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CRITICAL PATCH SIZE FOR PLANKTON AND PATCHINESS

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1. Introduction

Patchy distributions of plankton in the sea and lakes have been well documented (Cassie, 1963; Tonolli and Tonolli, 1960; Platt *et al.*, 1970; Steele, 1976, 1977; Harris, 1980). However, the precise mechanism that arises plankton patchiness is still a subject of considerable controversy. To name some proposed mechanisms they are: i) mechanical retention in wind-generated convective cells or frontal zones (Langmuir, 1938; Stommel, 1949; Floodgate *et al.*, 1981; Bowman and Esaias, 1978), ii) behaviorial reaction to distributions of environmental parameters such as temperature, salinity, light, and nutrients (Cassie, 1959; Forward, 1976; Heaney and Eppley, 1981), iii) exclusion of certain zooplankton by phytoplankton (Bainbridge, 1953), iv) food-chain association in predator-prey relations (Tonolli, 1958), in particular the phenomenon of spontaneous pattern generation through diffusive instability (Levin and Segel, 1976), and v) aggregative behaviors (swarming, schooling) for breeding and feeding (Clutter, 1969; Hamner and Carleton, 1979).

The patchiness itself most likely arises from a variety of mechanisms and processes under various conditions. However, many cases share in common a single process which acts generally as an "anti-patchiness" agent. This process is diffusion due to turbulence in surrounding media or random movements of organisms. Generally speaking, diffusion tends to counteract the formation of organism aggregation, and to give rise to a more uniform distribution (note an exception of diffusion-induced instability in predator-prey interactions). Thus an endless interplay occurs between the aggregative process of organism growth or reproduction and the antiaggregative process of diffusion, and a dynamical balance may be established in such a manner that the growth rate of organisms within a patch is equal to the loss rate of organisms due to diffusion into the surroundings where organisms cannot survive. Since the growth rate is proportional to the volume of the patch and the diffusion rate is proportional to the surface area of the patch, the patch size at the dynamical balance must be a minimum critical size or simply critical size, below which the population of plankton cannot be maintained and the patch disappears.

2. Model by Kierstead, Slobodkin and Skellam ("KISS model")

A simple nonetheless useful mathematical model for the critical patch size was given by Kierstead and Slobodkin (1953) and Skellam (1951) independently. This model is based on a simple diffusion and exponential growth equation for plankton concentration, which is expressed, in one-dimensional space, by

$$\frac{\partial S}{\partial t} = D\frac{\partial^2 S}{\partial x^2} + \alpha S , \quad 0 < t, \; 0 \le x \le L \tag{1}$$

subject to

$$\begin{aligned} &\text{at } t = 0;\ S = S_0(x) \\ &\text{at } x = 0;\ x = L;\ S \equiv 0 \end{aligned} \tag{2}$$

The solution is given by

$$S(x,t) = \sum_{n=1}^{\infty} a_n \sin \frac{n\pi}{L} x \; \exp\left\{ \alpha - \frac{n^2\pi^2}{L^2} D \right\} t \tag{3}$$

with

$$a_n = \frac{2}{L} \int_0^L S_0(x) \sin \frac{n\pi}{L} x \, dx$$

If $L < \pi(D/\alpha)^{\frac{1}{2}}$, $S(x,t)$ will approach zero as time progresses, while if $L > \pi(D/\alpha)^{\frac{1}{2}}$, $S(x,t)$ will increase indefinitely with time, thus a plankton bloom may occur. Therefore the critical (minimum) patch size L_c is determined from the equality condition, i.e.,

$$L_c = \pi(D/\alpha)^{\frac{1}{2}} \tag{4}$$

The above is applied for a linear habitat. For two dimensional space, e.g., a circular habitat, the critical diameter is obtained by

$$L_c = 4.81(\pi/\alpha)^{\frac{1}{2}} \tag{5}$$

This model has been a cornerstone in the later development of the subject. Hereafter it refers to the KISS model (KIerstead-Slobodkin-Skellam), and the critical size (4) refers to the KISS scale and denoted by L_o.

