

Instability of a uniform plankton distribution

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For a plankton model system, a horizontally uniform distribution becomes unstable if the zooplankton component carries out diurnal vertical migrations in an ocean with a speed difference between the currents in upper and lower waterlayers. With turbulent diffusion included in the model, the instability occurs beyond a threshold speed difference. A numerical estimation of the threshold and of the critical patch size gives reasonable values.

1. Introduction

Plankton is very inhomogeneously distributed in the ocean. In the vertical direction, the plankton concentration varies in a well-known dependence on physical factors, like light and nutrient concentrations (e.g. the model by Slagstad 1980, and references given there). But in the horizontal direction, the variations of the plankton densities (patchiness) do not follow so clearly the change of the environmental conditions. Indeed, on the large scale, well above 10 km, the plankton varies with the distance from the coastline, with the large scale ocean currents, determined by the geography of the bottom, and with other physical factors (e.g. Wroblewski 1976). But, on the intermediate scale, 1 km–10 km, large plankton fluctuations are observed that cannot be connected to the variations of the physical conditions (Platt and Denman 1975, Steele 1974, Ebenhöh 1979). A review of the mathematical analysis of patchiness can be found in Fasham (1978).

In this article, we shall prove that, in a model situation under quite general conditions, a horizontally uniform plankton distribution is dynamically unstable. This means a decay into patches occurs spontaneously. The model contains two plankton components: phytoplankton and zooplankton. The zooplankton carries out diurnal vertical migrations. It undergoes a daily shift against the non-migrating phytoplankton, due to its temporary residence in deeper waterlayers, if one assumes a velocity difference between surface ocean currents and deep water currents. Intuitively considered, such a shift should change nothing if the starting distribution is uniform (spatially homogeneous in horizontal direction). But the instability of the uniform plankton distribution, due to such an effective horizontal migration of the zooplankton, will be proved mathematically.

The turbulent diffusion tends to smooth out any spatial inhomogeneity, hence, it acts as a stabilizing factor. With diffusion included, one obtains a critical value for the speed difference that separates stable and unstable conditions. In § 2, a linear

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difference equation model is developed; in § 3, spatially uniform and periodic solutions are compared. Diffusion is added, in § 4, and the threshold speed difference is calculated.

2. A linear difference equation plankton model

In the following, P and Z stand for phyto- and zooplankton. As the starting point, a slightly modified Lotka–Volterra system is chosen:

$$\dot{P} = \lambda P - \alpha PZ - \epsilon P^2$$

$$\dot{Z} = \beta PZ - \gamma Z$$

This system differs from the classic Lotka–Volterra system only by the damping term with parameter ϵ . The quadratic term makes the model more flexible, since it allows the description of damped predator–prey oscillations. The plankton system may be considered as a system showing damped oscillations which become stimulated by the annual change of the physical conditions. A Lotka–Volterra system is, however, nothing more than a very crude simulation of the natural plankton system. The most crucial shortcomings of this simulation are

- (a) the limitation of phytoplankton growth due to nutrient shortage (only roughly contained in the term $-\epsilon P^2$) and
- (b) the neglect of size distribution and life cycle of the zooplankton.

For the purpose of an analytic stability analysis, however, the model must be kept as simple as possible.

The parameters λ , α , β and γ can be used for a fit of equilibrium densities of P and Z , of oscillation time and of relative oscillation amplitudes. But the stability properties do not depend upon all of these parameters. Two parameters disappear after proper scaling of P and Z :

$$\dot{P} = \lambda P(1-Z) + \epsilon P(1-P)$$

$$\dot{Z} = \beta(P-1)Z$$

For stability investigations it suffices to consider the model linearized in the neighbourhood of the equilibrium state $P_\infty = Z_\infty = 1$. With the introduction of the deviation $p = P - P_\infty$ and $z = Z - Z_\infty$, one obtains

$$\dot{p} = -\epsilon p - \lambda z$$

$$\dot{z} = \beta p$$

A final scaling of the deviations p and z and of the time gives

$$\left. \begin{aligned} \dot{p} &= -\epsilon p - z \\ \dot{z} &= p \end{aligned} \right\} \quad (1)$$

