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The Diffusive Instability in the Mathematical Model of the Lower Trophic Levels of the Marine Ecosystem*

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Abstract

Plankton patchiness has been observed for a long time. In the former studies, the plankton patchiness formation has been explained to be owing to divergence and convergence of the velocity field, or owing to environmental heterogeneity.

Recently, temporal and spatial variability of plankton and the environment in the mesoscale have been observed in detail. Because of the results of these observations, it has been proved that plankton patchiness does not always depend upon the heterogeneity of the environment.

We are concerned with the formative mechanism of plankton patchiness. In the Lotka-Volterra system, patchiness seems to be generated by diffusive instability. Firstly, we will carry out the numerical analysis to examine the possibility of diffusive instability in the ocean by using a simplified ecosystem model.

Introduction

Plankton patchiness in the ocean has been frequently observed. In former studies, the plankton patchiness formation has been explained to be generated by depending upon the divergence and convergence of the velocity field, or environment heterogeneity.

Recently, Powell¹⁾, Denman²⁾, Platt³⁾ and Steele⁴⁾ observed temporal and spatial variability of physical variables (temperature, salinity, velocity etc.) and biological variables (chlorophyll, nutrient, etc.) in the mesoscale. According to the results of their observations, plankton patchiness is not generated only by the heterogeneity of the physical environment. Namely, plankton patchiness formation should be discussed with the relationship between biological dynamics and the physical environment.

The theoretical studies dealing with temporal and spatial variability have been advanced in the various ways, that is, Segel⁵⁾ and Okubo⁶⁾ put the diffusion effect into the Lotka-Volterra system, and Jorne⁷⁾ gave the advection effect to the system with the diffusion effect. Mimura⁸⁾, moreover, expressed the growth rate, grazing rate, death rate in the forme of $F_i(u, v)$ in the Lotka-Volterra system. According to these studies, when a slight disturbance is given to the system, if predator diffuses

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more rapidly than prey, then the system becomes unstable, and is transformed to the largescale temporal and spatial structure.

We will examine the possibility of diffusive instability in the lower trophic levels of the marine ecosystem.

Mathematical model

The considerable differences between the marine ecosystem and the Lotka-Volterra system are as follows:

(1) The Lotka-Volterra system indicates only the prey-predator relationship, and is a perfect open system. On the contrary, the marine ecosystem includes feed back loops (especially in the excretion of zooplankton).

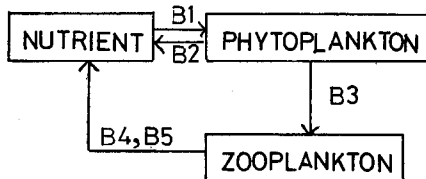


Fig. 1. Model kinetics, B1~B5 represent as follows:

- B1 nutrient uptake by phytoplankton
- B2 collective losses from phytoplankton
- B3 zooplankton grazing
- B4 zooplankton excretion
- B5 zooplankton standard excretion

(2) In the Lotka-Volterra system, the growth rate of the prey is constant, or, at least, depends only upon the biomass itself. In the marine ecosystem, the growth rate of phytoplankton always depends upon other variables especially nutrient.

We would like to make the simplified model of the lower trophic levels of the marine ecosystem by adding the feed back loop and the nutrient limitation effect in the Lotka-Volterra system (Fig. 1).

The Model Structure

We assume that the state variables are nutrient (N), phytoplankton (P), and zooplankton (Z). As in the biological process, we introduced nutrient uptake by phytoplankton (B1), the collective losses from phytoplankton (B2), zooplankton grazing (B3), and zooplankton excretion (B4, B5). In addition, we omit detritus, because if we assume the linear function of bacterial decomposition, the action of detritus has only the time lag effect.

Formulation

In formulation, we neglect the exogenous variables (light, temperature, etc.) and attempt to approximate each biological process in the nearest accuracy.

