figure 14) is followed by a dramatic decrease of the space-averaged plankton density oscillations

$$\langle p \rangle = \frac{1}{S} \int_{(S)} p(x, y, t) dx dy; \quad \langle h \rangle = \frac{1}{S} \int_{(S)} h(x, y, t) dx dy,$$
(36)

where $S = k^2$, k = 64. It emerges that in contrast to phytoplankton oscillations at f = 2, the oscillations at f = 1 are characterized by aperiodic bursts that occur at the moments of drastic changes in the fish school location (figure 15).

Thus, the plankton dynamics may depend on the fish school movement (Medvinsky *et al* 2000). Hence, the analysis of this movement is of particular interest in order to investigate plankton–fish interactions.

3.4 Fish school random walks resulting from fish-plankton interplay

3.4a *Regularity of irregular walks*: The motion of fish schools is controlled by various biotic and abiotic environmental factors as light, temperature, salinity, nutrient (e.g. plankton) supply, etc. (Radakov 1973; Bocharov 1990). On the other hand, fish school walks that are shown to be essentially controlled by plankton–fish interactions (Radakov 1973; Ebenhöh 1980; Misund *et al* 1998; Medvinsky *et al* 2000) have a strong feedback on the spatio-

temporal plankton dynamics (Medvinsky *et al* 2000). Therefore, it is not surprising that fish school movement resulting from the interplay of fishes and their environment, can be highly irregular (Medvinsky *et al* 2000; Tikhonov *et al* 2000).

An irregular behaviour exhibits very erratic features and is described by means of irregular functions. The irregular functions can display both (i) self-affine and (ii) multiaffine properties. If such a function (F) represents a stochastic process, it can be stated in the following way (Mandelbrot 1977, 1982; Feder 1988; Schroeder 1990):

$$\langle |F(x+l) - F(x)| \rangle \sim l^H, \qquad (37)$$

where $\langle ... \rangle$ means averaging in case (i), and

$$|F(x+l) - F(x)| \sim l^{h(x)},$$
 (38)

in case (ii). The exponent H in eq. (37) is called the Hurst exponent. Let us note that if H < 1 then F is not differentiable and that the smaller the exponent H the more singular is F. Thus, the Hurst exponent indicates how globally irregular the function F is. The exponent h(x) in eq. (38) is called the Hölder exponent. It measures how irregular the function F is at point x. The greater the Hölder exponent the more regular is the function F. Self-affine functions are qualified as fractal functions whereas multiaffine functions are qualified as multifractal (Feder 1988; Schroeder 1990; Peitgen *et al* 1992). Multifractal functions can be



Figure 12. Phytoplankton and zooplankton spatial distributions obtained in model (33)–(34). The density scale is given in the lower part of the figure; f = 2.

characterized by the multifractal spectrum D(h) that describes the distribution of the Hölder exponents and is the Hausdorff dimension of the subset where the Hölder exponent is equal to h:

$$D(h) = \dim_{\mathrm{H}} [x \ h(x) = h],$$
 (39)

where in general h can have positive as well as negative real values (Feder 1988; Peitgen *et al* 1992; Bacry *et al* 1993).

Multifractal processes can also be characterized by the $f(\mathbf{a})$ singularity spectrum which associates the Hausdorff dimension $f(\mathbf{a})$ to the subset of the support of the measure \mathbf{m} where the singularity strength is \mathbf{a} :

$$f(\boldsymbol{a}) = \dim_{\mathrm{H}} [x \ \boldsymbol{m}(B_x(\boldsymbol{e}))]$$
(40)

where $B_x(e)$ is an *e*-box centred at *x*, and

$$\mathbf{m}(B_x(\mathbf{e}) \sim \mathbf{e}^{\mathbf{a}(x)}.$$
(41)

Homogeneous measures are characterized by a singularity spectrum supported by a single point $(\mathbf{a}_0, f(\mathbf{a}_0))$. In other words, only one kind of singularity is present in the measure. Multifractal measures involve singularities of different strengths. In general context, the approach based on the $f(\mathbf{a})$ spectrum for singular measures has a similar status as the approach based on the D(h) spectrum of Hölder exponents (Bacry *et al* 1993).



Figure 13. Plankton vortex formation as a result of the fish school–plankton patch interaction. The location of the fish school is shown by the star; f = 2.