Here, the damping ϵ is the only parameter which remains. The other parameters are removed by simple scalings. The system (1) has a scaled oscillation time of $\Delta_0 = 2\pi/\sqrt{1-\epsilon^2/4}$ for $0 \leq \epsilon < 2$, and it shows exponential behaviour for $\epsilon \geq 2$. The observed oscillation time T_0 of 20 to 30 days (estimated e.g. from the length of the spring bloom) corresponds, hence, to a scaled time interval of Δ_0 ($\approx 2\pi$ for $\epsilon \lesssim 1$); and the time unit of 1 day corresponds to $\Delta = \Delta_0 \cdot 1 \text{ day}/T_0 \approx 0.2 \dots 0.3$.

A further simplification is possible by transforming the differential equation (1) into the linear difference equation system (2) with finite time-steps:

$$\begin{bmatrix} p \\ z \end{bmatrix} (t+\Delta) = \begin{bmatrix} 1-\epsilon\Delta & -\Delta \\ \Delta & 1 \end{bmatrix} \begin{bmatrix} p \\ z \end{bmatrix} (t) \quad (2)$$

In the next sections, the diurnal migration of the zooplankton and the turbulent diffusion is added to the system (2). There, interest will be concentrated on the change of the dynamic stability due to these extensions. In order to investigate the stability, the eigenvalues $\lambda_{1,2}$ of the matrix A from (2) have to be calculated:

$$A = \begin{bmatrix} 1-\epsilon\Delta & -\Delta \\ \Delta & 1 \end{bmatrix}$$

$$\lambda_{1,2} = \left(1 - \frac{\epsilon\Delta}{2}\right) \pm \sqrt{\left[\left(\frac{\epsilon\Delta}{2}\right)^2 - \Delta^2\right]} \quad (3)$$

We find $|\lambda|=1$ for $\epsilon=\Delta$, corresponding to the marginal undamped oscillations of the differential equation system (1) with $\epsilon=0$. Hence, by the transition from (1) to the difference equation system (2) the parameter ϵ changed its meaning slightly. For $\Delta < \epsilon < 2$, the system (2) shows damped oscillations with an oscillation period $\approx 2\pi$. For $2 \leq \epsilon \leq (1+\Delta^2)/\Delta$ the system (2) approaches the equilibrium in an exponential way. For $\epsilon > (1+\Delta^2)/\Delta$, nonsense oscillations of period 2Δ appear which become undamped for $\epsilon > (4+\Delta^2)/2\Delta$ (Fig. 1).