(1) Nutrient uptake (B1)

Nutrient uptake rate is shown as the Michaelis-Menten equation

$$\frac{V_m N}{K_1 + N} \quad (1-1)$$

where

- V_m : maximum uptake rate (hr^{-1})
 K_1 : phytoplankton Michaelis constant ($\mu g-at/l$)
 N : nutrient concentration ($\mu g-at/l$)

(2) The collective loss from phytoplankton (B2)

This process express the decrease of phytoplankton. It dose not include zooplankton grazing but includes the effects of excretion, autolysis, and natural death. This form is shown as follow.

$$D_p \cdot P \quad (1-2)$$

where

- D_p : collective loss rate (hr^{-1})
 P : phytoplankton biomass ($\mu g-at/l$)

(3) Zooplankton grazing (B3)

Zooplankton grazing depends upon phytoplankton biomass which is approximated as:

$$\frac{R_m \cdot P}{K_2 + P} Z \quad (1-3)$$

where

- R_m : maximum grazing rate (hr^{-1})
 K_2 : zooplankton Michaelis constant ($\mu g-at/l$)

(4) Zooplankton excretion (B4, B5)

According to Steele⁹, zooplankton excretion consists of the process which is dependent on grazing (B4) and independent on grazing (B5). The B4 rate is in proportion to grazing,

$$\Gamma \frac{R_m \cdot P}{K_2 + P} Z \quad (1-4)$$

where Γ is constant. B5 is expressed as

$$D_z \cdot Z \quad (1-5)$$

where

- D_z : standard excretion rate (hr^{-1})

Basic equation

We attempt the fundamental assumptions to reduce the state equations to tractable form:

- (1) The velocity field is assumed to be nondivergent.
- (2) The coefficient of eddy diffusivity is assumed constant.
- (3) Both eddy diffusivities of nutrient and phytoplankton are assumed to be the same.
- (4) All derivatives in the vertical and y directions are neglected.
- (5) Nutrient and phytoplankton are advected on the same velocity field.

And then, we introduced the dimensionless variables to reduce the number of parameters. The scaling relationships are listed in Table 1.

The nondimensional state equations are as follows:

Table 1. Definition of symbols and scaling relationship.

Dimensional quantity	Definition	Scaling factor	Nondimensional quantity
N	limiting nutrient concentration	N/N_i	N^*
P	phytoplankton biomass	P/N_i	P^*
Z	zooplankton biomass	Z/N_i	Z^*
R_m	zooplankton maximum grazing rate	R_m/V_m	β
K_1	phytoplankton Michaelis constant	K/N_i	α_1
K_2	zooplankton Michaelis constant	K/N_i	α_2
D_p	phytoplankton collective loss rate	D_p/V_m	ψ_1
D_z	zooplankton standard excretion rate	D_z/V_m	ψ_2
Γ	zooplankton excretion coefficient	$\Gamma \cdot N_i$	γ
t	time	$t \cdot V_m$	t^*
x	tangent-plane Cartesian coordinate		x^*
U	typical value of the horizontal velocity		U^*
D_1	eddy diffusivity of nutrient and phytoplankton		
D_2	eddy diffusivity of zooplankton diffusion ratio of phytoplankton and zooplankton		δ
V_m	phytoplankton maximum uptake rate		
N_i	total amount of biological limiting nutrient in the system		

$$\frac{\partial N^*}{\partial t^*} = -U_1 \frac{\partial N^*}{\partial x^*} + \frac{\partial^2 N^*}{\partial (x^*)^2} - \frac{N^* P^*}{\alpha_1 + N^*} + \psi_1 P^* + \gamma \frac{\beta P^* (Z^*)^2}{\alpha_2 + P^*} + \psi_2 Z^* \quad (2-1)$$

$$\frac{\partial P^*}{\partial t^*} = -U_1 \frac{\partial P^*}{\partial x^*} + \frac{\partial^2 P^*}{\partial (x^*)^2} + \frac{N^* P^*}{\alpha_1 + N^*} - \psi_1 P^* - \frac{\beta P^* Z^*}{\alpha_2 + P^*} \quad (2-2)$$

$$\frac{\partial Z^*}{\partial t^*} = -U_2 \frac{\partial Z^*}{\partial x^*} + \delta \frac{\partial^2 Z^*}{\partial (x^*)^2} + (1 - \gamma Z^*) \frac{\beta P^* Z^*}{\alpha_2 + P^*} - \psi_2 Z^* \quad (2-3)$$