The further development has been made into various directions. It includes i) generalization of the growth rate function and relaxation of the boundary condition; ii) scale and density dependencies in diffusivity, iii) addition of advection, iv) nonlinear population dynamics, and v) multispecies interactions. Interestingly enough these generalizations and improvements on the original model have shown that with a few exceptions, the KISS model is robust as a mathematical theory for the critical size problem.

In this article I will briefly review the main result of those later developments and present a new model which attempts to eliminate the arbitrariness of the boundary condition involved in the original KISS model.

3. Generalization of the KISS model

Platt and Denman (1975) and Wroblewski *et al.* (1975) included the effect of herbivore grazing on phytoplankton in the KISS model. Using an Ivlev type grazing function, they calculated the critical size to be

$$L_c = \pi \left\{ D/(\alpha - R_m\lambda) \right\}^{\frac{1}{2}}, \qquad \alpha - R_m\lambda > 0 \tag{6}$$

where R_m is the maximum grazing ration of the herbivore and λ is the Ivlev constant. As is expected, the effect of herbivore grazing reduces the net growth rate of the population, so that the critical size becomes larger than the KISS scale. If $\alpha \leq R_m \lambda$, all patches must vanish as time progresses.

The boundary condition of the KISS model that the plankton patch is surrounded by completely unsuitable water is rather arbitrary. In reality the transition from favorable to unfavorable conditions is gradual, and organisms move more or less freely both into and out of the favorable region. Ludwig *et al.* (1979) and Evans (1978) (unpublished manuscript) calculated critical size assuming that organisms can survive but not grow outside the favorable habitat, so that the diffusion-reaction equation outside is expressed by

$$\frac{\partial S}{\partial t} = D\frac{\partial^2 S}{\partial x^2} - \beta S \qquad \text{for } |x| > L/2 \tag{7}$$

where $\beta \geq 0$ is the death rate of organisms. (7) is solved by coupling with (1) subject to the continuity conditions for the population density and its flux at the boundaries, $|x| = L/2$. As a result the following criterion for critical size is obtained

$$L_c = L_o \left\{ \frac{2}{\pi} \tan^{-1}(\beta/\alpha)^{1/2} \right\} \tag{8}$$

where $\tan^{-1}(\beta/\alpha)^{1/2}$ takes the value of the principal branch. For infinite β the critical scale is reduced to the KISS scale, L_o. For finite β/α, L_c is less than L_o, decreasing to zero as β/α approaches zero; this limiting situation corresponds to a Malthusian population surrounded by reflecting barriers.

In reality for phytoplankton, a reasonable value for β/α might be 0.1 when population decay is simply due to plankton respiration outside the favorable area. For this value L_c is 20% of L_o. Thus the critical size does not differ much from the KISS scale when the conditions in the surrounding water are relaxed.

Gurney and Nisbet (1975) consider a model in which the growth rate varies continuously in space, in particular varying with distance from a habitat center in a parabolic fashion, i.e.,

$$\alpha(x) = \alpha_o \left\{ 1 - (x/x_o)^2 \right\} \tag{9}$$

where α_o is the maximum growth rate at the center. The favorable region extends from $-x_o$ to x_o, and beyond this region the death rate progressingly dominates. Unlike the KISS model the boundary conditions are applied only at infinity, i.e., $S \to 0$ at $|x| \to \infty$. Gurney and Nisbet solved the problem to obtain the minimum size of the favorable region for the population to survive. It is given by $2x_{cr} = 2(D/\alpha_o)^{1/2}$, which is compared to the KISS scale.