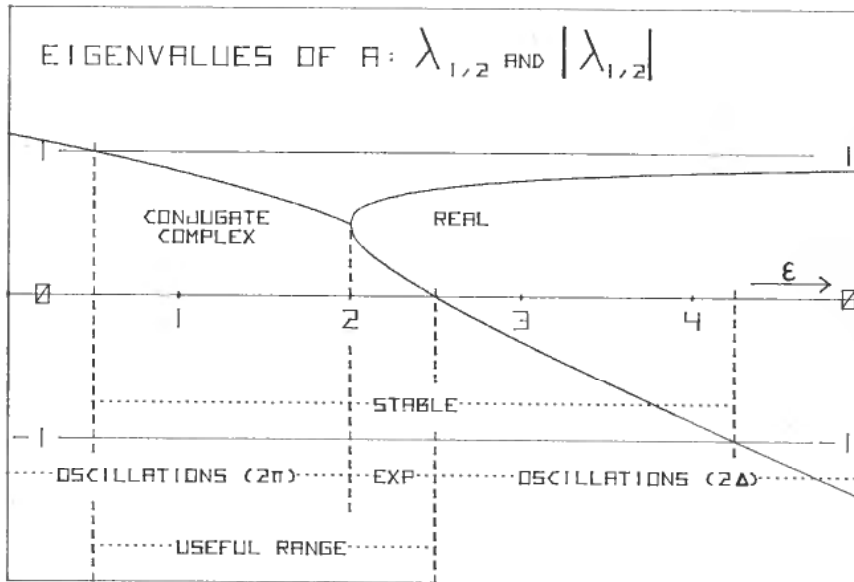


Figure 1. Eigenvalues of the matrix A (eqn. (3)) in the dependence on the damping parameter ϵ . In the case of complex eigenvalues ($\epsilon < 2$), the absolute values are given. For the time step Δ , the value 0.5 is chosen here as well as in the following figures. For a reduced Δ , the figures stay qualitatively unchanged but the different effects appear less pronounced.

Since the results in the next sections depend only slightly on the damping parameter ϵ , accurate numerical values for ϵ are not necessary. The statements on spatial stability will be valid for plankton systems with undamped or weakly damped oscillations ($\epsilon \approx \Delta$) as well as for the case of strong damping ($\epsilon \gtrsim 1$).

3. The effective horizontal migration of the zooplankton

A vertical migration of the zooplankton separates it from the phytoplankton for roughly half the day. If there is a horizontal velocity difference v between upper and lower waterlayers, then a selected patch of zooplankton, after a vertical down and up migration contacts the phytoplankton at a new position. There is a daily horizontal shift L of the zooplankton relative to the phytoplankton. The length L is determined by the vertical velocity profile and the vertical migration amplitude; it will be in the order of $\frac{1}{2}v$ day. A reasonable estimate for L is 1 km ($v=2$ km/day = 2.3 cm/sec). For a mathematical analysis of this situation, the space is divided in the direction of motion into compartments of length L . By choosing the scaled time interval to be equivalent to 1 day, any 'numerical diffusion' is avoided because the zooplankton component becomes shifted by exactly one compartment per day:

$$\begin{bmatrix} p_i \\ z_{i+1} \end{bmatrix} (t+\Delta) = A \begin{bmatrix} p_i \\ z_i \end{bmatrix} (t) \quad (4)$$

Here the index i (integer from $-\infty$ to ∞) denumerates the compartments. A special solution of (4) is the uniform solution (no dependence on i), thus, the solution of (2). But other solutions are possible; especially easy to construct are spatially periodic solutions.

For a spatial period $2L$ one finds from (4):

$$\begin{bmatrix} p_1 \\ z_1 \\ p_2 \\ z_2 \end{bmatrix} (t+\Delta) = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \end{bmatrix} \begin{bmatrix} A & O \\ O & A \end{bmatrix} \begin{bmatrix} p_1 \\ z_1 \\ p_2 \\ z_2 \end{bmatrix} (t) \quad (5)$$

where A and O are 2×2 matrices.

The stability of the system (5) is determined by the eigenvalues of the product matrix in (5). It can be seen that (5) decays into

$$\left. \begin{aligned} \begin{bmatrix} p_1 + p_2 \\ z_1 + z_2 \end{bmatrix} (t+\Delta) &= A \begin{bmatrix} p_1 + p_2 \\ z_1 + z_2 \end{bmatrix} (t) \\ \begin{bmatrix} p_1 - p_2 \\ z_1 - z_2 \end{bmatrix} (t+\Delta) &= \tilde{A} \begin{bmatrix} p_1 - p_2 \\ z_1 - z_2 \end{bmatrix} (t) \end{aligned} \right\} \quad (6)$$

with

$$\tilde{A} = \begin{bmatrix} 1 & 0 \\ 0 & -1 \end{bmatrix} \quad A = \begin{bmatrix} 1 - \epsilon\Delta & -\Delta \\ -\Delta & -1 \end{bmatrix}$$