The asterisk is dropped in equation (2-1), (2-2), (2-3) for the sake of simplicity. For the parameter values, we use following the values according to Suzuki, et. al.¹⁰⁾

$$\alpha_1 = 0.02, 0.05, 0.10, 0.20, 0.50$$

$$\alpha_2 = 0.05, 0.10, 0.20, 0.50, 1.00$$

$$\beta = 0.30, 0.50, 0.70, 1.00, 1.20$$

$$\gamma = 1.00, 2.00, 3.00, 4.00, 5.00$$

$$\psi_1 = 0.03, 0.05, 0.07, 0.10, 0.20$$

$$\psi_2 = 0.03, 0.05, 0.07, 0.10, 0.20$$

Assuming the existence of the uniform solution, the state equations are as follows:

$$\frac{dN}{dt} = f_1(N, P, Z) = -\frac{NP}{\alpha_1 + N} + \psi_1 P + \gamma \frac{\beta P Z^2}{\alpha_2 + P} + \psi_2 Z \quad (2-4)$$

$$\frac{dP}{dt} = f_2(N, P, Z) = \left\{ \frac{N}{\alpha_1 + N} - \psi_1 - \frac{\beta Z}{\alpha_2 + P} \right\} P \quad (2-5)$$

$$\frac{dZ}{dt} = f_3(P, Z) = \left\{ (1 - \gamma Z) \frac{\beta P}{\alpha_2 + P} - \psi_2 \right\} Z \quad (2-6)$$

and

$$N = 1 - P - Z \quad (2-7)$$

By the substitution of equation (2-7) into equations (2-5) and (2-6), the state equations are as follows:

$$\frac{dP}{dt} = g_1(P, Z) = \left\{ \frac{1 - P - Z}{\alpha_1 + 1 - P - Z} - \psi_1 - \frac{\beta Z}{\alpha_2 + P} \right\} P \quad (2-8)$$

$$\frac{dZ}{dt} = g_2(P, Z) = \left\{ (1 - \gamma Z) \frac{\beta P}{\alpha_2 + P} - \psi_2 \right\} Z \quad (2-9)$$

The values of the uniform solution are $P=P_0$ and $Z=Z_0$ and these values can be obtained in the solution of the following equations.

$$g_1(P_0, Z_0) = 0 \quad (2-10)$$

$$g_2(P_0, Z_0) = 0 \quad (2-11)$$

To examine the stability of the uniform solution to perturbations in concentration, we apply the following formula.

$$P(x, t) = P_0 + \Delta P(x, t) \quad (2-12)$$

$$Z(x, t) = Z_0 + \Delta Z(x, t) \quad (2-13)$$

If the perturbations ΔP , ΔZ are sufficiently small, we can linearize the equations (2-8), (2-9), that is, the linearized equations are as follows:

$$\frac{\partial(\Delta P)}{\partial t} = -U_1 \frac{\partial(\Delta P)}{\partial x} + \frac{\partial^2(\Delta P)}{\partial x^2} + a_{11}\Delta P + a_{12}\Delta Z \quad (2-14)$$

$$\frac{\partial(\Delta Z)}{\partial t} = -U_2 \frac{\partial(\Delta Z)}{\partial x} + \delta \frac{\partial^2(\Delta Z)}{\partial x^2} + a_{21}\Delta P + a_{22}\Delta Z \quad (2-15)$$

where

$$\begin{aligned}
 a_{11} &= - \left\{ - \frac{\alpha_1}{(\alpha_1 + 1 - P_0 - Z_0)^2} + \frac{\beta Z_0}{(\alpha_2 + P_0)^2} \right\} P_0 \\
 a_{12} &= - \left\{ \frac{\alpha_1}{(\alpha_1 + 1 - P_0 - Z_0)^2} + \frac{\beta}{(\alpha_2 + P_0)^2} \right\} P_0 \quad (2-16) \\
 a_{21} &= (1 - \gamma Z_0) \frac{\beta \gamma Z_0}{(\alpha_2 + P_0)^2} \\
 a_{22} &= -\gamma \frac{\beta P_0 Z_0}{\alpha_2 + P_0}
 \end{aligned}$$

Equations (2-14), (2-15) are in general full matrix equations and can be solved by the Fourier analysis method.

