Spatiotemporal Complexity of Plankton and Fish Dynamics*

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Abstract. Nonlinear dynamics and chaotic and complex systems constitute some of the most fascinating developments of late twentieth century mathematics and physics. The implications have changed our understanding of important phenomena in almost every field of science, including biology and ecology. This article investigates complexity and chaos in the spatiotemporal dynamics of aquatic ecosystems. The dynamics of these biological communities exhibit an interplay between processes acting on a scale from hundreds of meters to kilometers, controlled by biology, and processes acting on a scale from dozens to hundreds of kilometers, dominated by the heterogeneity of hydrophysical fields. We focus on how biological processes affect spatiotemporal pattern formation. Our results show that modeling by reaction-diffusion equations is an appropriate tool for investigating fundamental mechanisms of complex spatiotemporal plankton dynamics, fractal properties of planktivorous fish school movements, and their interrelationships.

Key words. chaos, order, scaling, aquatic ecosystems, predator-prey interaction, modeling

AMS subject classifications. 82C41, 92B05, 92D25, 92D40

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I. Introduction to Plankton and Fish School Patterns and Scales.

I.I. Patterns in Nonlinear Nonequilibrium Systems. Pattern formation in nonlinear complex systems is one of the central problems of the 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, and waves, and

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the emergence of macroscopic order from microscopic interactions in various nonlinear nonequilibrium systems in nature and society have been the subject of many theoretical and experimental studies.

The classical approach to the origin of spatial structures was developed by Turing (1952) and his followers (for references see Medvinsky et al., 1997). These investigations found that an initially uniform distribution of reacting components can become unstable. As the instability develops, a spatially nonuniform distribution (a spatial structure) of activators and inhibitors appears. Turing pattern formation is based on the coupling of linear diffusion and nonlinear local kinetics under conditions when the diffusivity of the activator is less than that of the inhibitor. Fairly recent experimental work by de Kepper et al. (1991) has demonstrated Turing structures in chemical reactions.

A major unsolved problem with Turing's approach is that the identification of activators and inhibitors that could be involved in the formation of patterns in chemical, biological, or social systems is still lacking, and may be unachievable. Nowadays, more realistic theoretical approaches are being considered. These account for complex spatiotemporal dynamics of open spatially confined systems as a result of the interaction between intrinsic dynamics of the system and external forcing by the 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 roles of predator invasion, planktivorous fish cruising and feeding, and the interaction of neighboring habitats in the formation of the complex transient spatiotemporal plankton patterns which occur in the ocean.

1.2. Plankton and Models of Plankton Dynamics: An Overview. Plankton are floating organisms of many different phyla living in the pelagic of the sea, in freshwater lakes, or in larger rivers. They are to a large extent subject to water movements (Sommer, 1994, 1996; Baretta-Bekker, Duursma, and Kuipers, 1998, p. 235). 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 are picoplankton (less than $2 \mu m$), nanoplankton (2–20 μm), microplankton (20–200 μm), mesoplankton (0.2–2 mm), macroplankton (2–20 mm), and megaplankton (greater than 20 mm) (Raymont, 1980; Baretta-Bekker, Duursma, and Kuipers, 1998, p. 235).

In the 17th century, the Dutch pioneer microscopist Anton van Leeuwenhoek was probably the first human being to see minute creatures, which he called *animal-cules*, 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* (from the Greek *planktos* = wandering).

Phytoplankton are microscopic plants that drive all marine ecological communities and the life within them. Photosynthesis by the world's phytoplankton generates half of the oxygen that mankind needs for maintaining life and absorbs half of the carbon dioxide that may be contributing to global warming. Besides oxygen and carbon dioxide, other substances are also recycled by phytoplankton, including phosphorus, nitrogen, and sulphur (Bain, 1968; Ritschard, 1992; Duinker and Wefer, 1994; Malin, 1997). Hence, phytoplankton are one of the main factors controlling the further development of the world's climate, and there is a vast literature on this subject; cf. 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 turn, the abundance of the plankton species is affected by a number of environmental factors such as water temperature, salinity, sunlight intensity, and biogen availability (Raymont, 1980; Sommer, 1994). Temporal variability of the species composition is caused by seasonal changes and, according to theories originating in papers of Lotka (1925) and Volterra (1926), is also due to trophical prey-predator interactions between phyto- and zooplankton.

Because of their evident importance, the dynamics of plankton systems have been under investigation for more than a hundred years. From the beginning, plankton studies have regularly combined field observations, laboratory experiments, and mathematical modeling. It was in the 19th century that fisheries first stimulated interest in plankton dynamics, because strong positive correlations between zooplankton and fish abundance were found. The German expedition of 1889 just mentioned 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 for understanding and predicting fish stock dynamics and their correlations with biological and physical factors and human interventions; cf. Cushing (1975), Gulland (1977), Steele (1977).

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

The control of phytoplankton blooming by zooplankton grazing was modeled 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 Lotka–Volterra equations to describe the prey-predator relation 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 were introduced by Ivlev (1945), with a 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 also in use (cf. 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 slow relaxation to the steady state after a supercritical external perturbation such as sudden temperature increase and nutrient inflow is suitable for modeling red or brown tides (Beltrami, 1989, 1996; Truscott and Brindley, 1994a,b).

Concerning temporal variability of plankton species abundance, an issue of particular interest is the limits of its predictability. At early stages, development of mathematical models of marine ecosystems was driven by the idea that the more species were explicitly included in a model, the higher would be its predictive ability. As a result, a number of many-species models appeared that allowed for detailed structure of the food web; cf. DeAngelis (1992), Jörgensen (1994), Yodzis (1994). However, the actual predictive ability of this class of models is not very high, rarely exceeding a few weeks. In fact, increasing the number of agents may sometimes make the accuracy of a model worse rather than better. This apparent paradox can be explained in terms of dynamical chaos (May, 1974). Although strict evidence of chaotic behavior of natural populations is still lacking, stronger indications of its existence are appearing (Scheffer, 1991b, 1998; Godfray and Hassell, 1997; Huisman and Weissing, 1999). Chaotic population dynamics fundamentally changes the very basis of system predictability (Scheffer, 1991b) and makes what one might call "schematic" models of as much use as many-species ones. Indeed, few-species models can sometimes be even more instructive, since they take into account only principal features of community functioning; cf. Pascual (1993), Petrovskii and Malchow (1999, 2001a), Petrovskii et al. (2001).

Another interesting problem is the dynamics of externally forced systems. Periodic forcing appears natural due to daily, seasonal, or annual cycles of photosynthetically active radiation, temperature, nutrient availability, etc. (Evans and Parslow, 1985; Truscott, 1995; Popova et al., 1997; Ryabchenko et al., 1997). Natural forcings are of course perturbed by environmental noise. A number of forced models have been investigated for parts of the food chain or for all of it, from nutrients, phytoplankton, and zooplankton to planktivorous fish, and many different routes to chaotic dynamics have been demonstrated (Kuznetsov, Muratori, and Rinaldi, 1992; Ascioti et al., 1993; Doveri et al., 1993; Rinaldi and Muratori, 1993; Scheffer et al., 1997; Scheffer, 1998; Steffen and Malchow, 1996a,b; Steffen, Malchow, and Medvinsky, 1997; Petrovskii and Malchow, 2001b; Malchow, Petrovskii, and Medvinsky, 2002).

The abundance of plankton species changes not only in time but also in space. Spatial heterogeneity of plankton distributions, known as "patchiness," is seen 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 centimeters to thousands of kilometers. A number of explanations have been suggested, in particular, relating the spatial structure of a plankton system to marine turbulence (Platt, 1972) or to the inhomogeneity of the temperature field in the ocean (Denman, 1976). A well-studied stripy plankton pattern is due to the trapping of populations of sinking microorganisms in Langmuir circulation cells (Stommel, 1948; Leibovich, 1993). Other physically determined plankton distributions have been reported too, such as steep density gradients due to local temperature differences, nutrient upwelling, turbulent mixing, or internal waves (Yoder et al., 1994; Franks, 1997; Abraham, 1998).

On a small scale of some tens of centimeters, and under relative physical uniformity, differences in "diffusive" mobility of individuals and the capability of locomotion might also create finer spatial structures, due, for example, to bioconvection and gyrotaxis (Platt, 1961; Winet and Jahn, 1972; Pedley and Kessler, 1992; Timm and Okubo, 1994). For certain bacteria, though not yet for plankton, the mechanism of diffusion-limited aggregation (Witten and Sander, 1981) has been proposed and experimentally verified for the spatial fingering of colonies (Matsushita and Fujikawa, 1990; Ben-Jacob et al., 1992).

Thus, mathematical models of plankton population dynamics have to account not only 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 growth, interactions, and transport that yields the whole variety of spatiotemporal population structures, and in particular the phenomenon of patchiness (cf. Fasham, 1978; Okubo, 1980). Mathematical modeling of these effects requires the use of reaction-diffusion and perhaps advection equations. A good introduction to the latter field has been provided by Holmes et al. (1994).

Since the classic paper by Turing, dissipative mechanisms of spontaneous spatial and spatiotemporal pattern formation in a homogeneous environment have been of interest in biology and ecology. Turing showed that the nonlinear interaction of two or more agents with widely different diffusion coefficients can give rise to spatial structure. Segel and Jackson (1972) were the first to apply Turing's ideas 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 as 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.

Skellam (1951) and Kierstead and Slobodkin (1953) were perhaps the first to consider the critical size problem for plankton patches, presenting a model, now called KISS (Kierstead–Slobodkin–Skellam), that couples exponential growth and diffusion of a single population. 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, Petrovskii, and Piskunov, 1937).

Populations with an Allee effect (Allee, 1931; Allee et al., 1949), where the existence of a minimum viable number of species yields two stable population states, namely, extinction or survival at the carrying capacity, show a spatial critical size as well (Schlögl, 1972; Nitzan, Ortoleva, and Ross, 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, while others go extinct. However, bistability and the emergence of a critical spatial size do not necessarily require an Allee effect, for logistically growing prey with a parameterized predator of type II or III functional response can also exhibit two stable steady states and the related hysteresis loops (cf. Ludwig, Jones, and Holling, 1978; Wissel, 1989).

The consideration of dynamic predation leads to a full spectrum of spatial and spatiotemporal patterns, including regular and irregular oscillations, propagating fronts, target patterns and spiral waves, pulses, and stationary spatial patterns. Some of these structures were first observed in oscillating chemical reactions (cf. 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 kilometer scale (Wyatt, 1973). They have also been found in parasitoid-host systems (Boerlijst, Lamers, and Hogeweg, 1993). For other motile microorganisms, traveling waves such as targets or spirals have been found in the cellular slime mold *Dictyostelium discoideum* (Gerisch, 1968, 1971; Keller and Segel, 1970, 1971a,b; Segel and Stoeckly, 1972; Segel, 1977; Newell, 1983; Alt and Hoffmann, 1990; Ivanitsky, Medvinsky, and Tsyganov, 1991; Siegert and Weijer, 1991; Steinbock, Hashimoto, and Müller, 1991; Vasiev, Hogeweg, and Panfilov, 1994; Höfer, Sherratt, and Maini, 1995). These amoebae are chemotactic species, i.e., they move actively up the gradient of a chemical attractant and aggregate. Chemotaxis is a kind of density-dependent cross-diffusion, and it is an interesting open question whether there is preytaxis in plankton or not. However, there is some evidence of chemotaxis in certain phytoplankton species (Ikegami et al., 1995). Bacteria like *Escherichia coli* or *Bacillus subtilis* also show a number of complex colony growth patterns (Adler, 1966; Adler and Templeton, 1967; Ivanitsky, Medvinsky, and Tsyganov, 1991, 1994; Medvinsky et al., 1991; 1993a; 1993b; 1994; Shapiro and Hsu, 1989; Shapiro and Trubatch, 1991; Reshetilov et al., 1992), different from the diffusion-limited aggregation patterns already mentioned. Their emergence requires cooperation and active motion of the species, which has also been modeled as density-dependent diffusion and predation (Kawasaki, Mochizuki, and Shigesada, 1995; Kawasaki et al., 1995; Mimura, Sakaguchi, and Matsushita, 2000).

