Nonequilibrium plankton community structures in an ecohydrodynamic model system

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Abstract. Due to the local and global impacts of algae blooms and patchiness on water quality, carbon cycling and climate, models of plankton dynamics are of current interest. In this paper, the temporal and spatial patterns in natural plankton communities are interpreted as transient and stationary nonequilibrium solutions of dynamical nonlinear interaction-diffusion-advection systems. A simple model of phytoplankton-zooplankton dynamics (Scheffer, 1991) is presented in space and time. After summarizing the local properties as multiple stability and oscillations, the emergence of spatial and spatio-temporal patterns is considered, accounting also for diffusion and weak advection. In order to study the emergence and stability of these structures under hydrodynamic forcing, the interaction-diffusion-advection model is coupled to the hydrodynamic equations. It is shown, that the formation of nonequilibrium spatio-temporal density patterns due to the interplay of the deterministic nonlinear biological inter-actions and physical processes is a rare occurence in rapidly flowing waters. The two-timing perturbation technique is applied to problems with very rapid single-directed steady flows. A channel under tidal forcing serves as an example for a system with a relatively high detention time of matter. Generally, due to the different time and length scales of planktic interactions, diffusion and transport, initial non-equilibrium plankton patches are simply moved through the system unless the strong hydrodynamic forces do not destroy them before.

1 Introduction

The dynamics of spatial and spatio-temporal pattern formation in nonlinear systems far from equilibrium is of considerable interest in theoretical biology and ecology. Several scenarios and mechanisms of structure formation have been found, e.g.:

i) In his basic paper on the role of nonequilibrium reaction-diffusion prepatterns in biomorphogenesis, Turing (1952) proved that the interplay of nonlinear reactions and diffusion of at least two substances can give rise to diffusion-induced instabilities of a spatially homogeneous distribution, resulting in standing spatial structures. A main condition for the emergence of such structures is a significant difference of the diffusion coefficients. Early generalizers of Turing's work were Gmitro and Scriven (1966) as well as Prigogine and Nicolis (1967). Most of the following experimental and theoretical investigations have been done in the fields of physics as well as physical and biological chemistry, compare Nicolis and Prigogine (1977), Haken (1978) and Ebeling and Feistel (1982) for reviews. The existence of diffusive Turing structures has been verified only recently in a chemical system (Castets et al., 1990), i.e. for the chlorite-iodide-malonic acid reaction. Segel and Jackson (1972) were the first to apply Turing's idea to a problem in population dynamics: The dissipative instability in the prey-predator interaction of phytoplankton and an herbivorous species.

ii) A spatially homogeneous distribution can also be destabilized by a differential or shear flow of the key species (Okubo, 1967; Evans, 1977; Spiegel and Zalesky, 1984; Rovinsky and Menzinger, 1992; Doering and Horst-hemke, 1993). This mechanism is free from the restrictions of the Turing instability on the diffusion coefficients and can thus be expected to appear in a larger class of physical, chemical, and biological systems. Recently, Rovinsky and Menzinger (1993) have reported the differential flow-induced chemical instability in the ferroin-catalyzed Belousov-Zhabotinsky system, resulting in wave-like patterns.

iii) The emergence of convective Bénard cells in an initially uniform fluid, heated from below, is a well-known thermal effect (cf. Ebeling and Feistel, 1982). It has its analogue in biology. This so-called bioconvection (Platt, 1961) appears in dense populations of free-swimming microorganisms. Certain conditions are required for the occurence of bioconvection, e.g. an overcritical density of the population as well as a minimum depth of the culture, compare also Okubo (1980), Kessler (1986), and Pedley and Kessler (1992).

iv) Density-dependent dispersal of species towards fa-vourable habitats in heterogeneous environments has been described as diffusion in an environmental potential (Shige-sada and Teramoto, 1978). Spatio-temporally varying

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potentials necessarily destabilize uniform species distributions (Malchow, 1988).

An impressive summary of spatial and spatio-temporal pattern formation phenomena in nonlinear ecological and biological reaction-diffusion-advection-convection models has been given by Okubo (1980) and Murray (1989).

Because of their role in carbon cycling and in temperature control and, hence, due to their strong impacts on the global climate changes (cf. Charlson et al., 1987; Williamson and Gribbin, 1991), the modelling of plankton population dynamics is a current problem. In this paper, the local behaviour and the spatial patterning in a two-component plankton model due to Scheffer (1991) are summarized. Local bistability, limit-cycle oscillations, plankton front propagation and the generation and drift of planktic Turing patches have been found recently (Malchow, 1993). Then, the model and its patterns are coupled to tidal hydrodynamics in order to study their stability against strong forcing.