The critical size problem with spatially variable growth rates can be treated in a general way. For simplicity we shall restrict our attention to a largely hostile environment containing a single central region of viable habitat; the growth rate is given by

$$\begin{aligned} r(x) &> 0, \quad 0 \leq x \leq x_o \\ r(x) &< 0, \quad x_o < x \end{aligned} \tag{10}$$

with the assumption that all the properties of the space is symmetrical about the origin $x = 0$ so that the appropriate boundary conditions for S read

$$\begin{aligned} &\text{at } x = 0, \quad \partial S/\partial x = 0 \\ &\text{at } x \to \infty, \quad S \to 0 \end{aligned} \tag{11}$$

The basic equation for S can be written as

$$\frac{\partial S}{\partial t} = D\frac{\partial^2 S}{\partial x^2} + r(x)S \quad , \quad 0 \leq x \tag{12}$$

For further simplicity we consider $r(x)$ to be a non-increasing function of x. Let $\alpha > 0$ be the (maximum) value of r at $x = 0$, and express $r(x)$ in terms of a non-decreasing function $V(x)$ as

$$r(x) \equiv \alpha - \alpha V(x) \tag{13}$$

with

$$\begin{gathered} V(0) = 0, \quad V(x) \leq 1 \quad \text{for } 0 \leq x \leq x_0, \quad V(x) > 1 \quad \text{for } x_0 < x, \\ V(\infty) = \beta/\alpha \equiv \nu^{-1} \quad (0 \leq \beta) \end{gathered} \tag{14}$$

(12) is rewritten as

$$\frac{\partial S}{\partial t} = D\frac{\partial^2 S}{\partial x^2} + \{\alpha - \alpha V(x)\} S \tag{15}$$

Defining

$$\begin{aligned} t &\equiv \alpha^{-1}\tau \\ x &\equiv (D/d)^{\frac{1}{2}}\xi \equiv \ell\xi \\ x_0 &\equiv \ell\,\xi_0 \end{aligned} \tag{16}$$

We nondimensionalize (15) with respect to the independent variables

$$\frac{\partial S}{\partial \tau} = \frac{\partial^2 S}{\partial \xi^2} + \{1 - V(\xi; \xi_0, \nu)\} S \tag{17}$$

Assume

$$S = e^{\lambda\tau}\phi(\xi) \tag{18}$$

Substituting (18) into (17) we obtain

$$\frac{d^2\phi}{d\xi^2} + \{E - V(\xi)\}\phi = 0 \tag{19}$$

with

$$E = 1 - \lambda \tag{20}$$

(19) is subject to

$$\begin{aligned} &\text{at } \xi = 0, \quad d\phi/d\xi = 0 \\ &\text{at } \xi \to \infty, \quad \phi \to 0 \end{aligned} \tag{21}$$

(19) is just analogous to the Schrödinger wave equation with potential $V(\xi)$ and energy E (Schiff, 1955). Thus an eigenfunction ϕ that satisfies the boundary conditions (21) can exist for a particular value of E. There may be a finite or infinite number of discrete values of E, but our concern is only to the minimum value of E ($= E_m$), which depends only on ℓ and ξ_0. The minimum of E corresponds to the maximum of λ, i.e., the largest eigenvalue λ_0 which determines whether the population ultimately grows or decays in an exponential fashion. Therefore $\lambda = \lambda_0 = 0$, i.e., $E_m = 1$ determines the critical size x_{cr} for x_0

$$E_m(x_{cr}/\ell, \nu) = 1$$

or

$$\begin{aligned} x_{cr} &= \ell\ fn(\nu) \\ &= (D/\alpha)^{\frac{1}{2}}\ fn(\nu) \end{aligned} \tag{22}$$

We will give some examples.

a) KISS model

$$V(\xi) = \begin{cases} 0 & , \quad 0 \leq \xi \leq \xi_0 \\ \infty \ (\text{or } \nu = 0) & , \quad \xi_0 < \xi \end{cases} \tag{23}$$