Hence, two of the four eigenvalues of the product matrix in (5) are the old values $\lambda_{1,2}$ from (3). The other two eigenvalues are the eigenvalues $\mu_{1,2}$ from \tilde{A} :

$$\mu_{1,2} = -\frac{\epsilon\Delta}{2} \pm \sqrt{\left[\left(1 - \frac{\epsilon\Delta}{2}\right)^2 + \Delta^2 \right]} \quad (7)$$

$$-\mu_2 \approx 1 + \frac{1}{2}\Delta^2 > 1 \quad \text{for } \Delta \lesssim 0.5$$

There is always $|\mu_2| > 1$ (Fig. 2). This means dynamic instability of (5). The nature of this instability can clearly be seen in the reformulation (6) of (5). The matrix \tilde{A} acts on the differences of the plankton concentrations in the neighbouring compartments. An initial difference increases. In Fig. 3, a solution of the system (5) is compared with a solution of (3).

Solutions of the system (4) with arbitrary periods $2D = nL$ ($n \geq 2$) can be investigated in the same way. One has to calculate the eigenvalues $\mu_{1,2}(\phi)$ of the matrices A_ϕ

$$A_\phi = \begin{bmatrix} 1 & 0 \\ 0 & \exp(i\phi) \end{bmatrix} A \quad (8)$$

Eigenvalues: $\mu_{1,2}(\phi)$

$$\phi = \pi L/D = 2\pi/n$$

It turns out that the absolute largest eigenvalue occurs for $\phi = \pi$, hence, for the spatial period $2L$ (Fig. 4). This must be interpreted in such a way that the model plankton approaches a periodic structure with a characteristic length L which is proportional to v .

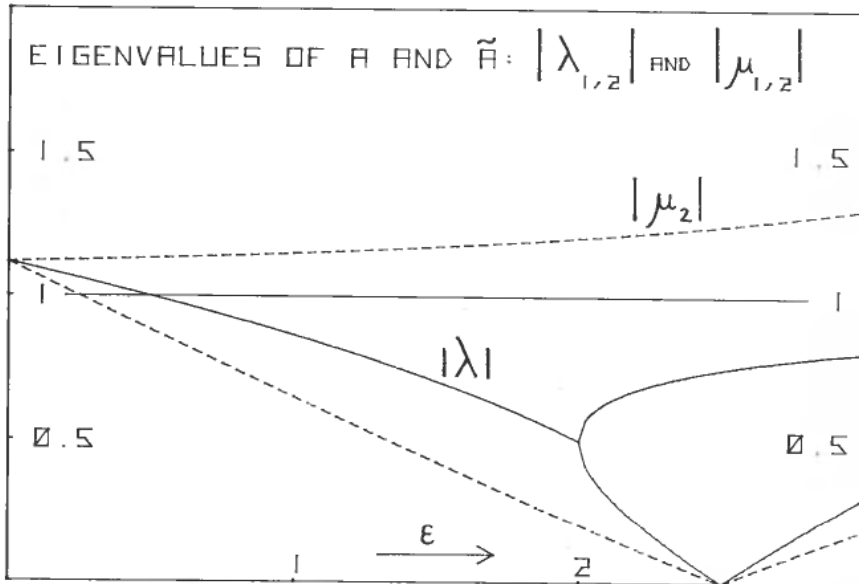


Figure 2. Absolute values of the eigenvalues of A (solid) and of \tilde{A} (broken). There is always $|\mu_2| > 1$ which means instability ($\Delta = 0.5$, see Fig. 1).