2 A Skeleton Model for Plankton Interactions

The trophic interactions of nutrients, phytoplankton, zooplankton and fish, considered here, are sketched in Fig. 1:
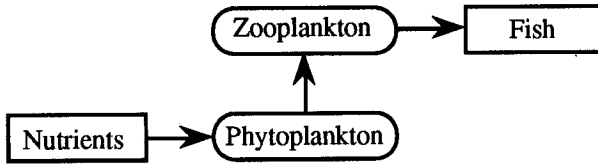

Fig. 1. Trophic levels of the considered system.

Phytoplankton and zooplankton biomass are treated as the dependent dynamical variables whereas the environmental factors of nutrient concentration and fish density act as the external control parameters, driving the system away from equilibrium. Scheffer (1991) formulated the following minimal model for this interaction sequence:

$$\frac{\partial P}{\partial t} = f(P,Z) = \frac{\alpha N}{H_N + N} P - cP^2 - \frac{\gamma P}{H_P + P} Z, \tag{1}$$

$$\frac{\partial Z}{\partial t} = g(P,Z) = \frac{e\gamma P}{H_P + P} Z - \delta Z - \frac{FZ^2}{H_Z^2 + Z^2}; \tag{2}$$

with P and Z as phytoplankton and zooplankton biomass respectively. N denotes the nutrient level of the system and F the predation rate of the present fish stock on zooplankton. α is the growth rate of phytoplankton, γ the grazing rate of zooplankton on phytoplankton, c the competition coefficient of phytoplankton, e the prey assimilation efficiency of zooplankton and δ the mortality and respiration rate of zooplankton. H_P, H_Z and H_N are the half saturation constants of functional responses and nutrient limitation. P, Z, H_P and H_Z are measured in [mg.dw l^{-1}]. N and H_N are

given in relative units, e is a dimensionless parameter. The dimension of α, γ, δ is [d^{-1}], whereas F is measured in [mg.dw d^{-1} l^{-1}]. c is expressed in [mg.dw^{-1} l^{-1} d^{-1}].

The nutrient limitation of logistic phytoplankton growth as well as the dependence of the zooplankton grazing rate on phytoplankton density are of Monod type. Hence, in the absence of zooplankton, phytoplankton growth will saturate at $P_0 = \alpha N/[c\,(H_N + N)]$. Growth limitations by different nutrients are not considered separately, but an overall carrying capacity, depending on the total nutrient level, is assumed (Rosenzweig, 1971). The zooplankton predation by fish follows a type-III functional response (Holling, 1959; Yodzis, 1989). This sigmoidal response can be caused by the existence of refuges for the prey or by the possibility of switching to alternative preys (Murdoch and Oaten, 1975; Murdoch and Bence, 1987).

2.1 Local Properties of the Model

The local behaviour of system (1,2) has been analysed graphically by Scheffer by means of zero-isocline representations:

$$\frac{\partial P}{\partial t} = 0 \quad \Rightarrow \quad Z = \frac{H_P + P}{\gamma}\left(\frac{\alpha N}{H_N + N} - cP\right), \tag{3}$$

$$\frac{\partial Z}{\partial t} = 0 \quad \Rightarrow \quad P = H_P \frac{\delta\left(H_Z^2 + Z^2\right) + FZ}{(e\gamma - \delta)\left(H_Z^2 + Z^2\right) - FZ}. \tag{4}$$

It is readily seen that the nutrient level N only influences the shape of the phytoplankton isocline (3), whereas the predation rate of fish F only affects the zooplankton isocline (4). Combining the graphical with a usual numerical bifurcation analysis, the following stationary states and bifurcations can be found for fixed parameters but decreasing predation rate F of fish on zooplankton:

(I) High fish predation rate: Existence of a non-oscillating (stable node-type) phytoplankton-dominated state;

(IIa) Generation of another non-oscillating (stable node-type) but zooplankton-dominated state and an unstable saddle point through a fold catastrophe (Thom, 1975; Ebeling & Malchow 1979), emergence of two-node bistability;

(IIb) Change of the stable-node zooplankton-dominated state to a stable focus (damped oscillation), emergence of focus-node bistability;

(III) Vanishing of both the stable-node phytoplankton-dominated state and the saddle point through a fold catastrophe,

(IV) Low and zero fish predation rate: Hopf bifurcation of the stable-focus zooplankton-dominated state to an unstable focus and a stable limit cycle (remaining of the typical phase-shifted prey-predator oscillations).

