Chaos and regular dynamics in model multi-habitat plankton–fish communities

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This work is focused on the role of diffusive interaction between separate habitats in a patchy environment in plankton pattern formation. We demonstrate that conceptual reaction–diffusion mathematical models constitute an appropriate tool for searching and understanding basic mechanisms of plankton pattern formation and complex spatio-temporal plankton dynamics.

1. Introduction

In our previous paper (Medvinsky *et al* 2001), the dynamics of a plankton system have been considered mainly under suggestion that the properties of the environment do not depend on time or position in space. Strictly speaking, this is not so in real oceans. Most of the hydrophysical factors controlling the functioning of the biological community, e.g. temperature, salinity, intensity of turbulent mixing, etc., are functions of time and space. This leads to a possibility of a spatial structure in the aquatic community induced by the heterogeneity of underlying hydrophysical and hydrochemical fields. 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 in the community like those that have been considered in Medvinsky *et al* (2001), and the forced patterns induced by the heterogeneity of the environment. The physical nature of the environmental heterogeneity, and thus the value of dispersion of varying quantities and typical times and lengths, can be essentially different in different cases. To assess the applicability of the homogeneous models, as well as to provide the information necessary for their development for a more realistic case of an inhomogeneous environment, we begin with a brief description of the main types of spatial inhomogeneities appearing in the ocean. We want to note that this brief and rather schematic account should be considered more as an introduction to the subject than as a full review. For those who are interested in more details, there is a vast specialized literature on this and similar issues arising in marine sciences; here we are concerned with this subject only as much as is necessary for our current purposes.

2. Inhomogeneity of marine environment

Before proceeding to the consideration of particular cases of hydrophysical heterogeneity, it is convenient to outline the processes that could be of primary interest. First of all, one should take into account that the ocean is a highly stratified system and there is always a distinct asymmetry between the vertical and horizontal directions. Since we are mainly interested in the phenomena appearing as a result of the interplay between physical and biological processes, the result reviewed in this section will relate to the dynamics of the upper productive ocean layer. The thickness of this layer, being dependent on a number of factors such as the geographical position of the region and the season of the year, is estimated to be from a few dozen to a few hundred metres. Since the biological spatial patterns considered in the previous article (Medvinsky *et al*

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2001) typically arise on scale from a hundred metres to a few kilometres, they seem to correspond more to horizontal dynamics of an aquatic community. Thus, here we are also more interested in the horizontal spatial structure of marine environment.

The next point is that a typical time of the evolution of particular inhomogeneities should not be too short. The ocean is a multiscale system and its applicability of the assumptions of its steadiness and the homogeneity depends on the scale of the process under consideration. A typical time for a plankton system is usually defined as the period it takes for the community to double its abundance. Roughly estimated, its value fluctuates 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 time of existence not less than one month.

According to one definition, plankton is the general name for species which exhibit low ability for 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, e.g. see Phillips (1977), Pond and Pickard (1978) Pedlosky (1987) and the references therein; in a wider sense, it is the principal issue in physical oceanography. The nature of the velocity field heterogeneity depends on the scale of the process. For instance, on small scale (from a few centimetres to a few dozen metres) this heterogeneity is mainly caused by turbulence and has the form of stochastic turbulent pulsations. On large scale (hundred kilometres and more), the heterogeneity of the velocity field has the form of ocean currents and is induced by processes acting on a planetary scale, e.g. the interplay of different climatic zones and the rotation of the Earth (Pedlosky 1996). On intermediate scales from a kilometre to dozens of kilometres, the inhomogeneity of the velocity field is usually caused by the interplay of different factors, one of the most important being the impact of the wind. Heterogeneity of the field of (horizontal) advective currents apparently leads to the formation of spatial structures in plankton communities (Vozjinskaya 1964; Abbot and Zion 1985; Walsh *et al* 1989; Capella *et al* 1992; Sur *et al* 1996; some examples can also be found in Raymont 1980). Detailed consideration of the results related to this problem, however, lies beyond the scope of this paper since we are more interested in the patterns formed due to biological interactions and not caused by ocean hydrodynamics.

The influence of ocean turbulence on the functioning of an aquatic community via its impact on feeding and growth rates has been reported in a number of papers, e.g. MacKenzie *et al* (1994), Jenkinson and Biddanda (1995), Marrase *et al* (1997). On the other hand, the inhomogeneity of the turbulent mixing in the ocean (intermittence, 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 spatio-temporal patterns in the community. This is, however, not so obvious as it may seen to be. The matter is that the intensity of turbulent mixing in the ocean is not only spatially intermittent but also transient. Particularly, there are theoretical results indicating that a single turbulent patch tends to decay with time (Barenblatt 1996; Barenblatt *et al* 1987), the estimated time of decay usually being much less than characteristic times for an aquatic community. Thus, intermittence of the ocean turbulence affects the dynamics of the community in terms of spatially homogeneous time-averaged values (Qzmidov 1968) rather than leading to the formation of a forced spatial structure.

Now, the point of primary interest is the possibility of formation of spatial structures not directly induced by water motion. There is 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 attention will be paid to the field of temperature. The reason is that, temperature is considered to be one of the main quantities controlling the abundance of aquatic species (Raymont 1980; Laurs *et al* 1984; Hofmann *et al* 1992). Particularly, strong correlation between the sea surface temperature and the chlorophyll concentration has been reported by many workers (e.g. see Denmann 1976; Hood *et al* 1990 and Barnard *et al* 1997). On the other hand, due to recent progress in remote sensing technology, the properties of the spatial temperature field in the ocean is studied better than the properties of other fields (Njoku *et al* 1985).