Allowing for spatial dependences in the plankton community opens up new routes to chaotic dynamics. Diffusion-induced spatiotemporal chaos along a neutral gradient was found by Pascual (1993). Chaotic oscillations behind propagating diffusive fronts are found in a prey-predator model (cf. Sherratt, Lewis, and Fowler, 1995; Sherratt, Eagan, and Lewis, 1997) and a three competitive species model (Petrovskii et al., 2001); a similar phenomenon is also observed in a model of a chemical reactor (Merkin et al., 1996; Davidson, 1998). Recently, it has been shown that the appearance of chaotic spatiotemporal oscillations in a prey-predator system is a somewhat more general phenomenon and must not be attributed to the species front propagation or to the inhomogeneity of environmental parameters (Petrovskii and Malchow, 1999, 2001a).

Conditions for the emergence of three-dimensional spatial and spatiotemporal patterns after differential-flow-induced instabilities (Rovinsky and Menzinger, 1992) of spatially uniform populations were derived by Malchow (1996, 1998, 2000a,b) and illustrated by patterns in a minimal phytoplankton-zooplankton model due to Scheffer (1991a). Instabilities in the uniform distribution can arise if phytoplankton and zooplankton move with different velocities, regardless of which one is faster. This mechanism of generating patchiness is more general than the Turing mechanism, which depends on strong conditions on the diffusion coefficients, and one can expect it to be widely applicable in population dynamics.

This discussion should make it clear that the dynamics of the plankton communities and, in particular, processes of plankton pattern formation, have been under intensive investigation in recent decades. Considerable progress has been made in understanding the principal features. However, many mechanisms of the spatiotemporal variability of natural plankton populations are still not known. Pronounced physical patterns like thermoclines, upwelling, fronts, and eddies often set the framework for the biological processes; cf. section 4. However, under conditions of relative physical uniformity, the temporal and spatiotemporal variability can be a consequence of the coupled nonlinear biological and chemical dynamics (Levin and Segel, 1976; Steele and Henderson, 1992). Daly and Smith (1993) concluded that "... biological processes may be more important at smaller scales where behavior 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; see also Wroblewski et al. (1975, 1976).

Physical and biological processes may differ significantly not only in spatial but also in temporal scale. In particular, the effect of external hydrodynamic 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 subject to 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 dependent on the interplay of various physical (light, temperature, hydrodynamics) and biological (nutrient supply, predation) factors (cf. Platt, 1972; Denman, 1976; Fasham, 1978). In nature, it has been observed that the direction of motion of plankton patches does not always coincide with that of the water (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 of less than a few dozen kilometers (Weber, El-Sayed, and Hampton, 1986). This indicates that biological factors play an essential role in the emergence of plankton patchiness (Steele and Henderson, 1981). The question arises: Can biological factors, such as predator-prey growth and interactions, be a cause of plankton pattern formation without any hydrodynamic forcing?

In this article, we apply schematic few-species models to demonstrate that predator-prey interactions can give rise to complex spatiotemporal dynamics of both plankton and plankton–fish communities.

2. Complex Patterns in a Minimal Model of Plankton Dynamics.

2.1. Mathematical Model. In this section, the spatiotemporal dynamics of an aquatic community is modeled by a two-species prey-predator (i.e., phytoplankton-zooplankton) system. We show that the formation of a patchy spatial distribution of species can be described by this relatively simple model. The environment is assumed to be uniform, i.e., the system parameters do not depend on space or time.

According to a widely accepted approach (Murray, 1989; Levin, Powell, and Steele, 1993; Malchow, 1993; Holmes et al., 1994; Shigesada and Kawasaki, 1997; Sherratt, 2001), the functioning of a prey-predator community can be described by a reaction-diffusion system of the form

(2.1)
$$u_t(\mathbf{r},t) = D\nabla^2 u(\mathbf{r},t) + f(u,v),$$

(2.2)
$$v_t(\mathbf{r},t) = D\nabla^2 v(\mathbf{r},t) + g(u,v).$$

Here, $u(\mathbf{r}, t)$ and $v(\mathbf{r}, t)$ are the abundance of prey and predator, respectively, \mathbf{r} is the position vector, t is time, and D is the diffusion coefficient. We assume that the diffusivities are equal for both species, which 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, must have the following structure: f(u, v) = $P(u) - E(u, v), g(u, v) = \kappa E(u, v) - \mu v$. 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 parameter μ is the mortality rate of the predator, and κ is the coefficient of food utilization.

The particular choice of the functions P(u) and E(u, v) in (2.1)–(2.2) may vary 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 systems (Raymont, 1980; Fasham, 1978), we assume that the local growth of the prey is logistic and that the predator shows the Holling type II functional response. Then, having chosen the simplest mathematical expressions for P(u) and E(u, v) (Murray, 1989; Shigesada and Kawasaki, 1997), we arrive at the equations

(2.3)
$$u_t = D\nabla^2 u + \frac{\alpha}{b}u(b-u) - \gamma \frac{u}{u+H}v,$$

(2.4)
$$v_t = D\nabla^2 v + \kappa \gamma \frac{u}{u+H} v - \mu v,$$

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where α, b, H , and γ are constants: α is the maximal growth rate of the prey, b is the carrying capacity for the prey population, and H is the half-saturation abundance of prey. In a schematic, few-species model such as (2.1)–(2.2), it makes little sense to look for a more detailed parameterization.

The next step is to introduce dimensionless variables. Considering

(2.5)
$$\tilde{u} = u/b, \quad \tilde{v} = v\gamma/(\alpha b), \quad \tilde{t} = \alpha t, \quad \tilde{\mathbf{r}} = \mathbf{r}(\alpha/D)^{1/2},$$

and new dimensionless parameters h = H/b, $m = \mu/\alpha$, and $k = \kappa \gamma/\alpha$, from (2.3)–(2.4) we arrive at the following equations containing only dimensionless quantities:

(2.6)
$$u_t = \nabla^2 u + u(1-u) - \frac{u}{u+h}v,$$

(2.7)
$$v_t = \nabla^2 v + k \frac{u}{u+h} v - mv.$$

Tildes are omitted here and below. More details about the choice of dimensionless variables in the system (2.3)–(2.4) as well as possible implications can be found in Petrovskii and Malchow (2001a).

Before proceeding to the study of spatiotemporal pattern formation, we consider the local dynamics of the system, i.e., the properties of (2.6)-(2.7) without diffusion terms. One finds by linear stability analysis that the system

(2.8)
$$u_t = u(1-u) - \frac{u}{u+h}v$$
, $v_t = k\frac{u}{u+h}v - mv$

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

(2.9)
$$u_* = \frac{rh}{1-r}$$
 and $v_* = (1-u_*)(h+u_*),$

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

Although the parameter space of (2.8) is three-dimensional, the properties of the local dynamics mainly depend on H and the ratio r = m/k, showing less pronounced dependence on k separately; cf. Petrovskii and Malchow (1999, 2000, 2001a). In

particular, the state (u_*, v_*) moves to the biologically meaningful region u, v > 0 when

$$(2.10) h < \frac{1-r}{r}$$

and becomes unstable for parameter values

$$(2.11) h < \frac{1-r}{1+r}$$

In the latter case, the steady state is surrounded by a stable limit cycle and the kinetics of the system is oscillatory. These results provide helpful information for choosing parameter values for numerical simulations of the full problem (2.6)-(2.7). In the case of existence of a stable stationary point (i.e., when (2.10) holds and (2.11) does not), the dynamics of the system typically reduces to relaxation to the spatially homogeneous state $u(x,t) \equiv u_*, v(x,t) \equiv v_*$. The details of the process depend on the type of the initial conditions. For example, for a finite initial distribution of species the relaxation usually takes place after propagation of diffusive fronts (Dunbar, 1986; Murray, 1989; Petrovskii, Vinogradov, and Morozov, 1998; Petrovskii and Malchow, 2000). Since we are more concerned here with the formation of transient spatiotemporal patterns, it is the parameter values satisfying condition (2.11) that are of primary interest (Kopell and Howard, 1973; Sherratt, Lewis, and Fowler, 1995; Petrovskii and Malchow, 1999).

2.2. Results of Computer Simulations: One-Dimensional Case. The spatiotemporal dynamics of a diffusion-reaction system depend on the choice of initial conditions. Recently, (2.6)–(2.7) have been considered in a few papers (Sherratt, Lewis, and Fowler, 1995; Shigesada and Kawasaki, 1997; Petrovskii and Malchow, 2000) in connection with the problem of biological invasion, where the initial conditions are naturally described by finite functions and the dynamics of the community mainly consists of a variety of diffusive populational fronts. In the present article we are interested in another situation that seems to be more general from the biological point of view. At the beginning of the process, both populations are spread over the whole area. In a real community, the details of the initial spatial distribution of the species can be determined by quite specific causes. The simplest form of the initial distribution would be spatially homogeneous. However, in this case the distribution of the species remains homogeneous for all time, and no spatial pattern can emerge. To get nontrivial dynamics, one has to perturb the homogeneous distribution.

In this subsection, we focus on the one-dimensional dynamics of the system (2.6)–(2.7) with u = u(x,t), v = v(x,t), and $\nabla^2 = \frac{\partial^2}{\partial x^2}$. Several different forms of perturbed initial conditions will be considered. We begin with the "constant-gradient" distribution

(2.12)
$$u(x,0) = u_*,$$

(2.13)
$$v(x,0) = \phi_1(x) = v_* + \epsilon x + \delta,$$

where ϵ and δ are parameters.

The results of our computer simulations show that the type of the system dynamics is determined by the values of ϵ and δ . If ϵ is small, the initial conditions (2.12)–(2.13) evolve to a smooth heterogeneous spatial distribution of species (Petrovskii and Malchow, 1999). The spatial distributions vary gradually in time, the local



Fig. 1 Spatial distribution of populations (solid lines for prey, dashed for predator) for a case where the regular phase is gradually displaced by the chaotic phase: (a) t = 640, (b) t = 2640.

temporal behavior of the dynamical variables u and v following the limit cycle of the homogeneous system. This regime is not self-sustained, and the smooth spatial pattern arising in this case slowly relaxes to the spatially homogeneous distribution of species (Petrovskii and Malchow, 2001a).

For another set of parameters (e.g., if ϵ exceeds a critical value ϵ_{cr} depending on δ), the features of the spatial distribution become essentially different; cf. Petrovskii and Malchow (1999). Figure 1 shows the spatial distribution of species at t = 640 and 2640 for k = 2.0, r = 0.4, h = 0.3, $\epsilon = 10^{-6}$, and $\delta = -1.5 \cdot 10^{-3}$. In this case, the initial distribution (2.12)–(2.13) leads to the formation of a strongly irregular "jagged" transient pattern inside a subdomain of the system (Figure 1(a)). The size of this region grows steadily with time and, eventually, irregular oscillations prevail over the whole domain (Figure 1(b)). This regime is persistent. Long-time numerical simulations show that after the irregular spatiotemporal oscillations occupy the whole domain, the dynamics of the system does not undergo any farther changes.