In a certain parameter configuration, the Hopf bifurcation (IV) can precede the decay (III) of the phytoplankton-dominated state, resulting in local limit cycle-node bistability of the model. Three typical isocline graphs are superposed in Fig. 2.
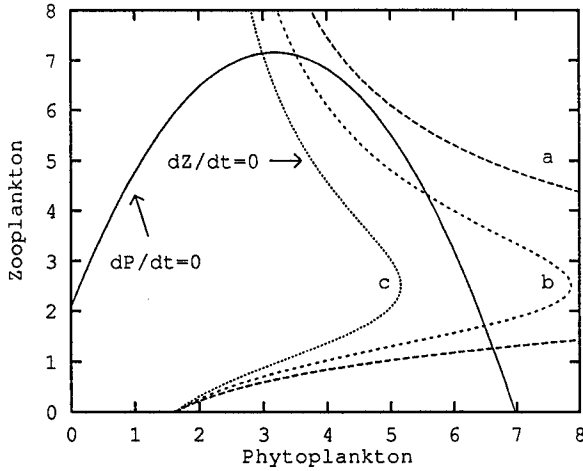
Fig. 2. Zero-isocline graphs for parameters:
$\alpha = 1.45$, $\delta = 0.175$, $\gamma = 0.4$, $e = 0.6$, $c = 0.2$, $N = 2.5$, $H_N = 0.1$, $H_P = 0.6$, $H_Z = 2.5$, (a) $F = 0.28$, node monostability, (b) $F = 0.24$, focus-node bistability, (c) $F = 0.20$, limit-cycle oscillations.

The parameter values are chosen within a realistic range. Phytoplankton growth limitation has been chosen to get a maximal phytoplankton carrying capacity of 7 to 10 mg.dw l⁻¹ which is thought realistic under eutrophic conditions. The zooplankton grazing rate, its assimilation efficiency, mortality and respiration are taken close to the values given by Rose & Swartzman (1988) for medium-sized *Daphnia*.

It can be concluded (Scheffer 1991), that a gradual change in fish density can cause discontinuous changes in phytoplankton and zooplankton density. Furthermore, planktivorous fish tends to damp the planktic predator-prey oscillations.

2.2 Spatio-temporal Patterns

Horizontal and vertical freshwater and marine algae patterns are well-known from direct measurements, airplane photographs or satellite images. The mechanisms of their formation are not known in detail yet, but there must be a permanent interplay of biological, chemical, and physical processes to generate, to stabilize or to destroy, to move etc. these patterns. Several experimental and modelling attempts have been made to achieve more detailed knowledge (cf. Nihoul, 1975, 1986; Steele, 1978; Brown and Barnwell, 1987; Ambrose et al., 1988; Cosper et al., 1989; Michaelis, 1990).

Spatial and spatio-temporal patterns in plankton communities have been interpreted as nonuniform nonequilibrium solutions of nonlinear interaction-diffusion systems with constant but weak advection (Malchow, 1993). The results will be briefly summarized now.

Following Scheffer's minimal approach, the considerations have been restricted to two-species models

$$\frac{\partial P}{\partial t} = f(P,Z) - \vec{\nabla}\vec{j}_P, \quad \frac{\partial Z}{\partial t} = g(P,Z) - \vec{\nabla}\vec{j}_Z; \quad (5)$$

with the fluxes

$$\vec{j}_K = \vec{V}(\vec{r},t)K(\vec{r},t) - D_K\vec{\nabla}K(\vec{r},t); \quad K = P, Z; \quad (6)$$

where $\vec{\nabla} = \vec{e}_x(\partial/\partial x) + \vec{e}_z(\partial/\partial z)$ is the Nabla operator in Carthesian (rectangular) co-ordinates $x \in [0, L]$ with unit vector $\vec{e}_x$ in horizontal direction, and $z \in [0, D]$ with unit vector $\vec{e}_z$ in vertical direction, i.e. a horizontally one-dimensional cross-section is modelled only. The vector $\vec{r} = \{x, z\}$ determines the position, whereas the vector $\vec{V}(\vec{r},t) = \{u(z,t), w\}$ gives the velocity at position $\vec{r}$. The velocity field is divergence-free: div $\vec{V}(\vec{r},t) = \vec{\nabla}\vec{V}(\vec{r},t) = 0$.

The vertical velocity component w describes the settling of species, and it is assumed to be constant in space and time. The component u models the horizontal drift which might vary with depth z. Furthermore, the motion of plankters is regarded as passive (Fickian) diffusion. Hence, the diffusion coefficients D_P and D_Z are treated as constants, i.e. time-, density- as well as temperature effects are neglected.

Throughout the paper, Neumann boundary conditions are applied.

The reference and derived magnitudes of the used quantities have again been chosen to achieve parameter values within a realistic range of densities, wind shear, sinking rates as well as vertical and horizontal diffusivity scales. Accounting for the local properties of Scheffer's model for different parameter domains, the formation of spatio-temporal patterns in the corresponding distributed system has been investigated (cf. Malchow, 1993).

Firstly, the parameter region of local bistability has been considered. The dynamics of systems with two alternative stable homogeneous solutions has been investigated extensively, compare Malchow and Schimansky-Geier (1985). The two homogeneous states can coexist in space, forming a diffusive front between them. In one-component systems, the standing front is structurally unstable and any fluctuation will force it to move. The direction depends on the local kinetics. As a result, only one solution will "survive". In more-component systems, this front can be stabilized, i.e. conditions for the stable spatial coexistence of the homogeneous distributions can be found. There are several analogues to nucleation phenomena. In particular, there is a critical nucleus size of one homogeneous solution surrounded by the other. Only nuclei of overcritical size can grow.