Following the standard method, we consider one set of Fourier components for the perturbations.

$$\Delta P = \tilde{P} \exp(ikx + \sigma t) \quad (2-17)$$

$$\Delta Z = \tilde{Z} \exp(ikx + \sigma t) \quad (2-18)$$

where \tilde{P} , \tilde{Z} are the time dependence and the Fourier component of wave number k .

Substituting equations (2-17), (2-18) into (2-14), (2-15), the characteristic equation become as follows:

$$\begin{vmatrix}
 a_{11} - k^2 + ikU_1 - \sigma & a_{12} \\
 a_{21} & a_{22} - \delta k^2 + ikU_2 - \sigma
 \end{vmatrix} = 0 \quad (2-19)$$

Results

A detailed analysis for the general diffusive instability is made by Segel⁵⁾ and Jorne.⁷⁾ Now, we are interested in the possibility of the diffusive instability in the lower trophic levels of a marine ecosystem.

We considered two models to understand the diffusion and advection effects, respectively. The models are:

- (1) In the absence of the advection effect, including the diffusion effect only (MODEL I).
- (2) Including both diffusion and advection effects (MODEL II).

MODEL I

Substituting $U_1=0$, $U_2=0$ into equation (2-19), the characteristic equation become:

$$\begin{vmatrix}
 \hat{a}_{11}(k) - \sigma & a_{12} \\
 a_{21} & \hat{a}_{22}(k) - \sigma
 \end{vmatrix} = 0 \quad (3-1)$$

where

$$\hat{a}_{11}(k) = a_{11} - k^2$$

$$\hat{a}_{22}(k) = a_{22} - \delta k^2$$

From equation (3-1), the necessary conditions for the diffusive instability are:

$$a_{11} + a_{22} < 0 \quad \text{at } k = 0 \quad (3-2)$$

$$a_{11}a_{22} - a_{12}a_{21} > 0 \quad \text{at } k = 0 \quad (3-3)$$

$$\hat{a}_{11}(k)\hat{a}_{22}(k) - a_{12}a_{21} < 0 \quad (3-4)$$

Inequality (3-4) is equivalent to

$$Q(k^2) = \delta k^4 - (\delta a_{11} + a_{22})k^2 + a_{11}a_{22} - a_{12}a_{21} < 0 \quad (3-5)$$

For instability, it is sufficient that Q can be negative at its minimum. This minimum is assumed at $k=k_m$, when

$$k_m^2 = \frac{\delta a_{11} + a_{22}}{\delta} \quad (3-6)$$

If diffusive instability is generated, the wave number k_m mostly dominates.

Firstly, we performed the stability analysis of the critical points of the system in a steady state to understand the basical dynamic behavior.

Under the process of computation, for 5^6 parameter combinations, we:

- (1) obtained the values of P_0 and Z_0 (equation (2-10), (2-11))
- (2) understood the values of $a_{11} \sim a_{22}$ (equation (2-16))
- (3) carried out the stability check (inequality (3-2), (3-3))

We offer the results of three cases as follows (Fig. 2):

- (1) When zooplankton biomass is considerably larger than phytoplankton biomass, the equivalent point is unstable.
- (2) When nutrients are deficient, phytoplankton biomass is large and zooplankton biomass is small, the critical points become node stable.
- (3) When nutrients are not deficient, and phytoplankton and zooplankton are well balanced, the equivalent points become spirally stable.

From the view of ecological efficiency, case (1) is impossible.

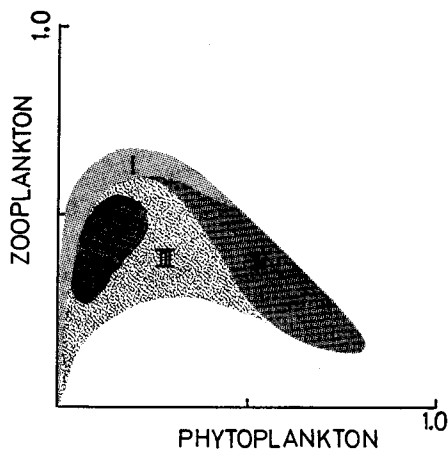


Fig. 2. Sorting of equivalent points, (I)~(IV) represent as follows:
 (I) unstable point
 (II) occurring diffusive instability point
 (III) node stable point
 (IV) spirally stable point

Through other conditions (case (2) and (3)), it is natural that the system is considered mostly stable.