For these parameters the temporal behavior of the concentrations u and v also becomes completely different. Figure 2 exhibits the "local" phase plane of the system obtained in a fixed point $\bar{x} = 480$ inside the region invaded by the irregular spatiotemporal oscillations. Instead of following the limit cycle, as happens in the 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 spatiotemporal chaos; see also 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 each moment separating the regions with different dynamic regimes, i.e., the jagged and smooth patterns. Our numerical results show that these interfaces propagate with approximately constant speed in opposite directions, so that the size of the chaotic region steadily grows. The phenomenon is essentially spatiotemporal: the chaos prevails as a result of the displacement of the regular regime by the chaotic one. The dynamics of the system looks similar to a phase transition between regular and chaotic phases.

Since the spatial distribution of the species abundance is essentially inhomogeneous, it seems that more information can be obtained from consideration of values



Fig. 2 Phase plane of the system at a fixed point inside the domain occupied by irregular spatiotemporal oscillations.



Fig. 3 Phase plane of spatially averaged densities of prey and predator for a case of irregular dynamics; parameters are given in the text. The dashed line shows the limit cycle of the spatially homogeneous system; the broken straight lines show the position of the steady state.

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 example will be considered below). Figure 3 shows a sketch of the phase plane $(\langle u \rangle, \langle v \rangle)$ for the parameters k = 2.0, r = 0.33, h = 0.43. While in the smooth pattern regime the trajectory (not shown) slowly approaches the limit cycle, for the regime of a jagged pattern the trajectory remains close to 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. This means that the amplitude of the temporal changes in the spatially averaged species abundance is much smaller in the case of a jagged pattern than for a smooth one.

The "two-phase" dynamics of the system (2.6)-(2.7) described above does not result from a specific choice of the initial conditions (2.12)-(2.13). It remains qualitatively similar for other quite different initial distributions. In particular, for the initial conditions

(2.14)
$$u(x,0) = u_*,$$

 $v(x,0) = v_* \text{ for } x \le x_0 \text{ or } x \ge x_0 + S,$
(2.15) $v(x,0) = v_* + A \sin\left(\frac{2\pi(x-x_0)}{S}\right) \text{ for } x_0 \le x \le x_0 + S,$

the spatially homogeneous limit cycle oscillation survives only for very small values of the amplitude A and magnitude S of the perturbation; cf. Petrovskii and Malchow (2001a). For somewhat larger but still small values of A and S, a smooth regular pattern arises. For larger values of A and S, the initial distribution evolves to a jagged pattern. The "embryo" of the chaotic phase first appears in the vicinity of the initial finite perturbation of the homogeneous steady state. The moving interface now separates the domain occupied by irregular oscillations from the homogeneous region. In this case, the speed of the interface can be found analytically (Petrovskii and Malchow, 2001a); for a discussion of similar issues see also Petrovskii et al. (2001).

If started with somewhat more complex, e.g., nonmonotonic, 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 (Figure 4). As an example, consider the initial conditions

(2.16) $u(x,0) = u_* + \epsilon(x - x_1)(x - x_2),$

(2.17)
$$v(x,0) = v_*.$$

In this case, slightly perturbed initial conditions evolve to a complex spatial structure where two domains occupied by jagged patterns are separated by regions with smooth ones; see Figure 4, which shows a snapshot of the distribution at t = 600 for $\epsilon = 10^{-8}$, $x_1 = 1200$, and $x_2 = 2800$, with other parameters as in Figure 1. As in the previous case, the chaotic domains grow steadily, eventually displacing the regular phase and occupying the whole region.

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



Fig. 4 An intermittent spatial structure appearing from nonmonotonic initial conditions (2.16)– (2.17); parameters are given in the text. Solid line for prey, dashed for predator.

The scenario of pattern formation described above appears to be essentially different from those already known for two-component diffusion-reaction systems (Turing, 1952; Segel and Jackson, 1972; Rovinski and Menzinger, 1992; Pascual, 1993; Malchow and Shigesada, 1994; Malchow, 1995; Sherratt, Lewis, and Fowler, 1995). The model (2.6)-(2.7) describing formation of the jagged spatial structure is in a certain sense "minimal," because it does not contain the usual assumptions and restrictions, e.g., about different mobility of interacting species or environmental heterogeneity. In the rest of this section, we consider further this new mechanism of pattern formation. First, we produce evidence of the chaotic nature of the irregular spatiotemporal oscillations just described. Second, to estimate the applicability of this mechanism to the dynamics of ecological communities, we extend the results to two space dimensions.

2.3. Spatiotemporal Chaos. In this subsection we show that the formation of a jagged transient patchy structure in the distribution of the species corresponds to spatiotemporal chaos. The term "chaos" has a specific meaning, and a visible irregularity of the system behavior, however complex it may be, does not necessary mean chaotic dynamics. According to its rigorous definition, chaos means sensitivity to initial conditions, with small variations of the initial distribution of species leading to exponentially growing discrepancies between species distributions later. This feature 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 decrease of the autocorrelation functions; cf. Nayfeh and Balachandran (1995). Thus, to identify chaos in the dynamics of the system, a variety of methods can be used. We note that the concept of chaos appeared originally in connection with the temporal dynamics of a spatially homogeneous system. Meanwhile,



Fig. 5 Spatial distribution of prey abundance at (a) t = 550 and (b) t = 750 for perturbed (dashed) and unperturbed (solid) initial conditions.

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. In particular, the appearance of chaos in the two-species system is a crucial consequence of the formation of spatial patterns. The phenomenon is essentially spatiotemporal and thus, to distinguish it from the purely temporal chaotic dynamics of a homogeneous system, the term "spatiotemporal chaos" seems to be more appropriate.

To show that the formation of jagged transient patterns is chaotic, we test the sensitivity of the species distribution to variations in the initial condition. Figures 5–8 present results of this kind. First, (2.6)-(2.7) are solved for parameter values corresponding to oscillatory local kinetics of the system (cf. (2.11)) to provide the formation of jagged patterns. The initial conditions are taken in the form (2.12)-(2.13). Then (2.6)-(2.7) are solved with slightly perturbed initial conditions $u(x,0) = u_*$, $v(x,0) = \phi_1(x) + \Delta v$, the perturbation Δv being chosen in the form

(2.18)
$$\Delta v = \epsilon_{pert} \sin\left(\frac{2\pi(x-x_0)}{L_{pert}}\right)$$

for $x_0 \leq x \leq x_0 + L_{pert}$, otherwise $\Delta v = 0$.

Then the spatial distributions of species calculated in the two cases are compared. Figure 5 shows the prey abundance (a comparison for the predator leads to a similar result) obtained at t = 600 and 800 for perturbed (with $x_0 = 150$, $L_{pert} = 5$, and $\epsilon_{pert} = 0.01$) and unperturbed initial conditions (2.12)–(2.13) for parameter values $k = 2.0, r = 0.3, h = 0.4, \epsilon = 2 \cdot 10^{-4}, \delta = -3 \cdot 10^{-2}$. Up to $t \approx 600$ there is little difference between the solutions. For t > 600, the difference begins growing rapidly, and at t = 800 it is of the same order as the solutions themselves. Qualitatively similar behavior is observed for other values of L_{pert} and ϵ_{pert} and for other parameter values corresponding to the formation of irregular structures.

Figure 6 quantifies the growth of perturbations by showing the absolute value b(t) of the local difference between the prev concentrations at the fixed point $\bar{x} = 150$ for



Fig. 6 Local difference b(t) between perturbed and unperturbed solutions calculated at a fixed point $\bar{x} = 150$.

the two cases,

(2.19)
$$b(t) = |u_{pert}(\bar{x}, t) - u_{unpt}(\bar{x}, t)|.$$

These pointwise results would be conclusive in their own right if obtained for a system without a spatial structure. This is not so in our case. To address the appearance of prominent spatial patterns we also calculate a distance d(t) between the perturbed and unperturbed solutions that allows for the spatial variation of the system,

(2.20)
$$d(t) = \max |u_{pert}(x,t) - u_{unpt}(x,t)|, \quad 0 \le x \le L,$$

where L is the length of the domain. Values of d at different times are shown in Figure 7 (parameters are the same as above). The behavior of d(t) also confirms sensitivity of 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 spatially averaged solutions. In general, this approach is not equivalent to that based on (2.20). Indeed, one can imagine a situation where two spatial distributions differ significantly in a few points but appear quite close in terms of averaged values. We define the "distance-on-average" by

(2.21)
$$n(t) = |\langle u_{pert} \rangle(t) - \langle u_{unpt} \rangle(t)|.$$

The results of the calculation of n(t) shown in Figure 8 (parameters are the same as in Figures 5–7) are in a good agreement with those obtained by the other approaches.

The results of Figures 5–8 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 conclusion is robust with respect to the method of quantifying



Fig. 7 Distance d(t) between perturbed and unperturbed solutions defined by (2.20).



Fig. 8 Distance n(t) between perturbed and unperturbed solutions defined by (2.21) on the basis of spatially averaged values.

the difference between the perturbed and unperturbed solutions. The estimates of the characteristic time T obtained from different approaches (cf. (2.19)–(2.21)) are also consistent. The dominant Lyapunov exponent is obviously positive, its value being estimated to lie between 0.003 and 0.01.

Another way to demonstrate the chaotic nature of the irregular spatiotemporal oscillations of the species abundance is to calculate autocorrelation functions. The state of a prey-predator community is described by the two dynamical variables u and v, the densities of prey and predator. Thus, for the 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 the predator shows a similar behavior.

An immediate application of the standard definition leads to certain problems. According to the usual approach, if a dynamical variable ψ is a function of a variable τ , which may be time or position or anything else, the autocorrelation function is defined by

(2.22)
$$F(s) = \lim_{Z \to \infty} \frac{1}{Z} \int_0^Z \psi(\tau + s) \psi(\tau) d\tau.$$

In the problem under consideration, the prey density depends on two variables: position and time. If we apply (2.22) to characterize the spatial structure of the system, we arrive at

(2.23)
$$\tilde{F}(s,t) = \lim_{Z \to \infty} \frac{1}{Z} \int_0^Z u(x+s,t)u(x,t)dx$$

This equation has a few drawbacks. First, \tilde{F} depends not only on *s* but also on *t*. The situation when the properties of \tilde{F} are explicitly time-dependent appears rather exotic and makes the interpretation of the results 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 behavior. Another problem is that, in order to obtain reliable results in computer simulations, the value of Z must be chosen sufficiently large. The numerical grid should contain hundreds of thousands of nodes, which is hardly practical.

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

(2.24)
$$K(s) = \lim_{T \to \infty} \frac{1}{T} \int_0^T u(x_0 + s, t) u(x_0, t) dt.$$

This equation includes the usual definition as a special case if the system exhibits ergodic behavior. Although the value of K formally depends on the parameter x_0 , our numerical simulations show no significant dependence on x_0 .

The function K(s) is shown in Figure 9 (for $k = 2.0, r = 0.2, H = 0.3, x_0 = 100$, with averaging done over the time interval $t \in [4000, 12000]$). Note the great difference between the solid line, corresponding to irregular dynamics (jagged patterns), and the dashed line, corresponding to regular dynamics (smooth). One can see that, in the case of the regular dynamics, the behavior of the system is highly correlated over the whole domain. 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 correlations of the temporal behavior between different points



Fig. 9 Autocorrelation function K(s) for the regimes of jagged (solid) and smooth (dashed) patterns.

increases. In the limit $t \to \infty$, temporal oscillations throughout the system become synchronized and $K(s) \equiv 1$.