The successful growth of an initially small phytoplankton-dominated nucleus in the surrounding zooplankton-dominated "phase" has been demonstrated in Malchow (1993). The phytoplankton-dominated solution "wins the competion" and, finally, it homogeneously fills the whole space domain. The added constant shear, linearly decreasing with depth, disturbs the smoothness of the evolving structure.

Secondly, the capacity of the distributed model to form diffusion-induced Turing patterns has been elucidated. For simplicity, the external shear $\vec{V}(\vec{r},t)$ is neglected here. Following Turing's idea, one has to suppose stability of a spatially homogeneous stationary distribution

$$\left[P^S(\vec{r},t), Z^S(\vec{r},t)\right] = \text{const.}, \quad f(P^S,Z^S) = g(P^S,Z^S) = 0;$$

of the system (5,6) against spatially uniform perturbations. This distribution can loose its stability against certain spatially nonuniform perturbations for overcritical ratios of the diffusivities. The full set of conditions for inducing such a diffusive Turing instability of a homogeneous two-species distribution reads

(i) $\partial_P f^S + \partial_Z g^S < 0$, $\partial_P f^S \cdot \partial_Z g^S - \partial_Z f^S \cdot \partial_P g^S > 0$, (7)

with

$$\partial_K f^S = \frac{\partial f(P^S,Z^S)}{\partial K}, \quad \partial_K g^S = \frac{\partial g(P^S,Z^S)}{\partial K}, \quad K = P,Z, \quad (8)$$

and

(ii) $$\frac{D_Z \, \partial_P f^S + D_P \, \partial_Z g^S \geq}{2\sqrt{D_P D_Z \left(\partial_P f^S \cdot \partial_Z g^S - \partial_Z f^S \cdot \partial_P g^S\right)}} \quad (9)$$

The equality sign in eq.(9) corresponds to the critical point. If the zooplankton species is supposed to be the destabilizing activator of the system, then it additionally holds

(iii) $\partial_P f^S < 0$, $\partial_Z g^S > 0$, $\dfrac{D_P}{D_Z} \gg 1$. (10)

The latter conditions have already been derived by Segel & Jackson (1972). Several examples for the formation of spatially nonuniform patchy plankton distributions have been provided for system (5,6) in Malchow (1993), also taking into account external shear as well as space- and time-variable phytoplankton growth α due to its dependence on light and temperature. This problem is not the focus of the present work. For illustration of the possible spatial structures of system (5,6), a combination of a diffusive front between the phytoplankton- and zooplankton-dominated state and a Turing structure, evolving from the destabilized zooplankton-dominated level, is given in Fig. 3.

The final stationary solution is the stable coexistence of the phytoplankton-dominated state at the left-hand side and the Turing pattern at the right-hand side.

3 Coupling to Hydrodynamics

In order to study the effect of hydrodynamic forcing on the considered nonequilibrium planktic interactions and patterns, the biological interactions and fluxes (5,6) are coupled to the hydrodynamic equations. This coupling may create a number of problems due to the significantly diffent
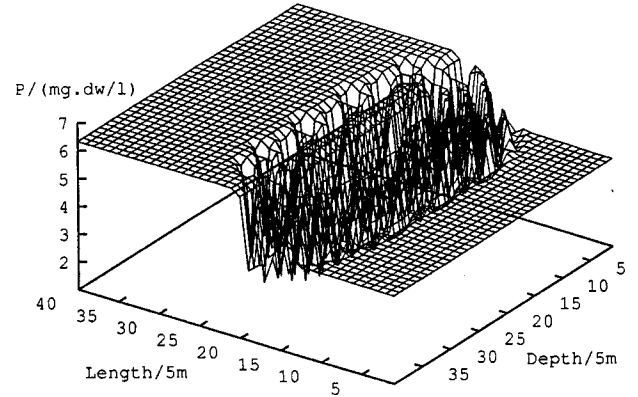
(a)
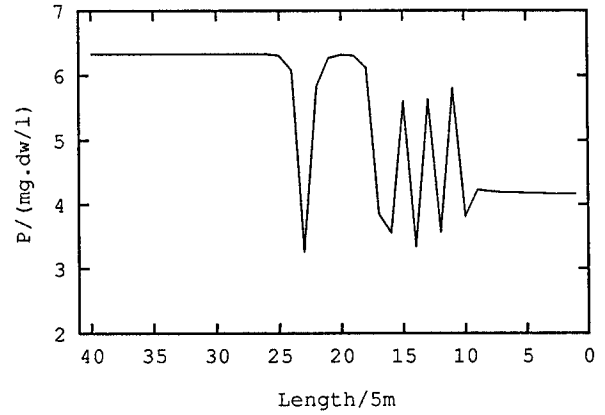
(b)