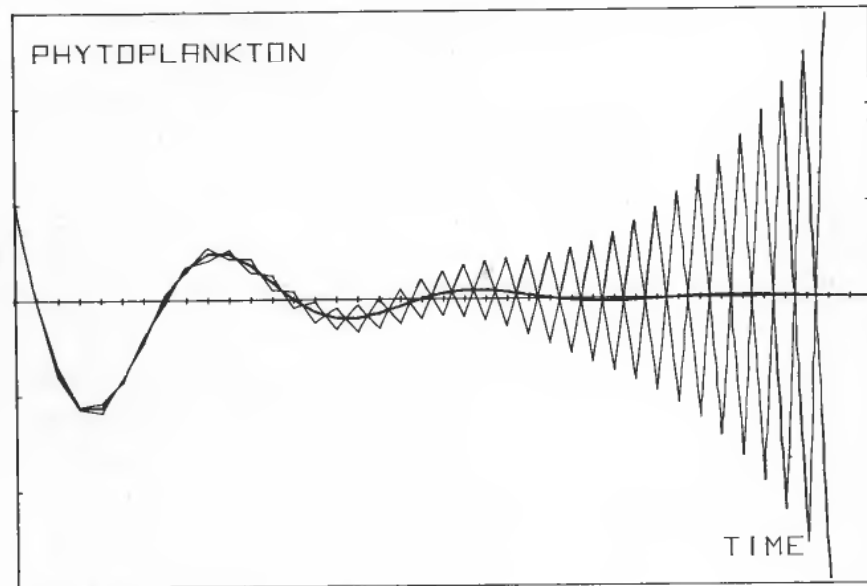


Figure 3. Comparison of the spatially uniform solution (smooth curve with slow damped oscillations, $\epsilon = 1$) with a spatially periodic solution. The uniform solution is unstable; a small initial difference between neighbouring compartments becomes amplified. The vertical axis gives the deviations of the phytoplankton density from the equilibrium value in arbitrary units. The time axis is divided into 1 day intervals corresponding to $\Delta = 0.5$ (see Fig. 1).

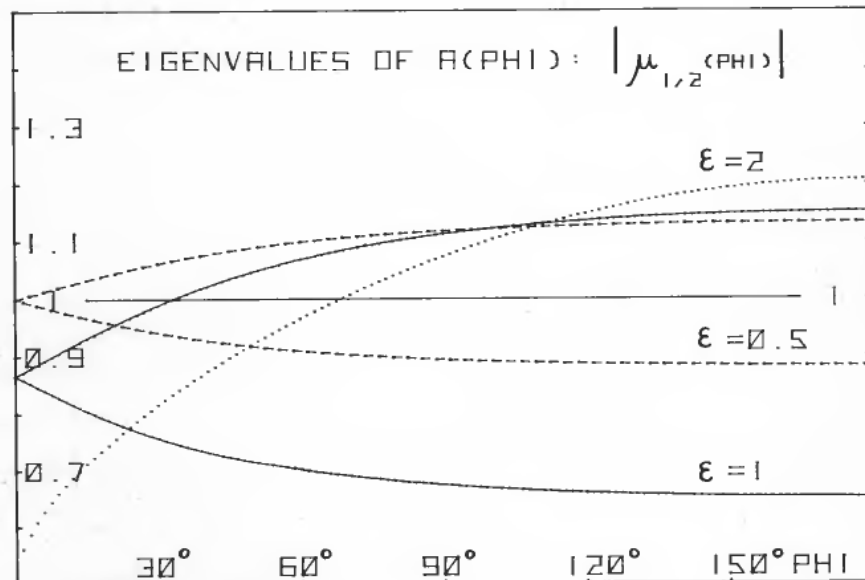


Figure 4. Eigenvalues of the matrices A_ϕ . The angle ϕ is proportional to the inverse of the spatial wavelength $2D$ (eqn. (8)) ($\Delta = 0.5$, see Fig. 1).

Of course, in nature the speed difference v between upper and lower waterlayers is not a constant. It changes strongly with tides and wind. A periodic structure cannot be expected in reality but this does not devalue the instability proof above.