This corresponds to the case of one-dimensional square well potential with a perfectly impenetrable wall at ξ_0. The minimum eigenvalue E_m is obtained by

$$E_m^{\frac{1}{2}} = \pi/2\xi_0$$

so that the critical size for x_0 is formed by setting $E_m = 1$.

$$x_{cr} = \frac{\pi}{2}\left(\frac{D}{\alpha}\right)^{\frac{1}{2}}$$

or

$$L_{cr} = 2\,x_{cr} = \pi (D/\alpha)^{1/2} = L_o$$

which recovers the KISS scale.

b) Evans and Ludwig *et al.* model

$$V(\xi) = \begin{cases} 0 \,, & 0 \le \xi \le \xi_o \\ \nu^{-1} = \beta/\alpha \,, & \xi_o < \xi \end{cases} \qquad (24)$$

This is the case of one-dimensional square well potential with finite potential step, and the minimum eigenvalue E_m is obtained by

$$\tan(E_m^{1/2}\xi_o) = (1 + \nu^{-1} - E_m)^{1/2}$$

Setting $E_m = 1$, we get

$$x_{cr} = (D/\alpha)^{1/2} \tan^{-1}(\beta/\alpha)^{1/2}$$

or

$$L_{cr} = 2(D/\alpha)^{1/2} \tan^{-1}(\beta/\alpha)^{1/2} = L_o\ \{2/\pi\ \tan^{-1}(\beta/\alpha)^{1/2}\}$$

which agrees to (8).

c) Gurney-Nisbet model

$$V(\xi) = (\xi/\xi_o)^2 \qquad (25)$$

This corresponds to the familiar potential for a harmonic oscillator, and the minimum eigenvalue E_m is given by

$$E_m = \xi_o$$

so that

$$x_{cr} = \ell = (D/\alpha)^{1/2}$$
$$L_{cr} = 2(D/\alpha)^{1/2}$$

d) Sverdrup's model (Sverdrup, 1953)

In this model $r(x)$ is taken as $r(x) = \alpha\, e^{-kx} - \beta (0 < \alpha < \beta)$, so that

$$V(\xi) = 1 - e^{-k'\xi} + \nu^{-1} \,, \quad k' \equiv k\ell = (D/\alpha)^{1/2} \ln \nu^{-1}/x_o \qquad (26)$$

It seems that the Schrödinger equation with this potential has not been studied.

$$\frac{d^2\phi}{d\xi^2} + \{E - (1 + \nu^{-1} - e^{-k'\xi})\}\phi = 0$$

The solution satisfying the boundary condition at infinity is obtained by

$$\Phi = A\, J_{2\gamma/k'}\left(\frac{2}{k'}\, e^{-\frac{k'}{2}\xi}\right)$$

with A is constant and $\gamma \equiv 1 + \nu^{-1} - E$

The condition at $\xi = 0$ leads to

$$J'_{2\gamma/k'}(2/k') = 0 \qquad (27)$$

The smallest positive root of (27) along with $\gamma(E = 1) = 1 + \nu^{-1}$ determines critical size for x_o:

$$x_{cr} = (D/\alpha)^{1/2} fn(\nu)$$

or

$$L_{cr} = 2(D/\alpha)^{1/2} fn(\nu)$$

Since the oceanic motion consists of a wide range of eddies, a mathematical model appropriate for oceanic diffusion cannot be described by a constant diffusivity; a more appropriate model should account for the scale dependence of diffusion. A crude approach is to introduce an appropriate scale dependence of diffusivity to the critical size formula and to solve for the size. For instance take the KISS scale formula for two-dimensional space

$$L_c = 4.81 \ (D/\alpha)^{\frac{1}{2}} \tag{28}$$

and use a scale dependent diffusivity

$$D = P(L_c/2) \tag{29}$$

where the linear dependence of D on the scale is after Joseph and Sendner (1958) whose oceanic diffusion model is characterized by the diffusion velocity P of order 1 cm/sec. Combining (28) with (29), we obtain