Fig. 3. Combination of a diffusive front between the phytoplankton- and zooplankton-dominated state and a Turing structure, evolving from the zooplankton-dominated level for $D_P/D_Z = 200$, $L=D=200m$, and all other parameters like in Fig. 2. (a) Three-dimensional plot of phytoplankton density, (b) two-dimensional cut at mean depth.

time and length scales of biological and physical processes (cf. Purcell, 1977; Zaret, 1980; Okubo, 1985; Nihoul, 1986; Nihoul et al. 1994). Therefore, advection and biological interactions can be of variable dominance. However, if one considers an area with a nearly vanishing or with a very rapid steady flow respectively, these processes can be separately treated, i.e. dominant biological interactions in very slowly moving waters and dominant transport of any species distribution in very rapidly moving waters. O'Brien & Wroblewski (1973) introduced a dimensionless parameter, containing the characteristic water speed and the maximum specific biological growth rate, to distinguish these two extremes. They can be treated by making use of the multiple-scale (two-timing) perturbation technique (Nayfeh, 1973) which has already successfully been applied to rapidly dispersing species in heterogeneous environments (Ei & Mimura, 1984; Shigesada, 1984; Malchow, 1988).

For very rapid flows the solution simply appears as the transported initial condition.

3.1 An Approximative Solution for Dominant Advection

For simplicity, advection with constant speed $u > 0$ and constant growth f of a single species P in one spatial dimension $x \in [0, L]$ are considered. The growth and advection processes are described by

$$\frac{\partial P(x,t)}{\partial t} + u\frac{\partial P(x,t)}{\partial x} = \varepsilon f(P), \qquad (11)$$

with initial and boundary condition $P(x,0) = s(x)$ and $P(0,t) = s(0) = P_B$ respectively. For later convenience, the growth function is written as the product of a parameter ε and the function f. To realize the case of very rapid advection processes, it is assumed that ε is small enough for making use of the two-timing perturbation technique. The growth function f and the advection term $u\,\partial P/\partial x$ are set to the same order of magnitude O(1). The formal procedure of constructing the approximative solution as a truncated expansion which is valid for all times up to O($1/\varepsilon$) closely follows the treatment given by Shigesada (1984) and Malchow (1988):

Two different time scales T_0 and T_1 are introduced by $T_0 = t$; $T_1 = \varepsilon t$, so that the time derivative is transformed to

$$\frac{\partial}{\partial t} = \frac{\partial}{\partial T_0} + \varepsilon\frac{\partial}{\partial T_1}. \qquad (12)$$

A solution is sought with the ansatz

$$\begin{aligned} P(x,t) &= P(x,T_0,T_1,\varepsilon) \\ &= P_0(x,T_0,T_1) + \varepsilon P_1(x,T_0,T_1) + \dots. \end{aligned} \qquad (13)$$

Substituting (12) and (13) into (11) and grouping together terms of the same order in ε, one finds in leading order O(1) the advection equation

$$\frac{\partial P_0(x,T_0,T_1)}{\partial t} + u\frac{\partial P_0(x,T_0,T_1)}{\partial x} = 0 ; \qquad (14)$$

$$P_0(x,0,0) = s(x) ; P_0(0,T_0,T_1) = s(0) = P_B .$$

Its solution can be written as

$$P_0(x,T_0,T_1) = Y_0(T_1) Z(x,T_0) ; \qquad (15)$$

where the function Z is again the solution of an advection equation

$$\frac{\partial Z(x,T_0)}{\partial t} + u\frac{\partial Z(x,T_0)}{\partial x} = 0 ; \qquad (16)$$

$$Z(x,0) = \frac{s(x)}{\int_0^L s(x)dx} ;$$

$$Z(0,T_0) = \frac{s(0)}{\int_0^L s(x)dx} = \frac{P_B}{\int_0^L s(x)dx} .$$

Eq.(16) is satisfied by any function $Z(x,T_0) = Z(x - uT_0)$. For $T_0 \to \infty$ or at least $T_0 \geq L/u$, the whole area $x \in [0, L]$ will be spatially uniform at

$$Z(x,T_0) = \frac{P_B}{\int_0^L s(x)dx} = \text{const.} \qquad (17)$$

i.e. any spatially nonuniform initial condition has run out.

The function $Y_0(T_1)$ remained arbitrary up to now, but it will be determined from the next step of the perturbation scheme O(ε):

$$\frac{\partial P_1(x,T_0,T_1)}{\partial T_0} + u\frac{\partial P_1(x,T_0,T_1)}{\partial x}$$
$$= f(P_0) - \frac{\partial P_0(x,T_0,T_1)}{\partial T_1} ; \qquad (18)$$

$$P_1(x,0,0) = 0 ; P_1(0,T_0,T_1) = 0.$$

Integrating eq.(18) over $[0,L]$, one obtains

$$\frac{\partial Y_1(T_0,T_1)}{\partial T_0} + u\left[P_1(L,T_0,T_1) - P_1(0,T_0,T_1)\right]$$
$$= \int_0^L f(P_0)dx - \frac{\partial Y_0(T_1)}{\partial T_1} . \qquad (19)$$