In contrast, the behavior of the autocorrelation function for the case of jagged patterns shown in Figure 9 is typical for chaotic dynamics; cf. Nayfeh and Balachandran (1995). The irregular oscillations of small amplitude in K(s) are a consequence of the finiteness of the averaging interval T; our numerical simulations show that their amplitude decreases to zero as T increases. Since the modified definition (2.24) of the autocorrelation function takes into account both spatial and temporal dependence, the dynamical regime corresponding to the formation of jagged patterns can be classified as spatiotemporal chaos; this is consistent 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 spatiotemporal chaos in a prey-predator system was described in terms of the temporal behavior of spatially averaged densities.

2.4. Pattern Formation in the Two-Dimensional Case. Now we consider the extension of these results to two space dimensions. In this case, (2.6)-(2.7) take the form

(2.25)
$$\frac{\partial u(x,y,t)}{\partial t} = \frac{\partial^2 u}{\partial^2 x} + \frac{\partial^2 u}{\partial^2 y} + u(1-u) - \frac{u}{u+h}v$$

(2.26)
$$\frac{\partial v(x,y,t)}{\partial t} = \frac{\partial^2 v}{\partial^2 x} + \frac{\partial^2 v}{\partial^2 x} + k \frac{u}{u+h} v - mv,$$

with $0 < x < L_x$, $0 < y < L_y$. Equations (2.25)–(2.26) describe the dynamics of an aquatic community in a horizontal layer, the vertical distribution of species inside the layer being assumed homogeneous. The equations are solved numerically. The choice of length L_x and width L_y of the domain may be different in different computer ex-

periments; in the results shown below, $L_x = 900, L_y = 300$. At the domain boundary, zero-flux conditions are imposed. As above, the type of the system dynamics depends on the choice of the initial conditions. For a purely homogeneous initial distribution of species, the system stays homogeneous forever and no spatial pattern emerges. For a very weakly perturbed initial distribution (the shape of the perturbation can be different, following, e.g., (2.12)-(2.13) or (2.14)-(2.15)), a smooth pattern arises that is not persistent and gradually evolves to the homogeneous distribution. For somewhat stronger initial perturbations, however, the system evolves to the formation of a jagged spatial pattern that 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 two-dimensional generalization of (2.16)-(2.17). Specifically,

(2.27)
$$u(x, y, 0) = u_* - \epsilon_1 (x - 0.1y - 225)(x - 0.1y - 675),$$

(2.28)
$$v(x, y, 0) = v_* - \epsilon_2(x - 450) - \epsilon_3(y - 150),$$

where $\epsilon_1 = 2 \cdot 10^{-7}$, $\epsilon_2 = 3 \cdot 10^{-5}$, and $\epsilon_3 = 1.2 \cdot 10^{-4}$. (The initial conditions are deliberately chosen to be unsymmetric in order to make any influence of the corners of the domain more visible.) The values of parameters in (2.25)-(2.26) are chosen as k = 2.0, r = 0.3, h = 0.4. Snapshots of the spatial distribution arising from (2.27)-(2.28) are shown in Figure 10 for t = 0, 150, 200, 300, 400, 1000. Since both species exhibit qualitatively similar behavior, except in the early stages of the process when the influence of the initial condition is dominant, only the prey (phytoplankton) abundance is shown.

Figure 10 shows that for the two-dimensional system (2.25)-(2.26), the formation of the irregular patchy structure 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 center of each spiral is situated in a critical point (x_{cr}, y_{cr}) , where $u(x_{cr}, y_{cr}) = u_*, v(x_{cr}, y_{cr}) = v_*$ (cf. the results obtained in the one-dimensional case). The distribution (2.27)-(2.28) contains two such points; for other initial conditions, the number of spirals may be different. After the spirals form (Figure 10(b)), they grow slightly for a certain time, their spatial structure becoming more distinct (Figures 10(b) and 10(c)). The destruction of the spirals begins in their centers (Figure 10(d)). Once appearing, the "embryos" of the patchy structure steadily grow (Figures 10(d) and 10(e)), and finally the irregular 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:

(2.29)
$$u(x, y, 0) = u_* - \epsilon_1 (x - 180)(x - 720) - \epsilon_2 (y - 90)(y - 210),$$

(2.30)
$$v(x, y, 0) = v_* - \epsilon_3(x - 450) - \epsilon_4(y - 135)$$

with $\epsilon_1 = 2 \cdot 10^{-7}$, $\epsilon_2 = 6 \cdot 10^{-7}$, $\epsilon_3 = 3 \cdot 10^{-5}$, $\epsilon_4 = 6 \cdot 10^{-5}$. Figure 11 shows snapshots of the phytoplankton distribution at t = 0, 120, 160, 300, 400, 1200 for parameter values k = 2.0, r = 0.3, h = 0.4. Although the dynamics of the system preceding the formation of patchy spatial structure is somewhat less regular than in the previous case, it follows a similar scenario. Again the spirals appear, with their centers located in the vicinity of critical points (Figures 11(b) and 11(c)); the form of the spirals is not as perfect as it was in the previous case. The destruction of the spirals, which also begins near the critical points, leads to the formation of two growing embryos of



Fig. 10 Spatial distribution of prey (phytoplankton) for (a) t = 0, (b) t = 150, (c) t = 200. Parameters are given in the text. The irregular patchy structure (see Figure 10 (continued) on following page) arises as a result of the destruction of the spirals.

the patchy spatial pattern (Figures 11(d) and 11(e)), and finally to the appearance of irregularity in the whole domain.

The formation of a spiral structure in the spatial distribution of plankton may shed new light on some old problems. The existence of dipole-like structures in the plankton distribution in the ocean is widely known. Usually this is associated with a so-called mushroom-like structure of the field of advective currents; cf. Fedorov and Ginzburg (1989). Here, we have shown that a structure of this type may appear due to trophical prey-predator interactions in the aquatic community and need not be associated with the ocean hydrodynamics.

We have seen that, although at intermediate times the dynamics of the system can be quite regular, for larger times an irregular patchy spatial pattern appears. This pattern is in qualitative agreement with field observations; cf. Denman (1976), Weber, El-Sayed, and Hampton (1986), Greene et al. (1992), Levin, Powell, and Steele (1993). To determine how genuine the agreement may be, one must consider the scales of the spatial structures in question. An analysis of the results shown in



Fig. 10 (cont.) Spatial distribution of prey (phytoplankton) for (d) t = 300, (e) t = 400, (f) t = 1000. Parameters are given in the text. The irregular patchy structure arises as a result of the destruction of the spirals.

Figures 10(f) and 11(f), as well as the behavior of the autocorrelation function K(s)(Figure 9), indicates that there is a characteristic length of the patterns with a value between 10 and 25 in dimensionless units. In view of (2.5), the magnitude of this value in dimensional units is determined by the maximal phytoplankton growth rate α and the turbulent diffusivity D. The value of α depends on the time of the year; for the period of blooming it can be estimated to be from $4 \cdot 10^{-5}$ to 10^{-5} sec⁻¹, corresponding to the time of phytoplankton biomass doubling of between 6 and 48 hours. The situation with D is somewhat more complicated. For open-sea regions the intensity of turbulent mixing usually shows a clear dependence on the scale of the phenomenon (Ozmidov, 1968; Okubo, 1971, 1980). In particular, for the diffusion of a single plankton patch, the diffusivity may grow with time (Petrovskii, 1999). However, this property of the turbulent mixing is manifested much less in coastal regions, e.g., in bights and harbors. In this case of so-called small-scale turbulence, the value of the turbulent diffusivity can be estimated as $D = 10^3 \text{cm}^2 \text{sec}^{-1}$ (Ozmidov, 1968, 1998). Inserting these estimates for D and α in (2.5), we find that the dimensionless unit length corresponds to approximately 50 to 100 meters in original dimensional units.



Fig. 11 Spatial distribution of prey (phytoplankton) for (a) t = 0, (b) t = 120, (c) t = 160. Parameters are given in the text.

This gives the value of the characteristic length of the spatial patterns of 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. Spatiotemporal Plankton Pattern Formation and Fish School Cruising. In the previous section, the effectiveness of a "classical" two-species continuous model in describing pattern formation in a plankton community was demonstrated. However, the continuous approach based on ordinary or partial differential equations does not account for the individual intentional behavior of species in their environment or for their mutual adaptation. The elaboration of the concept of complex adaptive systems from Holland (1975) up to the present, together with the development of individual-based modeling strategies, have partly overcome this problem. Usually, several so-called agents behave according to a small number of well-defined rules which control growth, mutual interactions, and motion as well as interactions with the environment. This set of rules for processes on the microscale can create temporal, spatial, spatiotemporal, or functional structures on the macroscale.



Fig. 11 (cont.) Spatial distribution of prey (phytoplankton) for (d) t = 300, (e) t = 400, (f) t = 1200. Parameters are given in the text.

Here we apply this concept to study the dynamics of a coupled fish-plankton system. The fish will be taken to be localized in a school or superindividual (Scheffer et al., 1995), cruising and feeding according to well-defined rules. In such an approach, the spatiotemporal continuous dynamics of two interacting and dispersing populations (phytoplankton and zooplankton) and the rule-based behavior of a discrete agent (fish school) control each other in a hybrid model. A similar hybrid modeling technique was previously used by Savill and Hogeweg (1997) to describe morphogenetic processes in cell tissues.

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

We note that prey-predator interactions are the basic dynamics of any food chain. However, Goodwin (1967) also applied these ideas to model the class struggle, where the employment rate serves as the prey while the wage bill share acts as the predator (cf. Lorenz, 1993). Similar interactions have also been identified in couplings of economic and ecological systems like models of fisheries (Ruth and Hannon, 1997).

3.1. A Model of a Nutrient-Plankton-Fish Coupled System.

3.1.1. Continuous Plankton Dynamics. We consider a four-component nutrient-phytoplankton-zooplankton-fish model where at any location (X, Y) and time τ , the phytoplankton $P(X, Y, \tau)$ and herbivorous zooplankton $H(X, Y, \tau)$ populations satisfy the reaction-diffusion equations

(3.1)
$$\frac{\partial P}{\partial \tau} = RP\left(1 - \frac{P}{K}\right) - \frac{AC_1P}{C_2 + P}H + D_P\nabla^2 P,$$

(3.2)
$$\frac{\partial H}{\partial \tau} = \frac{C_1 P}{C_2 + P} H - MH - F \frac{H^2}{C_3^2 + H^2} + D_H \nabla^2 H$$

The parameters R, K, M, and 1/A denote the intrinsic growth rate and carrying capacity of phytoplankton and 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, and 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 is assumed in the Scheffer model (Scheffer, 1991a,b).

The local kinetics of the model, i.e., the case $D_P = D_H = 0$, have been investigated in detail (Steele and Henderson, 1981; Scheffer, 1991a,b). In the absence of zooplankton, phytoplankton would reach its carrying capacity K. Considering zooplankton at first as a nondynamic predator, i.e., neglecting (3.2), the possibility of two 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 prey-predator limit cycle oscillations, and the addition of planktivorous fish by the last kinetic term in (3.2) restores the possibility of bistability. Without external or internal noise, the initial conditions determine which of the two stable states will be reached. Fluctuations, which might be due to natural noise or also to any extreme event, could induce transitions between stable states.

The behavior of the local model under seasonal forcing has been studied also (Scheffer et al., 1997; Scheffer, 1998; Steffen, Malchow, and Medvinsky, 1997). These seasonal forcings are due to the natural variability of temperature, light, and nutrient supply. The local prey-predator cycles can be driven to quasiperiodic 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 appear to be stable even under weak seasonal forcings (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 interplay of growth, interactions, diffusion, and advection causes an instability of the uniform plankton distribution (Malchow, 1996) or if certain parameters, such as the nutrient distribution, possess a spatial gradient. In the latter case, diffusion-induced chaos may even appear (Pascual, 1993).