Inhomogeneity of the temperature spatial distribution in the ocean arises as a result of many underlying processes. As mentioned above, rather typically, 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 many dozens or hundreds years. Particularly, the difference between the temperature in different climatic zones leads to the existence of a steady average horizontal temperature gradient, its value being on the order of 0·01°C/km (Rodionov and Kostianoy 1998). The value of the average climatic gradient provides a natural scale for measuring the intensity of various temperature anomalies.

The smallest spatial scale of the temperature field is determined by turbulence. As usual, horizontal and vertical directions provide essentially different examples because of the impact 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), the value of L_{oz} typically being from a few dozens centimetres to a few metres, lateral turbulent exchange generally has a somewhat 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 induced by turbulent pulsations can hardly produce any stable spatial structures in an aquatic community because the amplitude of the temperature fluctuations is not large, its value being on the order of 0·1°C (Monin *et al* 1974). Also, the periods of fluctuations usually do not exceed a few minutes (Monin *et al* 1974) which is much less than the times typical for the community functioning.

Another mechanism for formation an inhomogeneous temperature field is vertical convection. Although in some cases the processes underlying this phenomenon are not quite clear (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, due to evaporation or cooling, higher than the density of the water in the subsurface layer. Development of this instability can lead to the formation of a cell structure on the sea surface with alternating cold and warm patches, every patch corresponding to a column of either descending or ascending water (Foster 1974; Joseph 1976). The typical size of these patches in the ocean is estimated to be on the order of 10 to 100 metres and the characteristic time of the pattern evolution from a few dozen minutes to a few hours, with the difference between cold and warm patches rarely exceeding 1°C (Fedora and Ginzburg 1988). We want to note that, generally, 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, free vertical convection can hardly be expected to lead to the formation of a distinct long-living horizontal spatial structure in the pelagic community because its relatively small scale and non-stationary nature.

An example of a stable long-living 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, e.g. temperature, salinity and/or density, is notably larger than its characteristic value for a given part of the World Ocean (Fedora 1983). Concerning temperature, such a typical value is given by the average climatic gradient. In practice, the temperature field in the ocean is usually considered to create a front when $|\nabla T| \geq 0{\cdot}5$–1·0°C/km. Specialized marine literature (Fedorov 1983; Rodionov and Kostianoy 1998) gives a great variety of examples of ocean fronts differing in their features, behaviour and underlying physical mechanisms. Briefly summarizing the properties that can be important for the purpose of this paper, the value of the temperature contrast across the front varies from less than 1°C to 5

The width of the front (i.e. its typical size along the temperature gradient) usually lies between a few hundred metres and a few kilometres while its length (the size along the front) varies from a few dozen to a few hundred kilometres. Concerning their inner spatial structure, ocean fronts typically can be either step-like (in some cases, multi-step) when the front separates the regions with cold and warm water, or intermittent, when the regions with cold and warm water alternate (cases of a more complicated geometry are also possible).

A remarkable property of ocean fronts is that they usually exist during quite a long time, from a few months (seasonal fronts) to many years (e.g. fronts created by large-scale ocean currents), i.e. much longer than the time typical for the functioning of a plankton system. Also the value of the temperature difference of a few °C typical for the temperature contrast 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 case of upwelling fronts. One can expect that the combination of these two factors can lead to the formation of a forced spatial structure in the pelagic community (Fiedler and Bernard 1987; Mackas *et al* 1991). Indeed, some results indicate that both the phytoplankton growth rate and the species abundance in the pelagic community may be somewhat different on different sides of the front (Hood *et al* 1990; Mackas *et al* 1991).

Ocean fronts give a common but not the only example of long-living inhomogeneities in the ocean temperature field. Another widely observed phenomenon providing a relatively stable spatial structure is mesoscale/synoptic eddies and rings (Robinson 1983; Kamenkovich *et al* 1987). The eddies typically have a horizontal size from a few dozens to 250–350 km and thickness from a few hundred metres to somewhat more than 1 km, the time of existence 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). The eddies can be either warm (when the temperature of the water inside the ring is higher than the temperature outside) or cold, the maximal temperature difference can be as high as 10–12°C. Besides the temperature, the values of other factors (e.g. salinity and nutrient concentration) inside and outside a ring also can differ significantly.

An important point is that, regardless their origin and the details of the hydrophysical structure, virtually all rings exhibit an anomalous biological activity (Angel and Fasham 1983), i.e. higher abundance of plankton species and higher phytoplankton growth rates; besides, 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 eddies (Bowman *et al* 1983). Another biological consequence arises due to high mobility typical for the rings. While ocean fronts are usually localized inside a certain region, synoptic rings can travel many hundred miles. In some cases, it can lead to a large-scale biological invasion when large masses of water containing the pelagic community taken at the place of the ring formation are brought to another place with quite a different community (Wiebe *et al* 1976).

It should be mentioned that there exists also a specific kind of synoptic eddies known as rotating lens-like eddies, for the Northeastern Atlantic also known as meddies (Armi and Zenk 1984; Armi *et al* 1988; Kostianoy and Belkin 1989). Unlike a usual synoptic ring with the volume of rotating water adjoining to the ocean surface, a lens as a whole is localized in the depth. Typically, a lens makes no observable traces on the ocean surface and that makes it a more difficult object to investigate. This is apparently the reason because the information available about biological phenomena related with the rotating lenses is rather poor. Nevertheless, since the lenses exist like isolated parcels of water with the properties different from the properties of the water around, they provide an appropriate example of long-living inhomogeneities in the ocean hydrophysical and hydrochemical fields. One can expect that farther researches will bring more results concerning biological anomalies associated with this phenomenon.