Secondly, we examined the possibility of diffusive instability. Thus, we found the possibility that the equivalent points where zooplankton biomass is slightly larger than phytoplankton biomass, the diffusive instability occurs (Fig. 3).

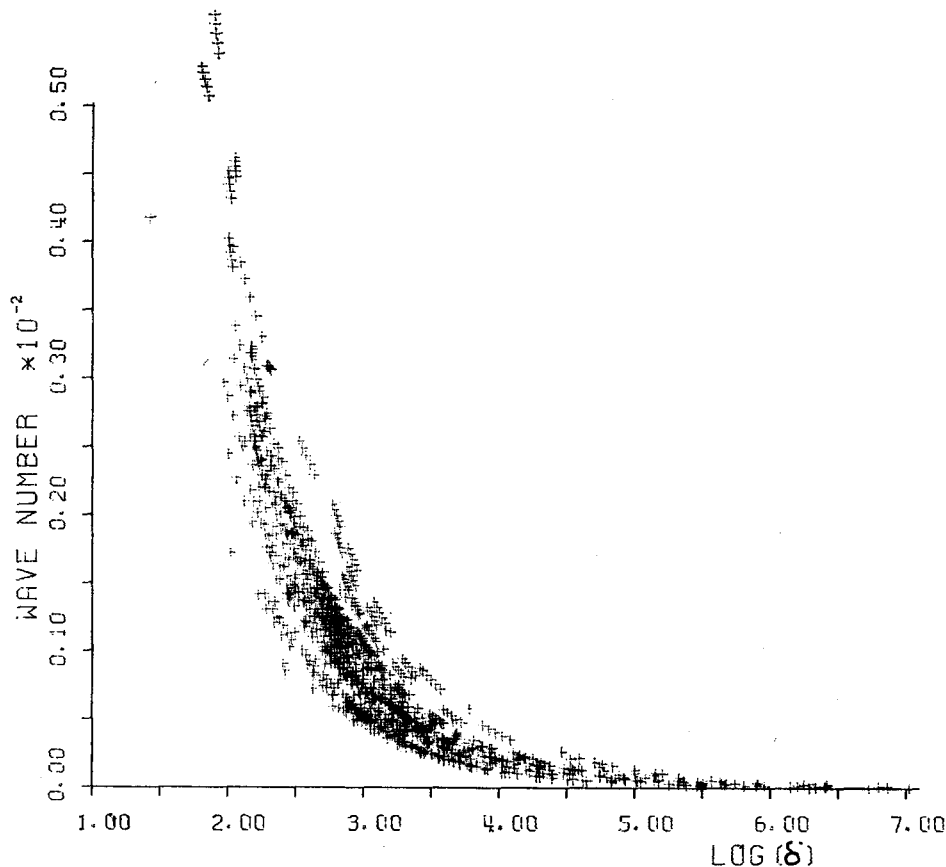


Fig. 3. Relationship between critical diffusion ratio of phytoplankton and zooplankton δ and dominant wave number k_m .

From equation (3-5) and (3-6), we calculated the critical diffusion ratio δ and the dominant wave number k_m at these equivalent points.

We obtained the results understanding that the calculated wave length is the order of 10^2 m which correspond with the observed patchiness scale. Nevertheless, if the ratio of diffusivity were not more than 10^2 , the diffusive instability would not be generated. (Fig. 3).

As $\delta=10^2$ is a normally impossible value in the marine ecosystem, we therefore must perform further investigation introducing the advection effect which destabilizes the system.

MODEL II

We introduce the advection effect. From equation (2-19), the eigen values are

$$\sigma = \alpha \pm i\beta \quad (3-7)$$

where

$$\alpha = \frac{1}{2} a \pm \frac{1}{2} \left[\frac{1}{2} (p + \sqrt{p^2 + q^2}) \right]^{1/2} \quad (3-8)$$

$$\beta = \frac{1}{2} b \pm \frac{q}{2[2(p + \sqrt{p^2 + q^2})]^{1/2}} \quad (3-9)$$

$$a = a_{11} + a_{22} - (1 + \delta) k^2 \quad (3-10)$$

$$b = k(U_1 + U_2) \quad (3-11)$$

$$p = \{a_{11} + a_{22} - (1 + \delta)k^2\}^2 - k(U_1 - U_2)^2 + 4\{(a_{11} - k^2)(a_{22} - \delta k^2) - a_{12}a_{21}\} \quad (3-12)$$

$$q = 2k(U_1 + U_2)\{a_{11} + a_{22} - (1 + \delta)k^2\} - 4k\{U_1(a_{22} - \delta k^2) + U_2(a_{22} - \delta k^2)\} \quad (3-13)$$