4. The turbulent diffusion

The turbulent diffusion reduces the differences of the plankton concentrations between neighbouring compartments. The simplest mathematical formulation of the effect of the turbulent diffusion is the action of a matrix K

$$K = \begin{bmatrix} 1 - \frac{1}{2}\kappa & \frac{1}{2}\kappa \\ \frac{1}{2}\kappa & 1 - \frac{1}{2}\kappa \end{bmatrix}, \quad 0 \leq \kappa \leq 1$$

on

$$\begin{bmatrix} p_1 \\ p_2 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} z_1 \\ z_2 \end{bmatrix}$$

If the turbulent diffusion were the only driving force, the characteristic lifetime of density differences between neighbouring compartments, T_κ , would be $1/\kappa$ days. Introducing K in system (5) one obtains:

$$\begin{bmatrix} p_1 \\ z_1 \\ p_2 \\ z_2 \end{bmatrix} (t + \Delta) = \begin{bmatrix} 1 - \frac{1}{2}\kappa & 0 & \frac{1}{2}\kappa & 0 \\ 0 & 1 - \frac{1}{2}\kappa & 0 & \frac{1}{2}\kappa \\ \frac{1}{2}\kappa & 0 & 1 - \frac{1}{2}\kappa & 0 \\ 0 & \frac{1}{2}\kappa & 0 & 1 - \frac{1}{2}\kappa \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \end{bmatrix} \begin{bmatrix} A & O \\ O & A \end{bmatrix} \begin{bmatrix} p_1 \\ z_1 \\ p_2 \\ z_2 \end{bmatrix} (t) \quad (9)$$

This system can be decomposed in the same way as the system (5):

$$\begin{bmatrix} p_1 + p_2 \\ z_1 + z_2 \end{bmatrix} (t + \Delta) = A \begin{bmatrix} p_1 + p_2 \\ z_1 + z_2 \end{bmatrix} (t)$$

$$\begin{bmatrix} p_1 - p_2 \\ z_1 - z_2 \end{bmatrix} (t + \Delta) = (1 - \kappa) \tilde{A} \begin{bmatrix} p_1 - p_2 \\ z_1 - z_2 \end{bmatrix} (t)$$

Two of the four eigenvalues of the product matrix in (9) are again the $\lambda_{1,2}$ of (3), while the two other eigenvalues $\nu_{1,2}$ now are the $\mu_{1,2}$ of (7) but reduced by a factor $(1 - \kappa)$:

$$\nu_{1,2} = (1 - \kappa)\mu_{1,2} \quad (10)$$

If κ exceeds a critical value, the system (9) is stable because $|\nu_2|$ is less than 1, even if $|\mu_2|$ is larger than 1.

A numerical value for κ can be derived from the measurements of the turbulent diffusion in the ocean. If the turbulent diffusion is described in analogy to the molecular diffusion by Fick's law with a diffusion constant κ_F , one finds that κ_F is dependent on the scale L of the diffusion process (Okubo 1971):

$$\begin{aligned}\kappa_F(L) &= \kappa_F(1 \text{ km})(L/1 \text{ km})^{1.15} \approx \kappa_F(1 \text{ km})(L/1 \text{ km}) \\ \kappa_F(1 \text{ km}) &= \kappa_1 \text{ km}^2/\text{day}\end{aligned}$$

Individual observations yield values from 0.01 to 0.1 for κ_1 with a mean value of 0.05. For solutions of eqn. (9) with spatial period $2L$, the constant κ in the matrix K and in (9) can now be obtained from κ_F :

$$\kappa(L) = \kappa_1 \pi^2 / (L/1 \text{ km}) \quad (11)$$

Now, from $|v_2| = 1$ and from the observed oscillation time T_0 (§ 2), a critical velocity difference v_{crit} can be calculated. By using eqns. (10), (7) and (11) one obtains:

$$\begin{aligned}\kappa_{\text{crit}} &= 1 - 1/|\mu_2| \approx \frac{1}{2}\Delta^2 \\ \Delta &\approx 2\pi \cdot 1 \text{ day}/T_0 \quad \text{with } T_0 = (20 \dots 30) \text{ days} \\ L_{\text{crit}}/\text{km} &= \kappa_1 2\pi^2 / \Delta^2 = (200 \dots 500)\kappa_1 \\ v_{\text{crit}} &= 2L_{\text{crit}}/\text{day}\end{aligned}$$