with

$$Y_1(T_0,T_1) = \int_0^L P_1(x,T_0,T_1)dx ; \qquad (20)$$

For $T_0 \to \infty$, it holds that $P_1(L,T_0,T_1) \to P_1(0,T_0,T_1)$. Moreover, the right-hand side of eq.(19) should tend to zero because otherwise $Y_1(T_0,T_1)$ will become unbounded due to the occurrence of secular terms. Hence, the function $Y_0(T_1)$ is fixed as the solution of

$$\frac{\partial Y_0(T_1)}{\partial T_1} = \int_0^L f\left(Y_0(T_1)\frac{P_B}{\int_0^L s(x)dx}\right)dx$$
$$= L \cdot f\left(Y_0(T_1)\frac{P_B}{\int_0^L s(x)dx}\right) ; \qquad (21)$$

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$$Y_0(0) = \int_0^L s(x)dx.$$

This follows by equating the r.h.s. of eq.(19) to zero and substituting the stationary value (17) into $Z(x,T_0)$. Finally, one finds the solution of eq.(11) as a truncated expansion which is valid for times up to $O(1/\varepsilon)$:

$$P(x,t) = Y_0(\varepsilon t)\, Z(x,t) + O(\varepsilon). \qquad (22)$$

$Y_0(\varepsilon t)$ is the solution of the ordinary differential equation (21). The short-time behaviour of system (11) is governed by the rapid advection process $O(1)$.

For sufficiently small system length L, it might be that the effects of the long-time behaviour $O(1/\varepsilon)$ will never be recognized. For constant speed u, the latter can be investigated better by a "moving-boat" technique, i.e. quantities as nutrients and fish stock, governing the plankton interactions, are assumed to be variable in space; $N = N(x)$, $F = F(x)$. Then one can concentrate on the local interactions with variable control parameters which are then described by nonautonomous differential equations through the transformation of space to time dependence $t = x/u$.

The time-scale separation, described above, is not possible for tidal hydrodynamics which is taken into account now.

3.2 Horizontally One-dimensional Tidal Hydrodynamics

The full set of tidal hydrodynamic equations of motion for the components of the velocity vector $\vec{V}$ can be reduced for the horizontally one-dimensional description, given above. The remaining governing equations are

$$\frac{\partial u}{\partial t} - A_v \frac{\partial^2 u}{\partial z^2} + g \frac{\partial \zeta}{\partial x} = 0, \qquad (23)$$

for the horizontal velocity component u, and

$$\frac{\partial \zeta}{\partial t} + \frac{\partial \zeta}{\partial x} u_S - w_S = 0, \qquad (24)$$

for the water surface elevation ζ. Here, A_v is the turbulent exchange coefficient and g the gravity constant. u_S and w_S are the velocity components at the water surface. Eq.(24) also represents the kinematic boundary condition for the surface. Furthermore, one has to take into account the continuity equation

$$\frac{\partial u}{\partial x} + \frac{\partial w}{\partial z} = 0, \qquad (25)$$

as well as the interaction-diffusion-advection equations (5,6). However, the Fickian diffusion coefficients in the latter expressions have to be replaced by the eddy diffusion coefficients because sub-scale processes cannot be resolved. The main assumptions, leading to eqs. (23-25), are (Sünder-mann, 1971):

1. All terms in the hydrodynamic equations of motion, containing the vertical velocity component w or its derivatives, are neglected.
2. Convective terms are discarded.
3. External forces except gravity vanish.
4. Then, the equation of motion for the vertical velocity component w is simply the equation for the hydrostatic pressure.
5. The air pressure is constant along the water surface. Hence, pressure gradients correspond to water level changes.

The additional appropriate boundary conditions can be formulated as:

1. At the water surface with wind speed U_W and wind-drag coefficient λ, it holds

$$A_v \frac{\partial u}{\partial z}\bigg|_S = \lambda\, |U_W|\, U_W. \qquad (26)$$

2. At the bottom with friction coefficient r, it holds

$$A_v \frac{\partial u}{\partial z}\bigg|_B = r\, |u_B|\, u_B. \qquad (27)$$

3. The velocity components normal to a closed boundary vanish.

4. At the seaward open boundary, one has the system-driving tide

$$\zeta_0(t) = A\cos(\sigma t - \kappa), \qquad (28)$$

with maximum water surface elevation A, tidal angular speed σ and phase κ.
5. At closed boundaries, it holds $\partial\zeta/\partial x = 0$.

The initial conditions are the motionless water $u = w = 0$ and $\zeta = 0$, as well as different nonequilibrium spatial plankton distributions, found without hydrodynamic coupling.