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As we have shown before (see § 2 and 3) the intrinsic spatio-temporal plankton and plankton-fish dynamics is apparently inhomogeneous, cf. figures 10, 11, 12, 14 and 15 (also figure 3). This kind of inhomogeneity in special distribution of species is not induced by heterogeneity of environment but arises purely as a result of inter-species interactions, i.e. interactions between phytoplankton and zooplankton or between phytoplankton, zooplankton and planktivorous fish. Below we show that this inhomogeneity can lead to fractal properties of fish school walks. However, the fractal properties can also be dependent on the coordinates resulting not in fractal but in multifractal behaviour, cf. eqs (37) and (38). The questions arise whether or not the complex movement of the fish school can be described by simple eqs (37) or (38) and (if such a description is appropriate) which of the equations gives the best fit to the fish school movement? The answer can be hardly given on the base of only qualitative arguments without detailed quantitative considerations of the system dynamics.

3.4b *Fish school trajectories*: According to the Ebenhöh rules, the fish school moves to the regions with the highest zooplankton density. Since the plankton distribution changes in time, fish school walks appear to be rather chaotic. Figure 16 demonstrates typical fish school trajectories: both high-persistent (at $f_0 = 1$) and low-persistent (at $f_0 = 15$). In both the cases $h_{th} = 0.35$, $dh_{th} = 0.01$, and $t_{th} = 0.08$.

One can see that the transition from low fish predation rate to high fish predation rate is followed by an obvious decrease of the persistence of the fish school movement; indeed at $f_0 = 1$ the fish school retains the direction of its movement for a very long time in comparison with the movement at $f_0 = 15$. The sophisticated treatment of the fish school walks let us reveal characteristic features of both types of the fish school behaviour.

3.4c Multifractal analysis of fish school walks: Recently, we have shown that fish school walks can be considered as a fractal Brownian motion with a Hurst exponent H depending on both the phytoplankton growth rate and the fish predation rate (Medvinsky *et al* 2000; Tikhonova *et al* 2000). But some care is required when using the Hurst exponent in order to analyse Brownian signals since such an approach may lead to conflicting estimates of H when the fractal function under consideration is not a homogeneous fractal function with a constant roughness associated to a unique exponent H (Arneodo *et al* 1996).

In the present work, we do not expect *a priori* that a fish school trajectory is represented by a homogeneous fractal function and carry out the multifractal analysis of fish school walks (Tikhonov *et al* 2000). We use a strategy (Bacry *et al* 1993; Muzy *et al* 1993; Arneodo *et al* 1995) which provides a practical way to determine singularity spectra D(h) (39) and f(a) (40) directly from any experimental signal. This approach is essentially based on the use of the wavelet transform (Meyer 1990; David



Figure 14. Plankton waves emitted by the point source occurred at f = 1. The density scale is given in the lower part of the figure.



Figure 15. (a) x and y projections of the fish school movement, and averaged phytoplankton density $\langle p \rangle$ oscillations for f = 1. (b) x and y projections of the fish school movement, and averaged phytoplankton density $\langle p \rangle$ oscillations for f = 2. Averaged zooplankton density $\langle h \rangle$ oscillations (not shown) are phase shifted and qualitatively similar to the phytoplankton oscillations.

1991; Kahane and Lemarié-Rieusset 1995; Hubbard 1996). It is a space-scale analysis which consists in expanding signals in terms of wavelets which are constructed from a single function, the analysing wavelet y, by means of translations and dilations. The continuous wavelet transform of a real-valued function F is defined as:

$$W_{\mathbf{y}}[F](b,a) = \frac{1}{a} \int_{-\infty}^{+\infty} F(x) \mathbf{y}\left(\frac{x-b}{a}\right) dx, \qquad (42)$$

where *b* is the space parameter and *a* the scale parameter. The analysing wavelet y is generally chosen to be well localized in both space and frequency. The main advantage of using the wavelet transform for analysing the regularity of a function *F* is its ability to be blind to polynomial behaviour by an appropriate choice of the analysing wavelet y. Throughout this section, we will use the analysing wavelet which is called the Mexican hat because of its particular shape.