Thus, our brief examination of the properties of heterogeneous ocean fields (particularly, water temperature) shows the presence of stable spatial structures (front and eddies) existing during the time much longer than the time typical for the plankton system dynamics. There are numerous evidences of the impact of these environmental patterns on the functioning of marine ecosystems. This should serve as a ground for constructing models taking into account the existence of the forced spatial structures in aquatic populations. An example of a model of this type will be considered in the next section.

3. Chaotic and regular plankton dynamics in spatially structured fish–plankton communities

3.1 *Introduction*

Brief inspection of the main structures in the ocean environment (cf. previous section) shows that the spatio-temporal dynamics of aquatic communities is to a large extent affected by the existence of stable mesoscale structures. It should be noted that the temporal dynamics of a community can depend significantly on the spatial structure of its environment (Nisbet *et al* 1993; Ranta *et al* 1997). In this section, we focus on the dynamics of plankton populations in a patchy environment. A minimal 1D reaction-diffusion model of the planktonic dynamics inside a patch is considered assuming that some plankton habitats are rich by fish while in others it is absent. We study the temporal behaviour 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, while some of the patches are populated by fish and others may be fish-free, can give rise to plankton spatial patterns. We also show that spatially averaged plankton dynamics depending on the fish predation rate and the distance between fish-populated habitats can exhibit both chaotic and regular behaviour. The chaotic plankton dynamics is characteristic of a wide parameter range.

3.2 *Model*

We consider the four-component basic marine food chain model described by eqs (33)–(34) of Medvinsky *et al* (2001). For numerical integration of these equations a simple explicit difference scheme is used. The 1D space is divided into a grid of 64 finite-difference cells of unit length. The border between habitats divides the space into two patches. The time step is set equal to 10^{-2}. Repetition of the integration with smaller step size showed that the numerical results did not change, ensuring the accuracy of the chosen time step. The dynamics is investigated with no-flux boundary conditions. The initial distributions for h and p in eqs (33)–(34) of Medvinsky *et al* (2001) are uniform and the same for each of the habitats.

The diffusion terms in eqs (33)–(34) of Medvinsky *et al* (2001) often describe the spatial mixing of the species due to the self-motion of the organisms (Skellam 1951; Okubo 1986). However, in natural waters it is turbulent diffusion that is supposed to dominate plankton mixing (Wroblewski and O’Brien 1976; Okubo 1980). Taking this into account we consider both phytoplankton and zooplankton as passive contaminants of the water turbulent motion. In this case in eqs (33)–(34) of Medvinsky *et al* (2001) $d_p = d_h = d$. Using the relationship between turbulent diffusivity and the scale of the phenomenon in the sea (Ozmidov 1968; Okubo 1971, 1980), with the minimum phytoplankton growth rate R_0 given by 10^{-6} s^{-1} (Jörgensen 1994), the characteristic length L/k (see § 3 of Medvinsky *et al* 2001) of about 2 km, typical of plankton patterns, one can show that d is about 5×10^{-2}.

3.3 *Two-patch ecosystem dynamics*

Figure 1 demonstrates the system (33)–(34) of Medvinsky *et al* (2001) solution diagrams, i.e. the dependence of the steady-state solution on the fish predation rate. One can see that the phytoplankton-dominated stationary states are typical for high fish predation rate f. When lowering f, an unstable and another stable steady-states appear, thus making the system bistable. Further lowering f, the phytoplankton-dominated stable steady-state and the unstable state disappear in a saddle-node bifurcation. For a lower value of f, at point H a Hopf bifurcation occurs, destabilizing the zooplankton-dominated steady-state while creating a stable limit cycle. Particularly, it means that in the absence of fish ($f = 0$) the local kinetics of the system is oscillatory (for all other parameters as in figure 1). The sophisticated treatment of local properties of models similar to the model (33)–(34) of Medvinsky *et al* (2001) has been carried out in (Scheffer 1989, 1991a; Malchow and Shigesada 1994; Steffen *et al* 1997).

Let us consider the simplest example of a spatially structured ecosystem consisting of two patches only. The dynamics in both patches obeys eqs (33)–(34) of Medvinsky *et al* (2001), and in one of the patches $f = 0$, i.e. fish density is negligible (for example, due to local changes in temperature or salinity). Figure 2 shows three sets of the 1D plankton spatial patterns which have emerged from initially (at $t = 0$) homogeneous plankton distributions as a result of the diffusion interaction of the habitat populated by fish (for $x \leq 32$) with $f = 0{\cdot}05$ (figure 2a), $f = 0{\cdot}18$ (figure 2b) and $f = 0{\cdot}395$ (figure 2c), and the patch ($x > 32$) where fish is absent ($f = 0$). It is readily seen from the consideration of the dependence of the steady-state solution of the system (33)–(34) of Medvinsky *et al* (2001) on the fish predation rate f (figure 1) that the values $f = 0{\cdot}05$ and $f = 0{\cdot}18$ correspond to oscillatory plankton kinetics while $f = 0{\cdot}395$ corresponds to the zooplankton-dominated steady state. One can see that increase of the fish predation rate is followed by transition from rather regular plankton patterns (see figure 2 for $f = 0{\cdot}05$) to irregular ones (figure 2 for $f = 0{\cdot}18$) and then to virtually unstructured plankton distributions (see figure 2 for $f = 0{\cdot}395$) in the fish-populated habitat, and from regular (figure 2a) to irregular (figure 2b, c) patterns in the fish-free habitat. Note that the interaction between the patches is essential to disturb the initially homogeneous distributions, otherwise no pattern could occur.