The equations are reformulated for an open channel of constant depth as a finite-difference scheme on a grid of 80 x 6 points, also considering the stability conditions (Sünder-mann, 1971; Roache, 1982; O'Brien, 1986; Rood, 1987), and then numerically integrated. The van-Leer algorithm (van Leer, 1974; Allen et al., 1991) is used for the advection scheme in order to minimize the numerical diffusion.

Some numerical results for the coupled plankton transport and interaction are given. The hydrodynamic parts of the program have been run over 4 tidal periods to provide a stationary water speed oscillation. Then, the transport and interaction modules have been switched on. At length $x=0$ the system is driven by the model tide with the angular speed of the M_2-tide, i.e. the semi-diurnal, principal lunar tide (Pond and Pickard, 1983). Furthermore, the system is forced at the surface $z=0$ by an periodically varying wind. The continuous forth-and-back motion of the water body

leads to the high detention times of suspended matter observed in estuaries and, hence, it makes the simultaneous consideration of hydrodynamics and biochemical interactions necessary. The used hydrodynamic parameters are:

$D_P = 3.47*10^{-4} \text{ m}^2 \text{ s}^{-1}, D_Z = 6.25*10^{-2} \text{ m}^2 \text{ s}^{-1}$
$A_v = 0.1 \text{ m}^2 \text{ s}^{-1}, \lambda = 3.2*10^{-6}, r = 6.0*10^{-3}$
$L = 80 \text{ km}, dx = 1000 \text{ m}, D = 20 \text{ m}, dz = 4 \text{ m}$
$A = 1.5 \text{ m}, \sigma = 1.4052*10^{-4} \text{ s}^{-1}, \kappa = -\pi/2$
$U_W = 10 \text{ m s}^{-1} \cos(\sigma t)$

Firstly, the transport and deformation of the phytoplankton-dominated state in the bistable node-node regime of Scheffer's model, starting with a rectangular nucleus of about 20km length and 12m depth, is presented in Fig. 4:
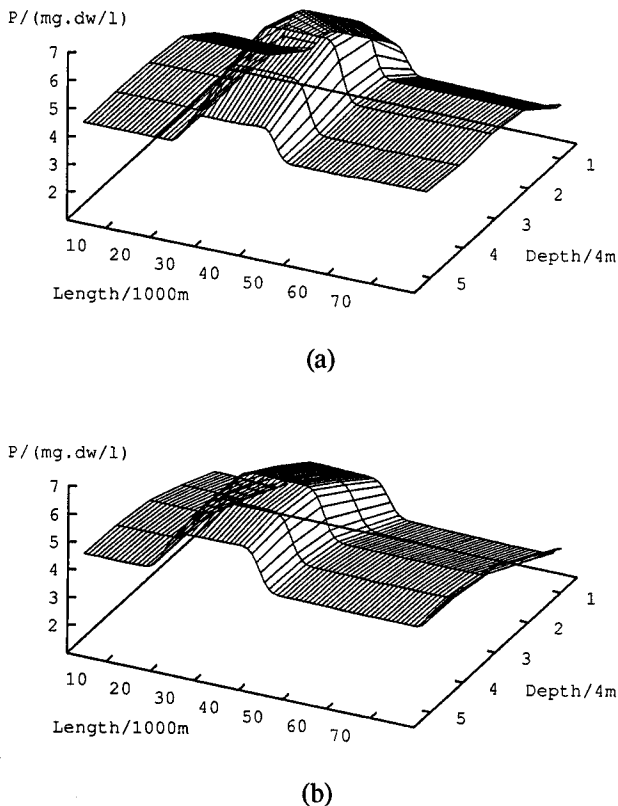

(a)

(b)

Fig. 4. Transport of the phytoplankton-dominated state in the bistable regime; (a) after 6 and (b) after 12 hours. F = 0.26, all other parameters like in Fig. 2.

The initial condition is simply transported and deformed. Switches of the zooplankton- to the phytoplankton-dominated state due to introduced local fluctuations have never been achieved. They are suppressed by the governing physical processes. For $t \rightarrow \infty$ the whole considered area is occupied by the zooplankton-dominated state due to the seaward overall net movement. Naturally, the same is valid for the inverse situation of an initial zooplankton-dominated nucleus surrounded by the phytoplankton-dominated "phase".

Secondly, the oscillatory regime is considered. A special initial condition has been designed to have a rectangular area of about 30km length and 12m depth at another part of the local limit-cycle oscillation than the rest, i.e. it is ahead of time. The resulting spatio-temporal patterns can be seen in Fig. 5.

The area ahead of time first reaches the part of the limit cycle with more rapid growth, resulting in a local maximum of phytoplankton density. Though it might be a rare event, the latter is an example for the capacity of deterministic nonlinear biological interactions to form localized spatial density structures which are moved by the governing hydrodynamic forces.

Thirdly, the interplay of nonlinear planktic interactions and turbulent diffusion could not generate or stabilize Turing patterns on their relevant time and length scale. As it appeared in the bistable regime, local fluctuations are damped out or simply advected by the powerful external forcing with its own patterns in space and time.