Hydrodynamic forces and their spatiotemporal flow patterns often govern the structures of drifting and swimming matter. Hydrodynamic processes are usually much faster than the plankton biology, a fact which makes it possible to use a special mathematical separation technique that is beyond the scope of this article (Malchow and Shigesada, 1994). A physically relatively uniform period and area are considered here.

For later convenience, the model (3.1)–(3.2) 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/k, which is the total length L of the area considered divided by an integer scale factor k that 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 $t = R_0\tau$. Equations (3.1)–(3.2) now become

(3.3)
$$\frac{\partial p}{\partial t} = rp(1-p) - \frac{ap}{1+bp}h + d_p \nabla^2 p,$$

(3.4)
$$\frac{\partial h}{\partial t} = \frac{ap}{1+bp}h - mh - f\frac{gh^2}{1+g^2h^2} + d_h\nabla^2 h,$$

where the new parameters are $r = R/R_0$, $a = C_1 K/(C_2 R_0)$, $b = K/C_2$, $m = M/R_0$, $f = F/(C_3 R_0)$, $g = K/(C_3 A)$, $d_p = k^2 D_P/(L^2 R_0)$, $d_h = k^2 D_H/(L^2 R_0)$.

For the numerical integration of (3.1)–(3.2), we used a simple explicit difference scheme. The two-dimensional space was divided into a rectangular grid of 64×64 quadratic finite elements with unit mesh size. The time step was set equal to 0.01. Repetition of the integration with smaller step sizes showed that the numerical results did not change, confirming the accuracy of the chosen time step. Periodic boundary conditions were used in both directions.

3.1.2. Discrete Fish School Dynamics. The predation rate of fish is usually taken to be a constant parameter of the plankton-fish interaction model (Scheffer, 1991a,b; Scheffer et al., 1997). This implies that fish are homogeneously distributed in space. But it is well known that fish can form mobile schools. For such 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., f = f(h, t, x, y) in (3.2). The function f describes plankton-density-dependent motion of the fish school towards favorable habitats. This motion can be simulated in different ways (Bocharov, 1990; Radakov, 1973).

In this article we take the behavior of fish schools to obey the rules introduced by Ebenhöh (1980). These are as follows:

- A localized feeding fish school moves to the neighboring region with the highest food concentration only if the local zooplankton density is grazed down to or below a certain threshold value h_{th} , resulting in a zooplankton density gradient higher than a defined threshold value δh_{th} .
- This move takes place only after some residence time τ_{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 fish and do not change their specific characteristics such as size, speed, and residence time. The model (3.1)–(3.2) with the function f describing the fish school movement following the Ebenhöh rules combines features of a cellular automaton and of a model based on partial differential equations.



Fig. 12 Phytoplankton and zooplankton spatial distributions obtained in model (3.3)–(3.4) for f = 2. The density scale is given in the lower part of the figure.

Our calculation of 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 $n\delta t$ the fish school is present at position (i, j), and zero otherwise. The zooplankton gradients $(\vec{\xi} \nabla h)$ were calculated numerically by the formula

(3.5)
$$(\vec{\xi}\vec{\nabla}h)_{ij}^{(n)} = |\xi_x| h_{i+sign(\xi_x),j}^{(n)} + |\xi_y| h_{i,j+sign(\xi_y)}^{(n)} - h_{ij}^{(n)},$$

where sign denotes the signum function.

3.2. Plankton Pattern Formation Resulting from Fish School Motion. The results presented here are based on numerical simulations for a set of parameters that guarantees limit cycle oscillations at each location in the absence of diffusion and fish (r = 2, a = 5, b = 5, m = 0.6, g = 2.5). In natural waters, turbulent diffusion often dominates plankton diffusion rates. Taking this into account, we consider both phytoplankton and zooplankton as passive drifters with the turbulent water motion. This implies $d_p = d_h = d$. Using the relationship between turbulent diffusivity and the scale of the phenomenon in the sea (Okubo, 1980), one can show that with the characteristic growth rate $R_0 = 10^{-5}s^{-1}$ or one division per day, typical of phytoplankton growth, and the characteristic length L/k = 1km, typical of plankton patterns, d is about 0.05.

Figure 12 demonstrates phytoplankton and zooplankton patterns that emerge as a result of the fish school-plankton interplay. It is apparent that the phytoplankton density is lower in the regions where zooplankton density is higher, and vice versa. Many previous observers have reported such an inverse relationship (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.

SPATIOTEMPORAL COMPLEXITY OF PLANKTON AND FISH DYNAMICS



Fig. 13 Plankton vortex formation as a result of fish school-plankton patch interaction for f = 2. The location of the fish school is indicated by the star.

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, Medvinsky, and Panfilov, 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 kilometer 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 (t = 450). The track made by the school oscillates with a phase shift compared to the surrounding zooplankton density. Once the fish school has escaped from the zooplankton patch (t = 460), its track expands and forms a U-like structure (t = 490). The edges of this structure bend in opposite directions and form a pair of spiral waves (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 nonoscillating active media, e.g., chemical ones (Murray, 1977). In the course of time the number of spiral waves increases, and complex spatial structures form like those of Figure 12. It has been verified that these spirals are stable for numerical runs of 10^6 iterations, which are equivalent to more than 50 years. However, such spirals are quite sensitive to physical disturbances like shear flows (Biktashev et al., 1998) or resource gradients (Malchow et al., 2000).



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

It is interesting that at small 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 oscillations of the space-averaged plankton densities

(3.6)
$$\langle p \rangle = \frac{1}{S} \int_{(S)} p(x, y, t) dx dy, \qquad \langle h \rangle = \frac{1}{S} \int_{(S)} h(x, y, t) dx dy,$$

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 sudden changes in the fish school location (Figure 15).

Thus we see that the plankton dynamics depends strongly on the fish school movement. The analysis of this movement is accordingly of particular interest in investigating plankton-fish interactions.

3.3. Fish School Random Walks Resulting from Fish-Plankton Interplay.

3.3.1. Regularity of Irregular Walks. The motion of fish schools is controlled by various biotic and abiotic environmental factors such as light, temperature, salinity, and nutrient (e.g., plankton) supply (Radakov, 1973; Bocharov, 1990; Wu et al., 2000). 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 spatiotemporal plankton dynamics (Medvinsky et al., 2000). In view of this interplay of fish and their environment, it is not surprising that fish school movements can be chaotic.

The behavior of chaotic systems exhibits highly 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; Li, 2000):



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

(3.7)
$$\langle | F(x+l) - F(x) | \rangle \sim l^H$$

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

(3.8)
$$|F(x+l) - F(x)| \sim l^{h(x)}$$

in case (ii). The number H in (3.7) is called the Hurst exponent. If H < 1, then F is nondifferentiable, and the smaller the exponent H, the more singular F is. Thus, the Hurst exponent indicates how globally irregular F is. The function h(x) in (3.8) is called the Hölder exponent. It measures how irregular F is at the point x. Self-affine functions are called fractal functions, whereas multiaffine functions are called multifractal (Feder, 1988; Schroeder, 1990; Peitgen, Jürgens, and Saupe, 1992). Multifractal functions can be 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,

$$(3.9) D(h) = \dim_H[x \mid h(x) = h],$$

where h can take positive as well as negative real values (Feder, 1988; Peitgen, Jürgens, and Saupe, 1992; Bacry, Muzy, and Arneódo, 1993).

Multifractal processes can be also characterized by the $f(\alpha)$ singularity spectrum, which associates the Hausdorff dimension $f(\alpha)$ with the subset of the support of the measure μ , where the singularity strength is α ,

(3.10)
$$f(\alpha) = \dim_H [x \mid \mu(B_x(\epsilon))],$$

where $B_x(\epsilon)$ is an ϵ -box centered at x and

(3.11)
$$\mu(B_x(\epsilon)) \sim \epsilon^{\alpha(x)}.$$

Homogeneous measures are characterized by a singularity spectrum supported at a single point $(\alpha_0, f(\alpha_0))$. In other words, only one kind of singularity is present in the measure. Multifractal measures involve singularities of different strengths. In a general context, the approach based on the $f(\alpha)$ spectrum for singular measures has a similar status to that based on the D(h) spectrum of Hölder exponents (Bacry, Muzy, and Arneódo, 1993).

The questions arise of whether or not the complex movement of the fish school can be described by the simple (3.7) or (3.8), and, if they can, which of the equations describes the movement best?

3.3.2. 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-persistence (at $f_0 = 1$) and low-persistence (at $f_0 = 15$). In both the cases, $h_{th} = 0.35$, $\delta h_{th} = 0.01$, and $\tau_{th} = 0.08$.

One can see that the transition from low to high fish predation rates is followed by a 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 reveals characteristic features of both types of fish school behavior.

3.3.3. Multifractal Analysis of Fish School Walks. Recently, we have shown that a fish school walk can be considered as 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 to analyze Brownian signals, since such an approach may lead to conflicting estimates of H when the fractal function under consideration is not homogeneous (Arnéodo et al., 1996).

Fig. 16 Fish school walks at different values of f_0 with the spatial distributions of Figure 12 taken as initial condition. As time passes these distributions do not undergo any qualitative changes. For details see Medvinsky et al. (2000).

In the present paper (see also Tikhonova et al., 2000), we do not assume that a fish school trajectory is necessarily represented by a homogeneous fractal function; we carry out a multifractal analysis of fish school walks. We use a strategy (Bacry, Muzy, and Arnéodo, 1993; Muzy, Bacry, and Arnéodo, 1993; Arnéodo, Bacry, and Muzy, 1995) that provides a practical way to determine the singularity spectra D(h)(3.9) and $f(\alpha)$ (3.10) directly from an experimental signal. This approach is based on the use of the wavelet transform (Meyer, 1990; David, 1991; Kahane and Lemarié-Rieusset, 1995; Li and Loehle, 1995). It is a space-scale analysis that consists of expanding signals in terms of wavelets that are constructed from a single function, the analysing wavelet ψ , by means of translations and dilations. The continuous wavelet transform of a real-valued function F is defined by

(3.12)
$$W_{\psi}[F](b,a) = \frac{1}{a} \int_{-\infty}^{+\infty} F(x) \,\psi\left(\frac{x-b}{a}\right) dx,$$

where b and a are the space and scale parameters, respectively. The analyzing wavelet ψ is generally chosen to be well localized in both space and frequency. The main advantage of using the wavelet transform for analyzing the regularity of a function F is its ability to be blind to polynomial behavior by an appropriate choice of ψ . Throughout this article, we use the analyzing wavelet called the "Mexican hat" (Li and Loehle, 1995).

The fastest way to estimate D(h) and $f(\alpha)$ suggests the analysis of the scaling behavior of the partition function Z(q, a) from the maxima of the modulus of the wavelet transform (Muzy, Bacry, and Arneodo, 1993),

(3.13)
$$Z = \sum_{i=1}^{N(a)} w_i(a)^q,$$

where i = 1, ..., N(a), N(a) is the number of the local maxima of $W_{\psi}[F](b, a)$ at each scale *a* considered as a function of *x*, and the function $w_i(a)$ can be defined in

terms of the wavelet coefficients (Muzy, Bacry, and Arnéodo, 1993; Bacry, Muzy, and Arnéodo, 1993) by

(3.14)
$$w_i(a) = \max_{\substack{(x, a') \in \ell_i \\ a' < a}} | W_{\psi}[F](x, a') |$$

with $\ell_i \in \mathcal{L}(a)$, where $\mathcal{L}(a)$ is a set of connected wavelet maxima lines ℓ_i , which reach or cross the *a*-scale.