The fastest way to estimate the function D(h) (39) and $f(\mathbf{a})$ (40) suggests the analysis of the scaling behaviour of the partition function Z(q, a) from the modulus maxima of the wavelet transform (Muzy *et al* 1993)

$$Z = \sum_{i=1}^{N(a)} (\mathbf{w}_i(a))^q,$$
(43)

where i = 1, ..., N(a), N(a) is the number of the local maxima of $W_y[F](b, a)$ at each scale *a* considered as a function of *x*, and the function $\mathbf{w}_i(a)$ can be defined in terms of wavelet coefficients (Muzy *et al* 1993; Bacry *et al* 1993) as:

$$\boldsymbol{w}_{i}(a) = \max_{\substack{(x,a') \in I_{i} \\ a' \leq a}} |W_{\boldsymbol{y}}[F](x,a')|, \tag{44}$$

 $l_i \in L(a)$ where L(a) is a set of connected wavelet maxima lines l_i which reach or cross *a*-scale.

In the limit $a \rightarrow 0^+$, the partition function Z(q, a) exhibits a power law behaviour:

$$Z(q,a) \sim a^{t(q)}.\tag{45}$$

The spectrum $f(\mathbf{a})$ (40) can be found by Legendre transforming $\mathbf{t}(q)$, i.e.

$$f(\boldsymbol{a}) = \min_{\boldsymbol{q}} (\boldsymbol{q}\boldsymbol{a} - \boldsymbol{t}(\boldsymbol{q})).$$
(46)

Since t(q) is typically differentiable, and $t''(q) \le 0$, we find that

$$\mathbf{a}\left(q\right) = \frac{d\mathbf{t}(q)}{dq},\tag{47}$$

$$f(q) = q\mathbf{a}(q) - \mathbf{t}(q). \tag{48}$$

Unfortunately, computing the Legendre transform has several disadvantages (for example, resulting from locally violating the inequality $t''(q) \le 0$). This may lead to various errors (Chhabra *et al* 1988). Therefore, another approach was developed to define singularity spectra in the spirit of the so-called canonical method (Chhabra *et al* 1988). It consists in using the two following functions:

$$h(a,q) = \frac{1}{Z(a,q)} \frac{\partial Z(a,q)}{\partial q},$$
(49)



Figure 16. Fish school walks at different values of f_0 (shown above each of the trajectories) for which plankton spatial distributions shown in figure 12 are taken as initial. In the course of time these distributions did not undergo qualitative changes. For more details see (Medvinsky *et al* 2000).

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where

$$\frac{\partial Z}{\partial q} = \sum_{i=1}^{N(a)} \mathbf{w}_i(a)^q \ln \mathbf{w}_i(a), \tag{50}$$

and, analogous to eq. (48)

$$D(a, q) = qh(a, q) - \ln Z(a, q).$$
 (51)

The spectra D(q) and h(q) are defined in the following way (Arneodo *et al* 1995):

$$D(q) = \lim_{a \to 0} \frac{D(a, q)}{\ln a},$$
(52)

$$h(q) = \lim_{a \to 0} \frac{h(a, q)}{\ln a}.$$
(53)

From eqs (52) and (53) one computes the D(h) singularity spectrum. In contrast to using the Legendre transform (47), (48) such an approach makes it possible to avoid any instabilities related to numerical differentiation



Figure 17. Multifractal analysis of realizations of fractional Brownian processes $B_{0.6}(x)$ (a) and $B_{0.9}(x)$ (b) indexed by H = 0.6 and H = 0.9. Each of the dependencies $\log_2 Z(a, q)$ vs $\log_2 a$, h(a, q) vs $\log_2 a$, and D(a, q) vs $\log_2 a$ for each of the processes was obtained from 32 realizations, each 2^{12} in length. q values are shown at each of the graphs. (c) The difference between t(q) obtained numerically [(eq. (45)] and its theoretical value t(q) = qH - 1 (Muzy *et al* 1993). (d) Spectra f(a) (dashed lines) and D(h) (solid lines).

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and attendant errors. On the other hand, the canonical method allows us to define and to evaluate the errors in calculating D(q) and h(q) as the variances in slope of the linear approximations (52) and (53) (Tikhonov *et al* 2000).