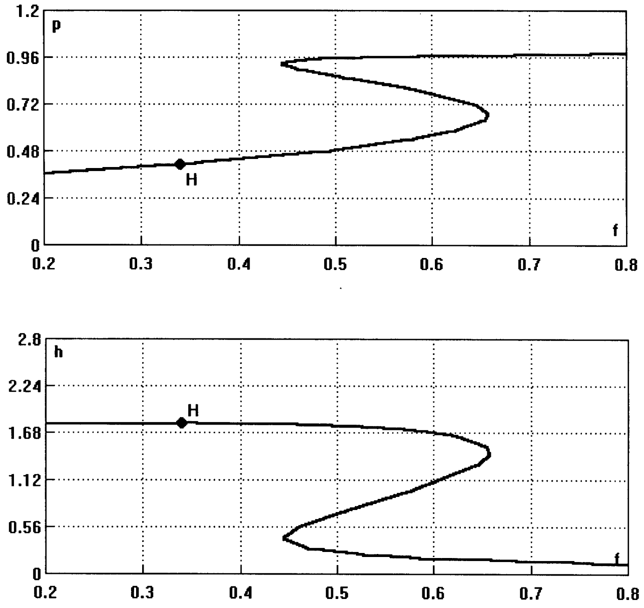


Figure 1. Solution diagrams of the model (33)–(34) of Medvinsky *et al* (2001) for the following set of parameters: $r = 5$, $a = b = 5$, $m = 0{\cdot}6$, $n = 0{\cdot}4$. The curves display the steady-state solutions for different values of f. H denotes a Hopf bifurcation.

In order to demonstrate the dependence of the plankton spatial patterns on the fish predation rate in more detail, we construct the pattern bifurcation diagram. Figure 3 shows the plankton abundance as a function of position x (the horizontal axis) calculated at $t = 5000$ for every value of f (the vertical axis) from $f = 0$ to $f = 0{\cdot}395$. 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 is growing, and then to the nearly homogeneous plankton distributions as the system passes through the Hopf bifurcation (figure 1). In contrast, at the fish-free habitat the Hopf bifurcation is not accompanied by essential changes in plankton structure (figure 3). 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 on such an inverse relationship between phytoplankton and zooplankton as an apparent consequence of phytoplankton grazing by zooplankton (Fasham 1978).

Although the distinctions between the three main types of the plankton structures shown in figure 2 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 patters a certain index. Also it seems important to follow the transformation of one pattern to another in more details, i.e. to follow how the properties of the structures change with small variations of f. To do this, we render the plankton spatio-temporal patterns (like the field shown in figure 2) into two-level structures where the values of plankton density less than a threshold value are taken equal to zero while those exceeding the threshold value are set equal to 1. The threshold value is chosen equal to the minimum peak of 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 spatio-temporal dynamics of the system.

To characterize the integral properties of the two-dimensional spatio-temporal 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 quality is robust. Figure 4 demonstrates the functions $D(f)$ for zooplankton patterns both at the fish-populated (figure 4a) and fish-free (figure 4b) 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 3 and 4 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 (figure 4a, b). Hence, the spatio-temporal plankton dynamics in the fish-free habitat seem to be less stable in comparison with the plankton dynamics in the fish-populated habitat with respect to changes in the fish predation rate.

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

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

where S_i is the area if the ith habitat; $i = 1$ corresponds to the fish-populated habitat, $i = 2$ to the fish-free one; $S_1 = S_2 = k^2/2$, $k = 64$. It emerges that the temporal dynamics of $\langle p\rangle_i$ and $\langle h\rangle_i$ depends significantly on the fish predation rate f. As an example, figure 5 demonstrates the dynamics of zooplankton space-averaged density for fish-populated and fish-free patches correspondingly. There exist three main types of the dynamics: (i) regular oscillations (when f is small); (ii) irregular oscillations in both fish-populated and fish-free patches (as f increases);