From equation (3-7), the diffusive instability occurs when:

$$a_{11} + a_{22} < 0 \quad \text{at } k = 0 \quad (3-14)$$

$$a_{11}a_{22} - a_{12}a_{21} > 0 \quad \text{at } k = 0 \quad (3-15)$$

$$a \pm \left[\frac{1}{2} (p + \sqrt{p^2 + q^2}) \right]^{1/2} > 0 \quad (3-16)$$

At first, we considered the condition that both phytoplankton and zooplankton are advected with the same velocity U .

Putting $U_1 = U_2 = U$ into equations (3-10), (3-11), (3-12), (3-13).

$$a = a_{11} + a_{22} - (1 + \delta) k^2$$

$$b = 2kU \quad (3-18)$$

$$p = \{a_{11} + a_{22} - (1 + \delta)k^2\}^2 - 4\{(a_{11} - k^2)(a_{22} - \delta k^2) - a_{12}a_{21}\}$$

$$q = 0$$

By substituting these parameter values into equations (3-8) and (3-9), real parts and imaginary parts of the eigen value are

$$\alpha = R_e(\sigma) = \frac{1}{2} (a + \sqrt{p}) \quad (3-19)$$

$$\beta = I_{mag}(\sigma) = \frac{b}{2} = kU$$

Inspecting the equation (3-18) shows that necessary conditions for diffusive instability are:

$$\begin{aligned} a_{11} + a_{22} &< 0 && \text{at } k = 0 \\ a_{11}a_{22} - a_{12}a_{21} &> 0 && \text{at } k = 0 \\ (a_{11} - k^2)(a_{22} - \delta k^2) - a_{12}a_{21} &< 0 \end{aligned} \quad (3-20)$$

These conditions are as same as MODEL I. In conclusion, if phytoplankton and zooplankton are advected with the same velocity, the advection effect does not increase the possibility of diffusive instability. But it increases oscillatory behavior with the frequency $f = \beta/2\pi$.

Then, we observe the case where the zooplankton has some individual movement and both phytoplankton and zooplankton are advected with different velocity. Here, the ratio of diffusivity is:

$$1 < \delta \leq 1.5$$

and we assume these parameter values:

$$U_1 = 5, 10, 20, 30, 50 \text{ cm/sec}$$

$$0.5 \leq \left| \frac{U_1}{U_2} \right| \leq 1.5$$

Between these ranges from the above mentioned, we investigate the equivalent point which diffusive instability are generated, numerically. As we estimate the diffusion ratio from the above, there are a few equivalent points where the diffusive instability occurs.

Conclusion

We examined the possibility of whether we can explain the plankton patchiness formation in the ocean from the study of diffusive instability by using a simplified mathematical model. And we obtained the following results:

- (1) Considering only the diffusion effect ($U \frac{\partial}{\partial x} = 0$), the calculated scale of plankton patchiness is 10^2 m and it is the same as the order of the observed patchiness scale. Though the calculated spatial scale of patchiness corresponds with the observed scale, the diffusion ratio of phytoplankton and zooplankton is large, (more than 100) and under the small diffusion ratio, instability can not occur.
- (2) The model with the advection effect: When zooplankton and phytoplankton are advected on the same velocity field, the system becomes apt to oscillate, but the necessary condition for the diffusive instability are the same as case (1).
- (3) Even if we assume that zooplankton had some individual movement and phytoplankton was advected with the different velocity from zooplankton, diffusive instability would not be generated when the diffusion ratio was so slight.

According to these results, if diffusive instability occurred in the marine ecosystem, zooplankton should be diffused more than a hundred times as fast as phytoplankton. It is, however, almost impossible. Since it is hard to explain the formation of plankton patchiness from diffusive instability in the marine ecosystem, we have to investigate other mechanisms which generate random movements of zooplankton.

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