4 Conclusions

The local properties of a skeleton model for phyto- and zooplankton interactions (Scheffer, 1991) have been summarized. Parameter ranges of local bistability, i.e. the local coexistence of a stable phytoplankton- and a stable zooplankton-dominated state, have been found. The typical prey-predator limit-cycle oscillations appear for a low or vanishing amount of fish and they are damped out for a high fish stock. This two-species system serves as a minimal biological water quality model to study the effects of coupling the biological to physical processes.

After the analysis of the local properties, the spatial pattern-generating capacity of the model on a two-dimensional spatial cross-section has been investigated. It has been referred to recently obtained results (Malchow, 1993) for dissipative structure formation in systems including passive species diffusion and constant weak advection. Conditions for the diffusive (Turing) instability of a homogeneous plankton distribution have again been given, and an example for the stable spatial coexistence of a phytoplankton-dominated state and a nonuniform structure has been provided, emerging after Turing instability of the zooplankton-dominated level.

In order to study the effect of hydrodynamic forcing on the considered nonequilibrium plankton interactions and patterns, the biological interactions and fluxes have been coupled to the hydrodynamic equations. It has been mentioned that approximate results are available for dominant single-directed advection and dominant interactions respectively when the time scales can be separated and multiple-scale perturbation techniques are applicable.

Generally, the latter is not possible for the coupling of biological processes and tidal hydrodynamic forces due to the continuous forth-and-back motion of the water body and the high detention time of suspended matter. Examples have been provided for both the simple transport and deformation of a spatially nonuniform initial plankton distribution and for the formation of a localized spatial density structure due to the nonlinearity of the underlying deterministic species interactions which is moved by the

P/(mg.dw/l)
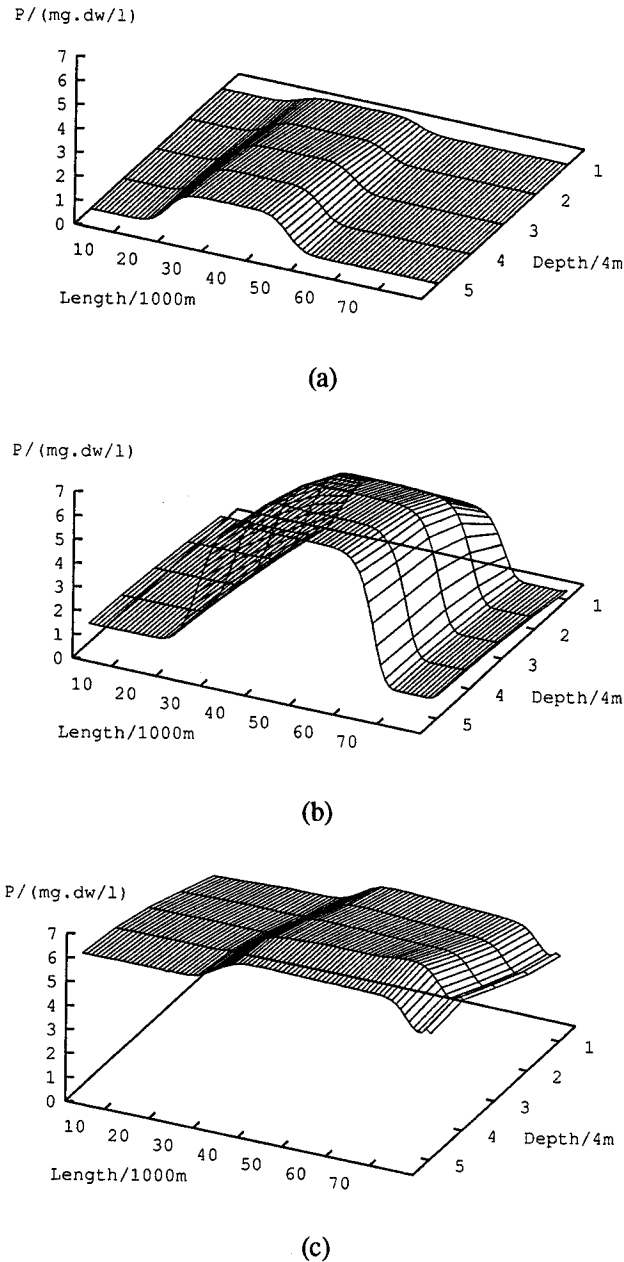

(a)

P/(mg.dw/l)

(b)

P/(mg.dw/l)

(c)

Fig. 5. Formation of spatio-temporal phytoplankton patterns in the oscillatory regime; (a) after 72, (b) after 180 and (c) after 252 hours. $F = 0.20$, all other parameters like in Fig. 2.

governing hydrodynamic forces.

However, switches from one deterministic steady state to another as a result of local or nonlocal fluctuations which are well-known for reaction-diffusion systems with weak advection, decoupled from hydrodynamic forcing, could not be reproduced. They are suppressed by the governing physical processes.

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