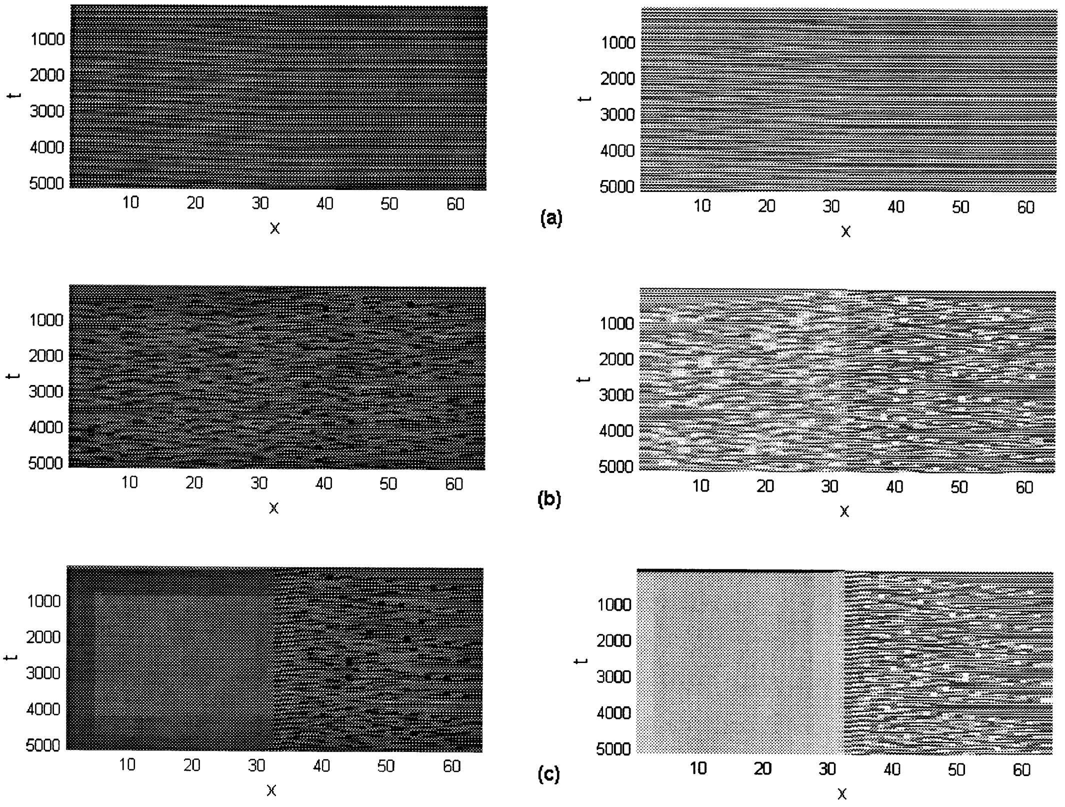


Figure 2. Spatio-temporal plankton patterns emerged from initially homogeneous plankton distributions in the two-habitat system for (**a**) $f = 0{\cdot}05$; (**b**) $f = 0{\cdot}18$ and (**c**) $f = 0{\cdot}395$; x is the spatial coordinate, t is time. The darker regions correspond to lower plankton densities.

(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; figure 1). The temporal behaviour 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 behaviour of the averaged densities (figure 5) and the spatio-temporal patterns in figure 2. 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 regular regimes the irregular ones demonstrate sensitivity to initial conditions, dependence which is characteristic of chaotic dynamics (figure 6). In order to investigate how common such a chaotic behaviour of the two-patch plankton system under consideration is, we built bifurcation diagrams for both fish-populated and fish-free patches.

Figure 7 demonstrates the bifurcation diagrams for (i) the fish-populated habitat and (ii) the fish-free one. Here, successive local maximums of the time-dependent space-averaged plankton density are plotted for the corresponding fish predation rate in a range of *f* that covers all types of the dynamics (figure 5). Regular oscillations produce one or a small number of points whereas successive maximums of irregular changes of the plankton density are spread over a range of values. The diagrams were obtained after the transition processes settled down, when the influence of the initial conditions vanished and a particular type of plankton dynamics became evident. Note the qualitatively different regions in the diagrams. For large values of the fish predation rate the plankton dynamics in the fish-populated habitat is regular (figure 7a) while in the fish-free patch the dynamics is irregular (figure 7b; an example of such a dynamics is shown in figure 5 at $f = 0{\cdot}395$). For smaller values of *f*, the regularity in the fish-populated patch is lost and the maximums visit a whole segment except for the very narrow

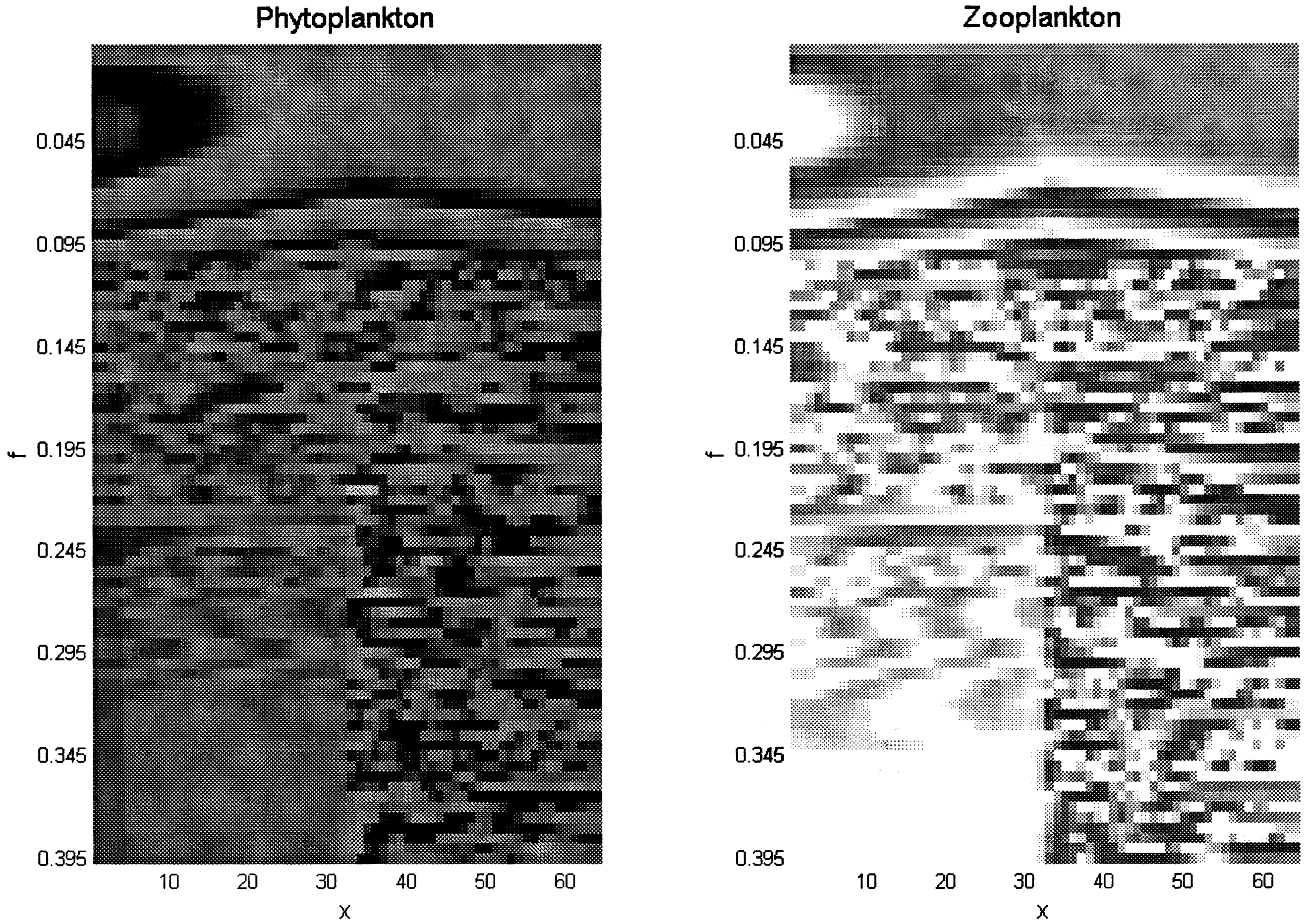
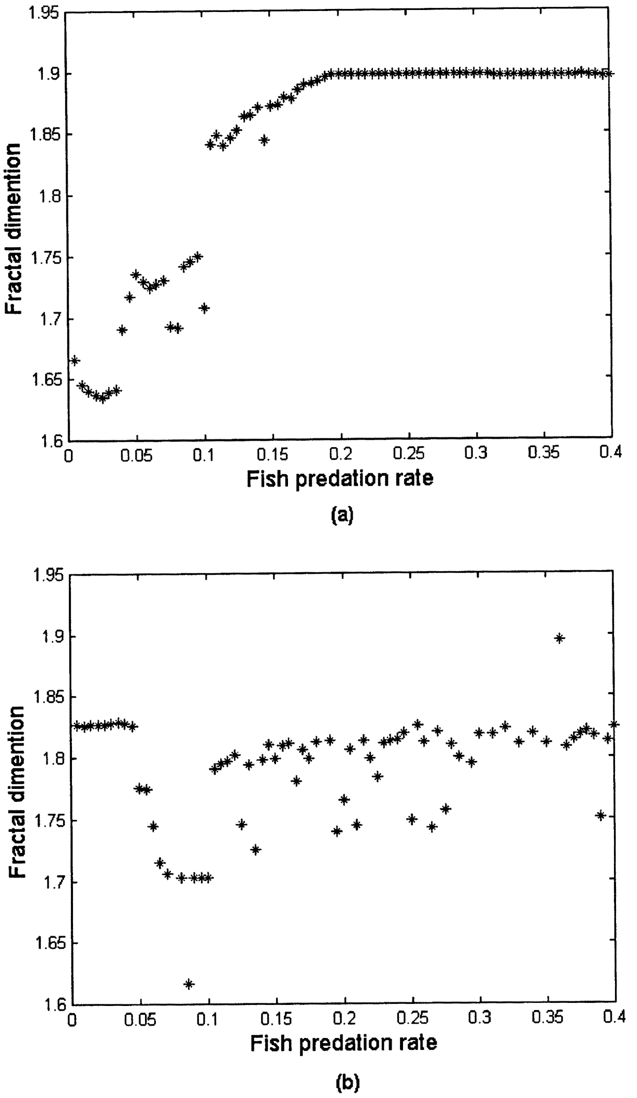