In the limit $a \to 0^+$, the partition function Z(q, a) follows a power law:

$$(3.15) Z(q,a) \sim a^{\tau(q)}.$$

The spectrum $f(\alpha)$ of (3.10) can be found by Legendre transforming $\tau(q)$, i.e.,

(3.16)
$$f(\alpha) = \min_{q} (q\alpha - \tau(q)).$$

Since $\tau(q)$ is typically differentiable with $\tau''(q) \leq 0$, we find that

(3.17)
$$\alpha(q) = \frac{d\tau(q)}{dq},$$

(3.18)
$$f(q) = q \alpha(q) - \tau(q).$$

Unfortunately, computing the Legendre transform has several disadvantages (for example, resulting from local violation of the inequality $\tau''(q) \leq 0$). This may lead to various errors (Chhabra et al., 1987). Therefore, another approach was developed to define singularity spectra in the spirit of the so-called canonical method (Chhabra et al., 1987). This consists of using the functions

(3.19)
$$h(a,q) = \frac{1}{Z(a,q)} \frac{\partial Z(a,q)}{\partial q},$$

where

(3.20)
$$\frac{\partial Z}{\partial q} = \sum_{i=1}^{N(a)} w_i(a)^q \ln w_i(a),$$

and, in analogy to (3.18),

(3.21)
$$D(a,q) = q h(a,q) - \ln Z(a,q).$$

The spectra D(q) and h(q) are defined by (Arnéodo, Bacry, and Muzy, 1995)

(3.22)
$$D(q) = \lim_{a \to 0} \frac{D(a,q)}{\ln a},$$

(3.23)
$$h(q) = \lim_{a \to 0} \frac{h(a,q)}{\ln a}.$$

From (3.22) and (3.23), one computes the D(h) singularity spectrum. In contrast to using the Legendre transform (3.17)–(3.18), such an approach makes it possible to avoid instabilities related to numerical differentiation. 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 (3.22) and (3.23).

Fig. 17 Multifractal analysis of realizations of fractional Brownian processes (a) B_{0.6}(x) and (b) B_{0.9}(x) indexed by H = 0.6 and 0.9. Each of the dependences log₂ Z(a, q) vs. log₂ a, h(a, q) vs. log₂ a, and D(a, q) vs. log₂ a for each of the processes was obtained from 32 realizations, each of length 2¹². Values of q are given at each of the graphs. (c) The difference between τ(q) numerically obtained from (3.15) and its theoretical value τ(q) = qH-1 (Muzy, Bacry, and Arnéodo, 1993). (d) Spectra f(α) (dashed) and D(h) (solid).

Figure 17 demonstrates how both approaches work in application to model realization of fractional Brownian motion. One can see that all the functions $\log_2 Z$ vs. $\log_2 a$, h vs. $\log_2 a$, and D vs. $\log_2 a$ are essentially linear, in agreement with (3.15), (3.23), and (3.22), respectively. Note (see Figure 17(c)) that the difference between the numerical and theoretical values of $\tau(q)$ is virtually independent of 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 τ remains nonzero for any finite realization, both the D(h) and $f(\alpha)$ fractal spectra are not just points but bell-like functions, the halfwidth of which are rather small in comparison with the half-width of any multifractal process.

The similar narrow fractal-like spectra are typical of fish school displacements under a fish predation rate $f_0 = 15$ (see Figures 18(c), 19(c)). It is evident 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 $H \approx 0.6$, which agrees with the results of Medvinsky et al. (2000). The singularity spectra change drastically as f_0 decreases.

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

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

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

4. Inhomogeneity of the Marine Environment. In the previous sections, the dynamics of a plankton system have been considered mainly under the hypothesis that the properties of the environment do not depend on time or position. This is not true in the ocean. Most of the hydrophysical factors controlling the functioning of the biological community, such as temperature, salinity, or intensity of turbulent mixing, are functions of t and \mathbf{r} . This leads to the possibility of a spatial structure in an aquatic community induced by the heterogeneity of the underlying hydrophysical and hydrochemical fields. In order to better understand the dynamics of an aquatic community in a real marine environment, it is important to distinguish between "intrinsic" patterns, i.e., patterns arising due to trophical interactions like those considered above, and "forced" patterns induced by the inhomogeneity of the environment. The physical nature of the environmental heterogeneity, and thus the value of the dispersion of varying quantities and typical times and lengths, can be essentially different in different cases. We now give a brief description of the main types of spatial inhomogeneities appearing in the ocean. This rather schematic account is an introduction to the subject, not a full review. For those interested in details, there is a vast specialized literature on this and similar issues arising in the marine sciences.

Before proceeding to the consideration of particular cases of hydrophysical heterogeneities, it is convenient to outline the processes that could be of primary interest. First of all, the ocean is a highly stratified system, and there is a distinct asymmetry between the vertical and horizontal directions. Since we are mainly interested in phenomena appearing as a result of the interplay between physical and biological processes, the results reviewed in this section will relate to the dynamics of the upper

Fig. 18 Multifractal analysis of small-scale (\bigcirc) and medium-scale (\triangle) fish school displacements for fish predation rates (a) $f_0 = 1$, (b) $f_0 = 4$, (c) $f_0 = 15$. Small-scale and medium-scale displacements were obtained by splitting the fish school trajectories (like those of Figure 16) into steps of length 2^3 and 2^5 , 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 shown for each value of f.

"productive" ocean layer. The thickness of this layer, which depends on a number of factors such as geographical position and season, ranges from a few dozen to a few hundred meters. Since the biological spatial patterns considered in previous sections typically arise on a scale from hundreds of meters to a few kilometers, they seem to correspond more to the horizontal dynamics of an aquatic community. Therefore, we focus our interest on the horizontal structure of the marine environment.

Fig. 19 Multifractal analysis of large-scale fish school displacements for fish predation rates (a) $f_0 = 1$, (b) $f_0 = 4$, and (c) $f_0 = 15$. 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 given at each of the graphs), $\tau(q)$, and the spectra $f(\alpha)$ (dashed) and D(h) (solid) are shown for each value of f.

The next point is that a typical time of the evolution of inhomogeneities should not be too short. The ocean is a multiscale system, and the applicability of an assumption of its steadiness or homogeneity depends on the scale of the processes under consideration. A typical time for a plankton system is usually defined as the

period it takes the community to double its abundance. This value varies between a few hours and a few days for phytoplankton species and between a few days and a few weeks for zooplankton species. Thus, one can expect that a distinct "forced" spatial structure in a marine plankton system can only be induced by environmental inhomogeneities with a typical lifetime of a month or more.

According to one definition, plankton are species which exhibit low capability of self-motion. Thus, the first apparent reason for the formation of spatial structures in a plankton system is water motion. There is an extensive literature concerned with the velocity field in the ocean; cf. Phillips (1977), Pond and Pickard (1978), Pedlosky (1987), and the references therein; in a wider sense, this is the principal issue of all of physical oceanography. The nature of the velocity field heterogeneity depends on the scale of the process. For instance, on a scale from a few centimeters to a few dozen meters, this heterogeneity is mainly caused by turbulence and has the form of stochastic turbulent fluctuations. On a scale of a hundred kilometers or more, the heterogeneity has the form of ocean currents and is induced by the processes acting on a planetary scale, e.g., the interplay of different climatic zones and the rotation of the earth (Pedlosky, 1996). On an intermediate scale from kilometers to dozens of kilometers, the inhomogeneity of the velocity field is usually caused by the interplay of different factors, one of the most important being wind. Heterogeneity of the field of (horizontal) advective currents apparently leads to the formation of spatial structures in plankton communities (Vozjinskaya, 1964; Raymont, 1980; Abbott and Zion, 1985; Walsh et al., 1989; Capella et al., 1992; Sur et al., 1996). Detailed consideration of results related to this problem, however, lies beyond the scope of this paper, since here we are mainly interested in patterns formed by biological interactions.

The impact of ocean turbulence on the functioning of an aquatic community via its influence on feeding and growth rates has been investigated in a number of papers (MacKenzie et al., 1994; Jenkinson and Biddanda, 1995; Marrase, Saiz, and Redondo, 1997). On the other hand, the inhomogeneity of the turbulent mixing in the ocean ("intermittency," "turbulent patches," "rips," etc.) is a widely observed phenomenon (Nihoul, 1980; Monin and Ozmidov, 1981). Naturally, one could expect that it should also contribute to the formation of spatial and spatiotemporal patterns. This is, however, not as obvious as it may seem. The reason is that the intensity of turbulent mixing in the ocean is not only spatially intermittent but also transient. In particular, there are theoretical results indicating that a single turbulent patch tends to decay with time (Barenblatt, Galerkina, and Luneva, 1987; Barenblatt, 1996), the estimated time of decay usually being much less than the characteristic times of an aquatic community. Thus, the intermittency of ocean turbulence affects the dynamics of the community in terms of spatially homogeneous time-averaged values (Ozmidov, 1986) more than it leads to the formation of a "forced" spatial structure.

Our main interest is the possibility of formation of spatial structures not directly induced by water motion. There are a variety of factors affecting the dynamics of an aquatic community via their impact on the growth rates, mortality, feeding rates, etc. In this brief review most of the attention will be paid to the field of temperature. One reason is that temperature is one of the main quantities controlling the abundance of aquatic species (Raymont, 1980; Laurs, Fiedler, and Montgomery, 1984; Hofmann et al., 1992). In particular, strong correlation between the sea surface temperature and the chlorophyll concentration has been reported in many papers (Denman, 1976; Hood et al., 1990; Barnard, Stegmann, and Yoder, 1997). Another reason is that, due to recent progress in remote sensing technology, the properties of the temperature spatial field in the ocean are known better than those of other fields (Njoku et al., 1985).

The inhomogeneity of the spatial temperature distribution in the ocean arises from many underlying processes. As mentioned above, the characteristic time of different anomalies in the temperature field depends on the spatial scale of the processes involved. Processes acting on a global scale may have characteristic times of dozens or hundreds of years. In particular, differences between climatic zones lead to a steady average horizontal temperature gradient on the order of 0.01° C/km (Rodionov and Kostianoy, 1998). This provides a natural scale for measuring the intensity of temperature anomalies.

The smallest spatial scale of the temperature field is determined by turbulence. As usual, the horizontal and vertical directions provide essentially different examples because of gravitation and stratification. While in the vertical direction the spatial inhomogeneities related to turbulent pulsations are estimated not to exceed the "Ozmidov length" L_{Oz} (Ozmidov, 1966, 1968), with value ranging from a few dozen centimeters to a few meters, lateral turbulent exchange generally has a more complicated nature and can depend on the scale of the particular phenomenon (Ozmidov, 1968; Okubo, 1971; Monin and Ozmidov, 1981). However, the spatial inhomogeneity of the temperature field induced by turbulent fluctuations can hardly produce any stable spatial structures in an aquatic community, because the amplitude of the temperature fluctuations is too small, on the order of 0.1° C (Monin, Kamenkovich, and Kort, 1974), which is much less than the times typical for community functioning.

Another mechanism for the formation of an inhomogeneous temperature field is vertical convection. Although in some cases the processes underlying this phenomenon are unclear (Monin and Krasitskii, 1985), a widely accepted hypothesis is that free vertical convection appears as a result of hydrodynamical instability when the water density in the upper ocean layer becomes higher than that of the water in the subsurface layer, due, for example, to evaporation or cooling. The development of this instability can lead (Foster, 1974; Joseph, 1976) to the formation of a cell structure on the sea surface with alternating cold and warm patches, each patch corresponding to a column of either descending or ascending water. The typical size of these patches is on the order of 10 to 100 meters, and the characteristic time of the pattern evolution is from a few dozen minutes to a few hours, with the difference between cold and warm patches rarely exceeding 1°C (Fedorov and Ginzburg, 1988). Vertical convection strongly affects the dynamics of the pelagic community, being responsible for seasonal thermocline breaking and bringing up deep waters with high biogen concentration. However, due to its relatively small scale and nonstationary nature, free vertical convection cannot be expected to lead to the formation of a distinct long-lived horizontal spatial structure.