This estimation does not take into account that for $\kappa \neq 0$ the most probable spatial wavelength $2D$ is larger than $2L$. The scale dependence of the diffusion constant κ

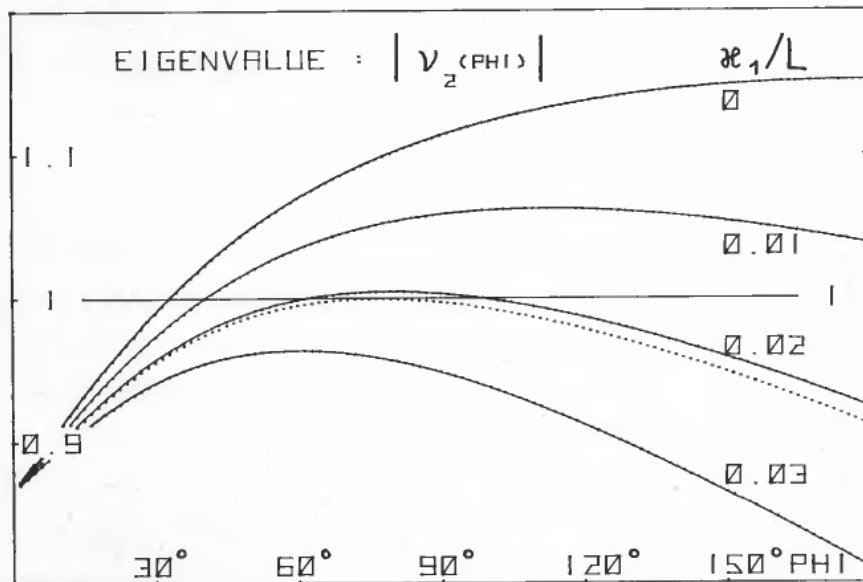


Figure 5. Eigenvalues of the matrices $(1 - \kappa(\phi))A_\phi$. The angle ϕ is proportional to the inverse of the spatial wavelength $2D$. Different curves correspond to different values of the quotient $\kappa_1/(L/\text{km})$. The curve with the critical value of this quotient is dotted ($\kappa = 1$ and $\Delta = 0.5$, see Fig. 1).

means that the maximum of $|\nu_2(\phi)| = (1 - \kappa)|\mu_2(\phi)|$ with $\phi = \pi L/D$ does not appear at $\phi = \pi$, as is the case for $|\nu_2(\phi)|$ (eqn. (8) and Fig. 4). The uniform distribution is marginally stable, if this maximum is 1 (Fig. 5). In this way more correct estimates can be obtained:

$$L_{\text{crit}}/\text{km} = (50 \dots 200) \kappa_1$$

$$v_{\text{crit}} = 2L_{\text{crit}}/\text{day}$$

$$D_{\text{crit}} = (2 \dots 4)L_{\text{crit}}$$

For $\kappa_1 = 0.05$ and $T_0 = 20$ days one finds $v_{\text{crit}} = 5$ km/day and $D_{\text{crit}} = 10$ km. D_{crit} can be interpreted as a characteristic diameter of a patch, which forms spontaneously if v exceeds v_{crit} .

5. Conclusion

In this paper, it has been proved that the vertical migration of the zooplankton destabilizes a horizontally uniform plankton distribution. Inhomogeneities in the plankton distribution become amplified due to the described mechanism (Fig. 6). Patchiness may be created in that way. There are certainly other mechanisms involved in the dynamics of patches (Steele 1974, Ebenhöh 1979), but an internal instability of the uniform distribution is most interesting.