Figure 3. Pattern bifurcation diagram for phytoplankton and zooplankton obtained after 500000 iterations; *x* is the spatial coordinate, *f* is the fish predation rate. The diagram is shown in the same gray colour scale as patterns in figure 2.

gap in the vicinity of $f = 0{\cdot}2$ where the plankton dynamics in this patch becomes regular again (figure 7a). The example shown in figure 5 at $f = 0{\cdot}18$ demonstrates irregular dynamics in both the patches. At $f < 0{\cdot}1$, the plankton dynamics in both the fish-populated and fish-free patch are regular (figure 7a, b; figure 5 at $f = 0{\cdot}05$ shows an example of such a dynamics). To provide a more quantitative insight into the nature of the temporal dynamics of the averaged densities, we also calculated the dominant Lyapunov exponent (l). The results for various values of the fish-predation rate in the fish-populated habitat (figure 7c) and in the fish-free patch (figure 7d) are in good agreement with the bifurcation diagrams (figure 7a, b) and clearly demonstrate the chaotic nature of the plankton irregular dynamics. Indeed, comparing figure 7a and c, as well as figure 7b and d, one can see that $l > 0$ and chaos always occur at values of f for which the regularity of the plankton dynamics is broken.

3.4 *Three-patch ecosystem dynamics*

Figure 8 shows an example of the plankton spatial patterns which emerge from an initially homogeneous distribution in the three-patch system consisting of two



(a)

(b)

Figure 4. The dependence of the fractal dimension of the zooplankton spatio-temporal patterns on the fish predation rate for (**a**) the fish-populated and (**b**) fish-free habitats.

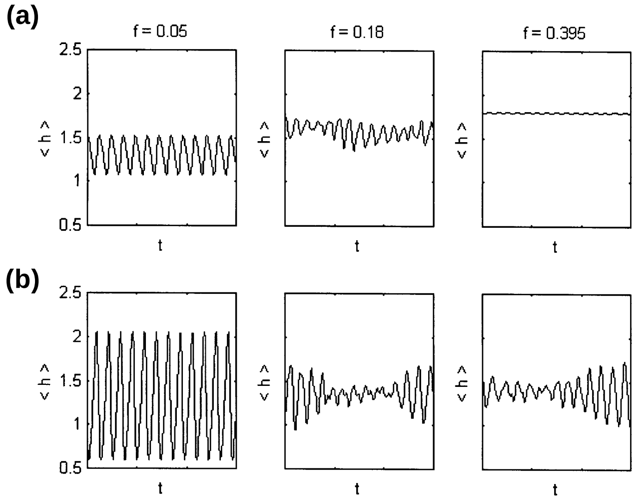


Figure 5. Three main types of oscillations of space-averaged zooplankton density depending on f. (**a**) At $x \leq 32$ (fish-populated habitat); (**b**) at $x > 32$ (fish-free habitat).