An example of a stable long-lived spatial structure in the temperature field is provided by ocean fronts. The term "ocean front" is normally used for an ocean region where the magnitude of the gradient of a certain parameter, such as temperature, salinity, or density, is notably larger than a typical value for that part of the World Ocean (Fedorov, 1983). In the case of temperature, such a typical value is given by the average climatic gradient. In practice, the temperature field is usually considered to contain a front when $|\nabla T| \ge 0.5 - 1.0^{\circ}$ C/km. The marine science literature (Fedorov, 1983; Rodionov and Kostianoy, 1998) gives a great variety of examples of ocean fronts differing in their features, behavior, and underlying physics. Briefly summarizing the properties that can be important for the purposes of this article, the value of the temperature difference across the front ranges from less than 1°C to 5–6°C. The width of the front (i.e., its typical size along the temperature gradient) usually lies between a few hundred meters and a few kilometers, while its length varies from a few dozen to a few hundred kilometers. In inner spatial structure, ocean fronts are typically either step-like (in some cases, multistep), when the front separates regions with "cold" and "warm" water, or intermittent, when the regions with cold and warm water alternate. Cases of more complicated geometry are also possible.

A remarkable property of ocean fronts is that they usually last for a long time, from a few months (seasonal fronts) to many years (e.g., fronts created by large-scale ocean currents), much longer than the time typical for the functioning of a plankton system. Also, the typical temperature difference of a few °C across the front is often sufficient to change significantly the growth rate of phytoplankton species (Raymont, 1980). Another point is that the waters on different sides of the front typically have different origin and can differ significantly in the biogen concentration, e.g., in the case of upwelling fronts. The combination of these two factors can lead to the formation of a "forced" spatial structure (Fiedler and Bernard, 1987; Mackas, Washburn, and Smith, 1991). Indeed, both the phytoplankton growth rate and the species abundance may be different on the two sides of the front (Hood et al., 1990; Mackas, Washburn, and Smith, 1991).

Ocean fronts give a common example of long-lived inhomogeneities in the ocean temperature field, but not the only example. Other widely observed phenomena providing a relatively stable spatial structure are mesoscale/synoptic eddies and "rings" (Robinson, 1983; Kamenkovich, Koshlyakov, and Monin, 1987). The eddies typically have a horizontal size from dozens to 250–350 km and thickness from a few hundred meters to somewhat more than 1 km, with lifetime varying from a few weeks to a few months. Mechanisms by which the eddies are formed can be different in different hydrographic regions (Sverdrup, 1938; The Ring Group, 1981; The Coastal Transition Zone Group, 1988; Barth, 1989). They can be either "warm," when the temperature of the water inside the ring is higher than the temperature outside, or "cold," and the temperature difference can be as high as 10–12°C. Besides the temperature, values of other factors like salinity and nutrient concentration can also differ significantly across a ring.

Regardless of their origin and the details of the hydrophysical structure, practically all rings exhibit anomalous biological activity (Angel and Fasham, 1983), i.e., higher abundance of plankton species and higher phytoplankton growth rates. Besides this, the plankton community inside the ring can be spatially structured (Haury et al., 1986; Hayward and Mantyla, 1990; Bucklin, 1991). Some authors also report higher abundance of certain fish species associated with the eddies (Bowman et al., 1983). Another biological consequence arises due to the high mobility typical for the rings. While ocean fronts are usually localized inside a certain region, synoptic rings can travel many hundreds of miles. In some cases this can lead to a large-scale biological invasion when large masses of water containing one pelagic community taken at the place of the ring formation are brought to another place with quite a different community (Wiebe et al., 1976).

There also exists also a kind of synoptic eddy known as rotating lens-like eddies, also known as "meddies" in the Northeastern Atlantic (Armi and Zenk, 1984; Armi et al., 1988; Kostianoy and Belkin, 1989). Unlike the usual synoptic ring, with the volume of rotating water adjacent to the ocean surface, a lens is localized in depth. Typically, a lens makes no trace on the ocean surface, and this makes it a difficult

object to investigate. Accordingly, the information available about biological phenomena related to rotating lenses is rather poor. Nevertheless, since the lenses exist like isolated parcels of water with properties different from those of the surrounding water, they provide an example of long-lived inhomogeneities in the ocean hydrophysical and hydrochemical fields. One can expect that further research will bring more results concerning biological anomalies associated with this phenomenon; cf. Cooper (1961).

Our brief examination of heterogeneous ocean fields, particularly water temperature, has shown the presence of stable spatial structures (fronts and eddies) with lifetimes much greater than those typical for plankton system dynamics. There is considerable evidence of the impact of these structures on marine ecosystems, which serves as a motivation for constructing models that take them into account. We now consider a model of this type.

5. Chaotic and Regular Plankton Dynamics in Spatially Structured Plankton-Fish Communities. Our brief inspection of the main structures in the ocean environment, in the previous section, showed that the spatiotemporal dynamics of aquatic communities is strongly affected by the existence of stable mesoscale physical structures (Nisbet et al., 1993; Ranta, Kaitala, and Lundberg, 1997). In this section, we focus on the dynamics of plankton populations in a patchy environment. A minimal one-dimensional reaction-diffusion model of the dynamics inside a patch is considered, assuming that some plankton habitats have high fish abundances while in others fish are absent. We study the temporal behavior of spatially averaged zooplankton and phytoplankton densities depending on such ecologically significant parameters as the fish predation rate and patch-to-patch distance. We show that the diffusive interaction between different habitats in a patchy marine environment can give rise to plankton spatial patterns. We also show that the spatially averaged plankton dynamics depends on both the fish predation rate and the distance between fish-populated habitats and can exhibit chaotic and regular behavior. Chaotic dynamics appears in a wide parameter range.

5.1. Model Equations. We consider the four-component basic marine food chain model described, in dimensionless variables, by (3.3)–(3.4)

For numerical integration of (2.3)–(2.4) a simple explicit difference scheme is used. The one-dimensional space is divided into a grid of 64 finite-difference cells of length one. The boundary between habitats divides the space into two patches. The time step is set equal to 10^{-2} . Repetition of the integration with a smaller step size showed that the numerical results did not change, confirming the accuracy of the chosen time step. The dynamics is investigated with no-flux boundary conditions. The initial distributions for h and p are uniform and the same for each of the habitats.

The diffusion terms in (2.1)-(2.2) often describe the spatial mixing of the species due to the self-motion of the organisms (cf. Skellam, 1951; Okubo, 1986). However, in natural waters it is turbulent diffusion that is thought to dominate plankton mixing (Wroblewski and O'Brien, 1976; Okubo, 1980). Taking this into account, we considered both phytoplankton and zooplankton as passive contaminants of the turbulent motion. 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; Ozmidov, 1968), with the minimum phytoplankton growth rate R_0 given by $10^{-6} \sec^{-1}$ (Jørgensen, 1994) and the characteristic length L/k of about 2 km, typical of plankton patterns, one can show that d is about 5×10^{-2} .

Fig. 20 Solution diagrams of the model (3.3)–(3.4) for parameters r = 5, a = 5, b = 5, m = 0.6, g = 0.4. The curves display the steady-state solutions for different values of f. H denotes a Hopf bifurcation.

5.2. Two-Patch Ecosystem Dynamics. Figure 20 presents solution diagrams for the system (2.3)-(2.4), i.e., the dependence of the steady-state solution on the fish predation rate f. One can see that phytoplankton-dominated stationary states are typical for high predation rates. As f is lowered, an unstable and another stable steady state appear, making the system bistable. As f is lowered further, the phytoplankton-dominated stable steady state and the unstable state disappear in a saddle-node bifurcation. For a lower value of f, at a point H a Hopf bifurcation occurs, destabilizing the zooplankton-dominated steady state while creating a stable limit cycle, which means that in the absence of fish (f = 0), the local kinetics of the system is oscillatory (for all other parameters as in Figure 20). The sophisticated treatment of local properties of models similar to (2.3)–(2.4) was carried out in (Scheffer, 1991a; Malchow and Shigesada, 1994; Scheffer, 1989; Steffen, Malchow, and Medvinsky, 1997).

Let us consider the simplest example of a spatially structured ecosystem, consisting of just two patches. The dynamics in both patches obeys (2.3)–(2.4), and in one patch f = 0, i.e., fish are absent (for example, due to local changes in temperature or salinity). Figure 21 shows three sets of one-dimensional plankton spatial patterns that have emerged from initially homogeneous plankton distributions in a patch populated by fish ($x \le 32$) with f = 0.05, 0.18, and 0.395 adjacent to a patch where fish are absent (x > 32, f = 0). The values f = 0.05 and 0.18 correspond to oscillatory plankton kinetics, while f = 0.395 corresponds to the zooplankton-dominated steady state. One can see that increase of the fish predation rate is followed by transitions from regular plankton patterns to irregular ones and then to virtually unstructured

Fig. 21 Spatiotemporal plankton patterns emerging from initially homogeneous plankton distributions in the two-habitat system for (a) f = 0.05, (b) f = 0.18, (c) f = 0.395. The darker regions correspond to lower plankton densities.

plankton distributions in the fish-populated habitat, and from regular to irregular patterns in the fish-free habitat. Note that the interaction between the patches is essential to disturbing the initially homogeneous distribution in the fish-free patch; otherwise, no pattern could occur.

To examine the dependence of these patterns on the fish predation rate in more detail, we construct the pattern bifurcation diagram for the three main types of plankton patterns shown in Figure 21. Figure 22 shows the plankton abundance as a function of x at t = 5000 for values of f from 0 to 0.395. One can see that, for the fish-populated habitat, the structures with a larger inner scale characteristic for the smaller f transform into small-scale irregular patterns as f grows, and then to nearly homogeneous plankton distributions as the system passes through the Hopf bifurcation (Figure 20). In contrast, in the fish-free habitat the Hopf bifurcation is not accompanied by essential changes in plankton structure (Figure 22). It is also seen that the phytoplankton density is lower in the regions where zooplankton density is higher, and vice versa. Many authors have reported such an inverse relationship between phytoplankton and zooplankton as an apparent consequence of phytoplankton grazing by zooplankton; cf. Fasham (1978).

Although the distinctions between the three main types of the plankton structures shown in Figure 21 are quite evident, it seems to be desirable to characterize the difference in a more quantitative way, e.g., to ascribe to each of the patterns a certain index. It also seems desirable to follow the transformation of one pattern to another in more detail, i.e., to follow how the properties of the structures change with small

Fig. 22 Pattern bifurcation diagram for phytoplankton and zooplankton obtained after 5×10^5 iterations. The gray scale is the same as in Figure 21.

variations of f. To do this, we render the plankton spatiotemporal patterns (like the "field" shown in Figure 21) into two-level structures, where the values of plankton density less than a threshold value are set equal to zero, while those exceeding the threshold value are set equal to unity. The threshold value is chosen equal to the minimum peak of the spatially averaged plankton density obtained in the course of the pattern formation. Note that we do not distinguish between space and time in order to reveal the features essential for spatiotemporal dynamics of the system.