The model in this paper allows the derivation of a critical speed difference and of a characteristic patch size depending on only two simple model parameters and on a diffusion constant. If the speed difference between upper and lower waterlayers exceeds the critical value, the uniform distribution decays into patches of a characteristic size. In the model, a constancy of that speed difference is assumed. This is never fulfilled in nature but the instability proof is not devalued by that complication.

An estimation of the characteristic patch size gives numerical values in the order of 10 km. These quite high values should not discourage us because the model is based on very simple Lotka-Volterra-like equations which are far from describing the real plankton. Furthermore the zooplankton may have a social behaviour that counteracts the diffusion.

Finally, other patch-creating mechanisms (e.g. inhomogeneity of the vertical turbulences, schools of fish), cannot be neglected. In a previous paper (Ebenhöh 1979), a 'dynamic patchiness model' is presented, in which several such mechanisms are presumed to act together. The cooperative action of different patch creating mechanisms makes it hard to 'prove' by observation the action of any one of these mechanisms individually. The satisfying result of the estimation of the critical velocity difference and of the characteristic patch size is an indication of the validity of the patch creation conception presented here. A suitable experimental check, however, would require detailed simultaneous measurements of the plankton densities, of the velocity profile and of the vertical migration amplitude.

An interesting extension of the model would be the assumption of a food-dependent amplitude of the vertical migration. This would lead to a feedback system with quite new stability properties. The zooplankton could be prevented from drifting into areas of poor food supply.

The vertical migration of the zooplankton seems to be a mechanically simple process (orientation on a light intensity reference level), with surprising consequences. In addition to the often discussed functions (e.g. protection against being seen,

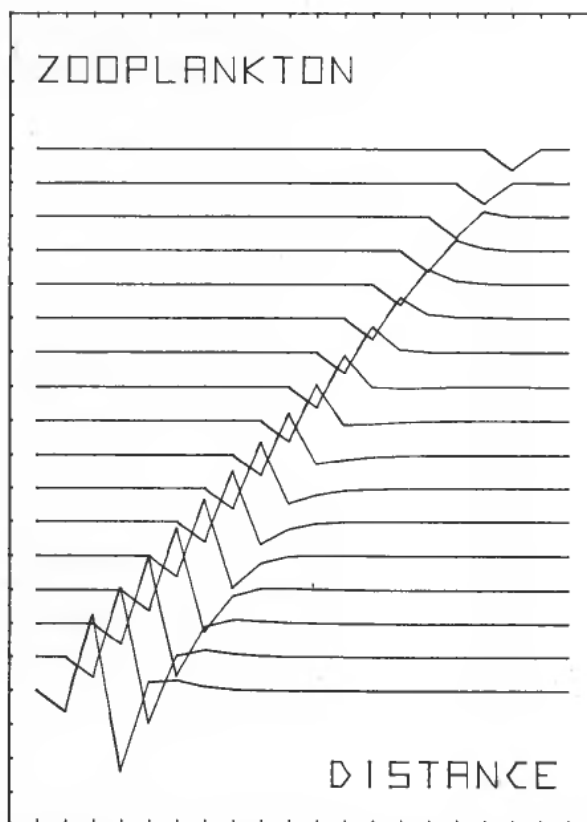


Figure 6. Amplification of a local distortion in the plankton distribution. Given are the deviations of the zooplankton density from the steady state value in arbitrary units. The curves follow from above in 1 day intervals. The start curve contains a local reduction of the zooplankton. The shift of the distortions in horizontal directions is due to the horizontal transport of the zooplankton in the deeper waterlayers relative to the surface water. The horizontal axis (distance) is divided into intervals of length L ($\epsilon=1$ and $\Delta=0.5$, see Fig. 1).

energy conservation), it may serve as a tactic for finding food (Isaac *et al.* 1974), and it may lead to a 'granulation' of the density distribution which is important for feeding and breeding of fish.

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