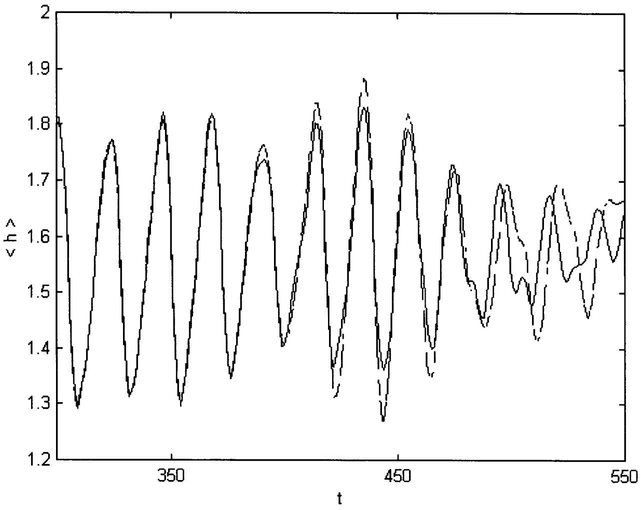


Figure 6. Sensitivity to initial conditions. Temporal $\langle h \rangle$ oscillations diverge for small initial differences. Trajectories of $\langle h \rangle$ are shown for two initial conditions differing by $0{\cdot}001$. Here $f = 0{\cdot}18$.

fish-populated habitats separated by the fish-free gap. The choice of the parameters corresponds to either the steady-state local kinetics ($f = 0{\cdot}395$ in figure 8a) or to the limit cycle local kinetics ($f = 0{\cdot}18$ in figure 8b). The following question arises: how does the type of plankton dynamics depend on the width of the fish-free gap?

To answer this question, we calculate the dominant Lyapunov exponent for various gap width values (d). It appears that regular oscillations (similar to those in figure 5 for $f = 0{\cdot}05$) are independent on d. In figure 9 l is plotted versus d for two other types of plankton dynamics shown in figure 5. The function $l(d)$ is remarkably non-monotone in case of irregular oscillations of space-averaged plankton density in both fish-populated patches and the fish-free gap (figure 9 for $f = 0{\cdot}18$). Note that there is a clear correlation between the gap width-variations of the dominant Lyapunov exponent in the fish-populated patches (solid line) and the fish-free gap (dashed line). Such a correlation is absent as a virtually constant plankton density in the fish-populated patches occurs while irregular oscillations appear in the fish-free gap (figure 9 for $f = 0{\cdot}395$). It easily seen that in the fish-populated patches l is virtually constant and equal to zero while in the fish-free gap is monotonically decreasing down to zero as the gap width d decreases approaching 14 (the bottom of figure 9). Thus, 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 under consideration, but also on patch-to-patch distances.

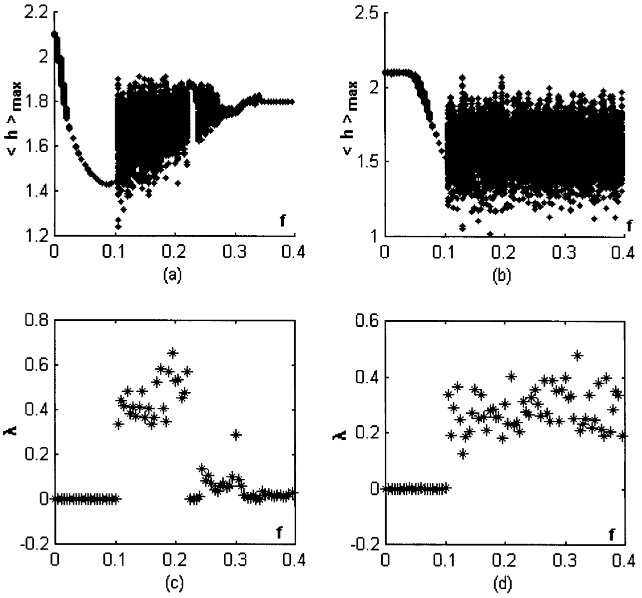


Figure 7. Bifurcation diagrams and dominant Lyapunov exponents for various values of fish predation rate f. (**a**) Bifurcation diagram for fish-populated patch. (**b**) Bifurcation diagram for fish-free patch. (**c**) Dominant Lyapunov exponent for fish-populated patch. (**d**) Dominant Lyapunov exponent for fish-free patch. All the calculations were carried out on the time interval $2000 \leq t \leq 5000$.

6. Summary

In this work we overview the processes underlying the dynamics of spatially inhomogeneous aquatic communities. It is well-known that the heterogeneity of the species spatial distribution can not be always reduced to the heterogeneity of marine environment: there are physical and biological scales of the problem. We consider different mechanisms of the formation of intrinsic biological patterns, i.e. the patterns not directly induced by any aspect of the ocean hydrodynamics. We show that formation of a realistic (i.e. transient and irregular) spatial structure in the plankton distribution may come as an immediate result of the interplay between the turbulent