To characterize the "integral" properties of the two-dimensional spatiotemporal plankton patterns, we use the fractal dimension (D) of the two-level plankton structures described above and study the dependence of D on the fish predation rate f. It should be noted that small changes in both the threshold and the range of t do not influence essentially the results of the analysis of the plankton patterns; in this sense this quantity is robust. Figure 23 demonstrates the functions D(f) for zooplankton patterns in the fish-populated and fish-free habitats. Because of the inverse relationship between phytoplankton and zooplankton density distributions, the phytoplankton patterns are characterized by qualitatively similar functions.

The comparison of Figures 22 and 23 demonstrates that each plateau of D(f) corresponds to more regular plankton distributions. This tendency is more conspicuous for small f in the fish-free habitat and for large f in the fish-populated habitat. The functions D(f) reveal some new details of the plankton patterns. Specifically, the smooth changes in D for the fish-populated habitat are seen to be accompanied by abrupt changes of the fractal dimension in the fish-free habitat (Figures 23(a) and

Fig. 23 Dependence of the fractal dimension of the zooplankton spatiotemporal patterns on the fish predation rate for (a) fish-populated and (b) fish-free habitats.

23(b)). Hence, the plankton dynamics seem to be less stable with respect to changes in the fish predation rate in the fish-free habitat than in the fish-populated habitat.

To study the plankton dynamics, we use phytoplankton and zooplankton densities, space-averaged over each of the habitats:

$$\langle p \rangle_i = \frac{1}{S_i} \int_{S_i} p\left(x,y,t\right) dx dy, \quad \langle h \rangle_i = \frac{1}{S_i} \int_{S_i} h\left(x,y,t\right) dx dy,$$

where S_i is the area of the *i*th habitat. Here i = 1 corresponds to the fish-populated habitat and i = 2 to the fish-free one, with $S_1 = S_2 = k^2/2$, k = 64. It emerges that

Fig. 24 Three main types of oscillations of space-averaged zooplankton density, depending on f. (a) $x \leq 32$ (fish-populated patch); (b) x > 32 (fish-free).

the temporal dynamics of $\langle p \rangle_i$ and $\langle h \rangle_i$ depend significantly on the fish predation rate f. As an example, Figure 24 demonstrates the dynamics of the zooplankton spaceaveraged density for fish-populated and fish-free patches. There are three main types of dynamics: (i) regular oscillations (when f is small); (ii) irregular oscillations in both fish-populated and fish-free patches (as f increases); (iii) virtually constant plankton density in the fish-populated patch while irregular oscillations appear in the fish-free habitat (when f undergoes further growth and becomes larger than the critical value characteristic of the Hopf bifurcation; see Figure 20). The temporal behavior of the averaged phytoplankton density is qualitatively the same. It should be mentioned that there is a clear correspondence between the three types of the temporal behavior (Figure 24) and the spatiotemporal patterns of Figure 21. Specifically, regular and irregular patterns lead to regular and irregular oscillations of $\langle p \rangle$ and $\langle h \rangle$, respectively, while nearly homogeneous patterns lead to virtually constant plankton density.

It is noteworthy that in contrast to the regular regimes, the irregular ones demonstrate the sensitivity to initial conditions that is characteristic of chaotic dynamics (Figure 25). In order to investigate how common such a chaotic behavior of the twopatch plankton system under consideration is, we constructed bifurcation diagrams for both fish-populated and fish-free patches.

Figure 26 shows these bifurcation diagrams. Successive local maxima of the timedependent space-averaged plankton density are plotted for the fish predation rates covering all the types of dynamics (Figure 24). Regular oscillations produce one or a small number of points, whereas successive maxima of irregular changes of the plankton density are spread over a range of values. The diagrams were obtained after the

Fig. 25 Sensitivity to initial conditions. Temporal $\langle h \rangle$ oscillations diverge for small initial differences. Trajectories of $\langle h \rangle$ are shown for f = 0.18 and two initial conditions differing by 0.001.

transition processes settled down, when the influence of the initial conditions vanished and a particular type of plankton dynamics became evident. Note the different qualitative regions in the diagrams. For large values of f, the plankton dynamics in the fish-populated habitat is regular (Figure 26(a)), while in the fish-free patch it is irregular (see Figure 26(b); an example of irregular dynamics is shown in Figure 24 at f = 0.395). For smaller values of f, the regularity in the fish-populated patch is lost and the maxima visit a whole segment, except for a narrow gap in the vicinity of f = 0.2 where the dynamics becomes regular again (Figure 26(a)). The example shown in Figure 24 at f = 0.18 demonstrates irregular dynamics in both patches. For f < 0.1, the dynamics in both patches is regular (cf. Figures 26(a) and 26(b); Figure 24 at f = 0.05 shows an example). To provide a more quantitative insight into the nature of the temporal dynamics of the averaged densities, we also calculated the dominant Lyapunov exponent (λ). The results for various values of the fish predation rate in the fish-populated and fish-free patches (Figures 26(c) and 26(d)) are in good agreement with the bifurcation diagrams and demonstrate the chaotic nature of the plankton dynamics. Indeed, comparing Figures 26(a) and 26(c), as well as Figures 26(b) and 26(d), one can see that $\lambda > 0$ and chaos always occur at values of f for which the regularity of the plankton dynamics is lost. A more sophisticated analysis (Medvinsky et al., 2001) has revealed that chaos underlying the irregular plankton oscillations (Figure 24) is characterized by positive values of at least four first Lyapunov exponents. This implies high-dimensional chaos responsible for the complex plankton dynamics. The sensitivity of the plankton oscillations to initial conditions typical of chaotic behavior has also been shown to be due to coexistence of a chaotic attractor and a limit cycle. Interestingly, the entire basin of attraction of the limit

Fig. 26 Bifurcation diagrams and dominant Lyapunov exponents for various values of the fish predation rate f. (a) Bifurcation diagram for the fish-populated patch. (b) Bifurcation diagram for the fish-free patch. (c) Dominant Lyapunov exponent for the fish-populated patch. (d) Dominant Lyapunov exponent for the fish-free patch. All calculations were carried out on the time interval $2000 \le t \le 5000$.

cycle appears to be riddled with "holes" leading to the competitive chaotic attractor (Medvinsky et al., 2001).

5.3. Three-Patch Ecosystem Dynamics. Figure 27 shows an example of the plankton spatial patterns that emerge from an initially homogeneous distribution in a three-patch system consisting of two fish-populated habitats separated by a fish-free gap. The choice of parameters corresponds to either the steady-state local kinetics (f = 0.395 in Figure 27(a)) or to the limit cycle local kinetics (f = 0.18 in Figure 27(b)). The following questions arise. How strongly correlated is the plankton dynamics in the patches separated by a gap? How does the type of plankton dynamics depend on the width of the gap?

To answer these questions, we calculated the dominant Lyapunov exponent for different gap widths δ . It appears that regular oscillations (similar to those in Figure 24 for f = 0.05) are independent of δ . In Figure 28, λ is plotted versus δ for two other types of plankton dynamics shown in Figure 24. The function $\lambda(\delta)$ is remarkably nonmonotone in the case of irregular oscillations of the space-averaged plankton density in both fish-populated patches and the fish-free gap (Figure 28 for f = 0.18). Note that there is a clear correlation between the gap width variations of

Fig. 27 Quasi-two-dimensional zooplankton and phytoplankton patterns emerging in the three-patch system from initially homogeneous plankton distributions, and the corresponding profiles of plankton density. (a) $y \le 16$ and $48 \le y \le 64$, f = 0.395 or (b) f = 0.18 whereas f = 0 for 16 < y < 48.

the dominant Lyapunov exponent in the fish-populated patches and the fish-free gap. Such a correlation is absent in the case f = 0.395, as a virtually constant plankton density appears in the fish-populated patches while irregular oscillations appear in the fish-free gap. In the fish-populated patches λ is virtually constant and equal to zero,

Fig. 28 Dependence of the dominant Lyapunov exponents in the fish-populated (solid) and fish-free (dashed) habitats on the distance between the fish-populated habitats.

while in the fish-free gap it decreases monotonically to zero as δ decreases to about 14 (Figure 28, bottom). These results show that in the natural patchy environment, plankton dynamics inside a given patch may depend not only on local parameters (such as the fish predation rate) relative to the patch in consideration but also on patch-to-patch distances.

6. Summary. In this article we explored the processes underlying the dynamics of spatially inhomogeneous aquatic communities. We have emphasized that spatial heterogeneity cannot always be reduced to the heterogeneity of the marine environment: there are "physical" and "biological" aspects of the problem. We have considered different mechanisms of the formation of intrinsic biological patterns and shown that the formation of transient and irregular spatial structure in the plankton distribution may result from the interplay between turbulent mixing and principal matter fluxes in the plankton community such as phytoplankton-zooplankton interactions. The formation of the plankton pattern is characterized by an intrinsic length, and the value of this length that emerges in our mathematical models, on the order of 1 km, is consistent with field observations.

The minimal model describing the formation of an irregular patchy plankton distribution has been shown to be the two-species prey-predator (phytoplanktonzooplankton) system with parameters independent of position and with no restrictions on the species diffusivities. We have demonstrated that the dynamical regime corresponding to pattern formation can be characterized as spatiotemporal chaos. The appearance of an irregular spatial distribution follows an unusual scenario and can be preceded by the formation of a distinct spiral pattern.

Another mechanism of the formation of irregular spatial patterns in a plankton community has been shown to be the impact of a planktivorous fish school. The interaction between mobile fish schools and the plankton system, although modifying the properties of the spatial structure, does not change the principal points of the system dynamics: the formation of spiral waves and spatiotemporal chaos. Additionally, it has been shown that the fish school motion has fractal properties.

By reviewing data from field observations, we have also shown that, in many cases, the dynamics of an aquatic community is affected by the existence of relatively stable mesoscale inhomogeneities in the field of ecologically significant factors such as water temperature, salinity, and biogen concentration. The characteristic size of these "forced" inhomogeneities provides another, external scale of the system. We developed the analysis of plankton pattern formation and corresponding spatiotemporal dynamics of the community in a patchy environment. By using a model allowing for both the formation of intrinsic biological patterns and forced spatial structure, we showed that the type of the system dynamics depends essentially both on the size of the patches and on the interpatch distance.

In the real ocean, there is a continuous competition between the creation of patterns by biological mechanisms and their destruction by turbulent flow. The effects of this competition can hardly be fully captured in terms of the mean-field equations (2.1)-(2.2) and (3.1)-(3.2), where the whole impact of marine turbulence is reduced to turbulent diffusion. Development of models allowing for more details of turbulent fluid motion remains a big open problem.

In terms of the mean-field approximation, we have shown that the chaotic spatiotemporal dynamics of an aquatic community appears in a class of relatively simple, schematic models that take into account only the principal interactions in the community. This may indicate a vital role of chaotic regimes in the spatiotemporal organization of aquatic ecosystems. Indeed, there is evidence that systems with chaotic dynamics have a greater potential for adapting to changing environmental conditions than nonchaotic ones (Wilson, 1992; Allen, Schaffer, and Rosko, 1993; Hastings, 1993; Pahl-Wostl, 1993; Huisman and Weissing, 1999; Petrovskii and Malchow, 2001b). At another level, the existence of chaos and related irregularities is often a sign of health of organisms (Garfinkel et al., 1992; West and Deering, 1995; Marks-Tarlow, 1999). There has even been the suggestion that the process of aging is characterized by loss of the plasticity and variability afforded by chaos in the basic physiological system (Lipsitz and Goldberger, 1992). Developments such as these make the problem of the relationship between chaotic and regular dynamics one of great interest.

This article has examined new challenges resulting from nonlinear interactions in aquatic communities. Schematic few-species reaction-diffusion models have been shown to be effective tools for investigating spatiotemporal pattern formation in plankton-fish dynamics.

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