Figure 17 demonstrates how both approaches work being applied to the model realization of fractional Brownian motion. One can see that all the functions $\log_2 Z(a,q) \operatorname{vs} \log_2 a, h(a,q) \operatorname{vs} \log_2 a$, and $D(a,q) \operatorname{vs} \log_2 a$ are essentially linear what agrees with eqs (45), (53) and (52), respectively. Notice (figure 17c) that the difference between numerical and theoretical values of t(q) is virtually independent on H and remains close to zero in a rather wide region of q. This region widens as the length of a realization increases. The error grows as |q| increases. Since the difference between numerical and theoretical values of t remains different from zero for any finite realization, both D(h) and f(a) fractal spectra are not



Figure 18. Multifractal analysis of small scale (O) and medium-scale (Δ) fish school displacements for different fish predation rates: $f_0 = 1$ (**a**), $f_0 = 4$ (**b**), and $f_0 = 15$ (**c**). Small-scale and medium scale displacements were obtained by splitting the fish school trajectories (like those shown in figure 16) into steps of length 2³ and 2⁵, respectively. Both the functions h(a, q) vs $\log_2 a$ (q values are shown at each of the graphs), and the spectra D(h) are presented for each of the f values. The error bars take into account the variances in slope of the linear approximations (52) and (53).

just points but form bell-like functions half-width of which is rather small in comparison with that characteristic of any multifractal process.

The similar narrow fractal-like spectra are typical of fish school displacements under a fish predation rate $f_0 = 15$ (figures 18c, 19c). It is seen that $h \approx 0.6$ corresponds to the maximum of *D*. Hence, these fish school displacements can be considered as fractional Brownian

motion with a Hurst exponent $H \approx 0.6$ what coincides well with the results obtained in (Medvinsky *et al* 2000). The singularity spectra change drastically as f_0 decreases.

Figure 18b demonstrates small-scale and medium-scale fish school displacements singularity spectra for $f_0 = 4$. These spectra are wider and have a shape very similar to that typical of multifractal spectra (Bacry *et al* 1993; Muzy *et al* 1993; Arneodo *et al* 1995, 1996).



Figure 19. Multifractal analysis of large scale fish school displacements for different fish predation rates: $f_0 = 1$ (**a**), $f_0 = 4$ (**b**), and $f_0 = 15$ (**c**). Large scale displacements were obtained by splitting the fish school trajectories (like those shown in figure 16) of length 2^{19} (for $f_0 = 4$ and $f_0 = 15$) and 2^{20} (for $f_0 = 1$) into steps of length 2^9 . The functions h(a, q) vs $\log_2 a$ (*q* values are shown at each of the graphs), t(q), the spectra f(a) (dashed lines) and D(h) (solid lines) are presented for each of the *f* values. The error bars take into account the variances in slope of the linear approximations (52) and (53).

Figure 18a demonstrates some results of the multifractal analysis of small-scale and medium-scale fish school displacements for $f_0 = 1$. One can see that small-scale displacements are characterized by essentially non-linear $h(\log_2 a)$ dependencies. As a result, the singularity spectrum can not be obtained. Such a spectrum for medium-scale fish school displacements is shown here. It is multifractal.

Finally, figure 19 demonstrates the results of the multifractal analysis of large-scale fish school displacements. One can see that the function t(q) for the fractal movement (figure 19c) is virtually linear, whereas the transition to multifractal D(h) and f(a) spectra is accompanied by a growing non-linearity of the t(q) function. Such a non-linearity is typical of multifractal patterns (Feder 1988).

3.4d Concluding remarks: In this section, a hybrid model of spatio-temporally continuous phytoplankton-zooplankton but discrete agent-like planktivorous fish dynamics is presented and investigated for inherent capacities of plankton patch formation which is known from natural aquatic populations (Radakov 1973; Bocharov 1990; Jörgensen 1994). Fish and plankton dynamics undergo continuous mutual adaptation. Fish school trajectories turned out to be essentially dependent on the fish predation rate f(figure 16). Any decrease of f is followed by a transition from low-persistent to high-persistent fish school movement. The low-persistent movement demonstrates fractal properties for all temporal scales, whereas high-persistent movements demonstrate pronounced multifractal properties for large-scale displacements. In this connection, the problem of changes in multifractal spectra D(h) and f(a)resulting from season changes are of particular interest. It is expected that future experiments and field observations will be able to prove whether fish school movement can be characterized in such a way.

In conclusion, the current results indicate that the rather simple conceptual minimal model (33)–(34) can describe a large variety of fish school movements which give rise to complex plankton spatio-temporal patterns resulting from prey–predator interactions and diffusion processes.

Obviously, the results presented in this paper are merely a starting point for further research. First of all, the effects of perturbations arising from diffusive interactions between neighbouring habitats in inhomogeneous environment would be worth studying. The analysis of the plankton dynamics in multi-habitat plankton–fish communities is the subject of our following paper (Medvinsky *et al* 2001).

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