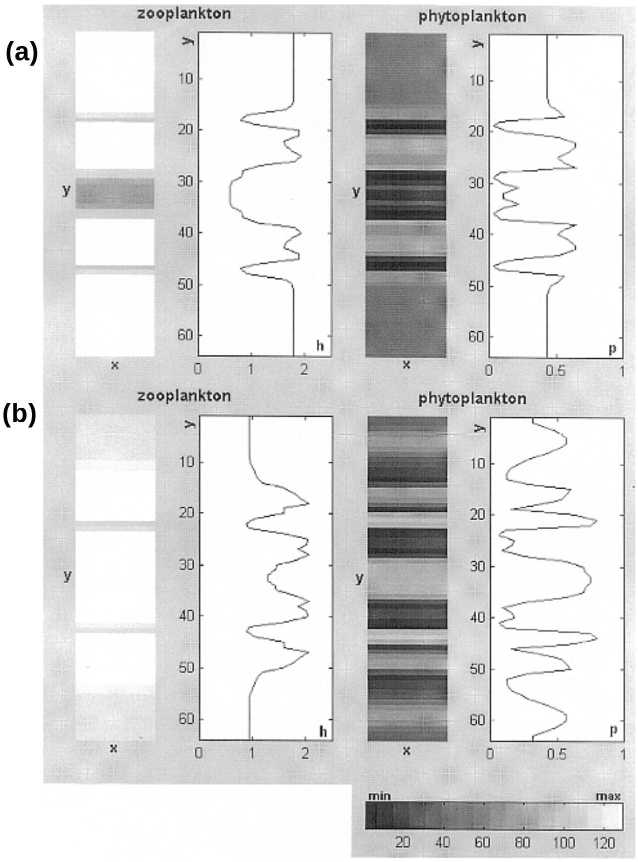


Figure 8. Zooplankton and phytoplankton quasi-2D spatial patterns emerging in the three-patch system from initially homogeneous plankton distributions, and the corresponding profiles of plankton density. For $x \leq 16$ and $48 \leq x \leq 64$, $f = 0{\cdot}395$ (**a**) or $f = 0{\cdot}18$ (**b**) while for $16 < x < 48$, $f = 0$.

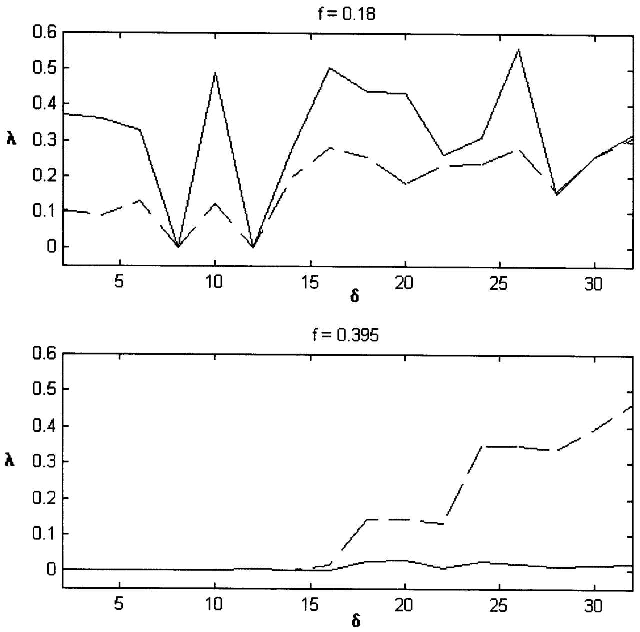


Figure 9. The dependence of dominant Lyapunov exponents in the fish-populated habitats (solid lines) and in fish-free habitats (dashed lines) on the distance between fish-populated habitats.

mixing and principal matter fluxes in the plankton community, e.g. phytoplankton–zooplankton interactions. Formation of the plankton pattern is characterized by an intrinsic length, the value if this length (estimated to be on the order of 1 km) is consistent with the data of field observations.

The minimal model describing the formation of irregular patchy plankton distribution is shown to be the two-species prey-predator (phytoplankton-zooplankton) system with the parameters not depending on the position and without any restraints on the values of the species diffusivities. We show that the regime of the system dynamics corresponding to the pattern formation can be qualified as spatio-temporal chaos. The appearance of irregular spatial distributions follows an unusual scenario and can be preceded by formation of a distinct spiral pattern.

Another mechanism of formation of irregular spatial patterns in a plankton community is shown to be the impact of a planktivorous fish school. The interaction between a mobile fish schools and the plankton system, although modifying the properties of the spatial structure, does not change the principle points of the system dynamics: formation of spiral waves and chaos in the plankton dynamics. The fish school motion is shown to have fractal features.

By reviewing data of field observations we also show 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, e.g. water temperature, salinity, biogen concentration etc. In this case, the characteristic size of these inhomogeneities provides another, external scale of the system.

We develop the analysis of plankton pattern formation and corresponding spatio-temporal dynamics of the plankton community in a patchy environment. Using a minimal reaction-diffusion model of the nutrient–plankton–fish food chain, we study the role of the diffusive interaction between fish-populated and fish-free habitats in a patchy environment in plankton pattern formation. We show that such interaction can give rise to spatio-temporal plankton patterns with the fractal dimension depending on the fish predation rate. The spatially averaged plankton dynamics turn out to be dependent on both the fish predation rate and the distance between fish-populated habitats and can exhibit chaotic and regular behaviour. The chaotic plankton dynamics is characteristic of a wide parameter range.

These results may indicate the vital role of chaotic regimes in the spatio-temporal organization of aquatic ecosystems. Indeed, there is increasing evidence that systems with chaotic dynamics have an even higher potential for adapting to changing environmental conditions than systems with a stable equilibrium point (Wilson 1992; Allen *et al* 1993; Hastings 1993; Pahl-Wostl 1993; Huisman and Weissing 1999). 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 is even the suggestion that the process of aging is characterized by loss of plasticity and variability afforded by chaos in basic physiological systems (Lipsitz and Goldberger 1992). In this connection the problem of interrelation between chaotic and regular dynamics is of great interest.

The paper demonstrates new challenges resulting from essentially nonlinear interactions in aquatic communities. Conceptual few-species reaction-diffusion models are shown to be an appropriate tool for searching and understanding basic mechanisms of the spatio-temporal pattern formation in coupled plankton-fish dynamics.

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