$$L_c = 11.5 \ P/\alpha \tag{30}$$

A more rigorous derivation relies on the following diffusion equation

$$\frac{\partial S}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(Pr^2 \frac{\partial S}{\partial r}\right) + \alpha S \tag{31}$$

where Joseph-Sendner's theory is applied to the two-dimensional horizontal diffusion with $D = Pr$. (31) is subject to the boundary condition that at $r = L_c/2$, $S \equiv 0$ and to an appropriate initial condition. Solving (31) under these conditions, we obtain

$$L_c = 7.34 \ P/\alpha \tag{32}$$

(Okubo, 1978). For more general treatments with $D = cr^m$ (c: constant, $m \geq 0$), consult Okubo (1978).

Estimated values of the critical size of phytoplankton for various oceanic diffusion models range from 1 km to 2 km for $\alpha = 1$ div/day and 20 to 50 km for $\alpha = 1$ div/10 days. These theoretical models of phytoplankton support the general observations that plankton patches appear to occur at scales of the order of 10-100 km in the open sea (Steele, 1976) and at 1-10 km in a semi-enclosed bay (Platt *et al.*, 1970). It is important to note that no matter what the model may be, the essential feature of the KISS model is preserved in the formulation of the critical size, i.e., the size is determined by the balance of diffusion rate and net growth rate (McMurtie, 1978).

When advection occurs in addition to diffusion, the critical patch size may be quite different from the KISS scale. For example, when a patch of plankton is placed in a zone of convergence, a flow pattern (advection) which tends to act against diffusion is present. It then becomes obvious to expect that the size of plankton bloom may be significantly smaller than the KISS scale.

A mathematical model for this case is given by

$$\frac{\partial S}{\partial t} = D\frac{\partial^2 S}{\partial x^2} + \frac{\partial}{\partial x}(US) + \alpha S \tag{33}$$

where $U(x)$ is the amplitude of the current converging to the center, $x = 0$. (33) is subject to the same boundary conditions as before. For a uniformly converging flow; $u(x) = v$ (constant), the critical size is obtained by

$$L_c = \pi (D/\alpha)^{\frac{1}{2}} \mu \tag{34}$$

where μ is the smallest positive root of the equation

$$m^{\frac{1}{2}} \tan\left\{(1-m)^{\frac{1}{2}} \pi\mu/2\right\} = (1-m)^{\frac{1}{2}} \tag{35}$$

with $m = v^2/4\alpha D$ (see Okubo, 1978 for detail). As $m \to 0$, $\mu \to 1$ and as $m \to \infty$, $\mu \to 0$. This model may explain the existence of very narrow bands of phytoplankton bloom in frontal zones (Bainbridge, 1957; Simpson and Pingree, 1978).

On the other hand, the critical size becomes larger than the KISS scale when a patch is placed in a diverging flow; as a matter of fact the critical size may become infinite, and a patch can never exist (Okubo, 1978). For a uniformly diverging flow, μ in (34) is the smallest positive root of the equation

$$m^{1/2} \tan\{(1-m)^{1/2}\pi\mu/2\} = -(1-m)^{1/2} \tag{36}$$

Thus, for $m \geq 1$, i.e., $v \geq 2(D\alpha)^{1/2}$, μ becomes infinite and so is L_c. For example, if $D = 10^5 \text{cm}^2/\text{sec}$, $\alpha = 1$ div/day, and $v = 2$ cm/sec, then $L_c \to \infty$, whereas the KISS scale is about 1 km. Even a relatively weak convergence of a few centimeters per second in the sea is capable of destroying phytoplankton blooms.

In passing density-dependent diffusion may create another dramatic change in the critical size problem. Mathematical models for density-dependent dispersal of population have been developed by Gurney and Nisbet (1975), Gurtin and MacCamy (1977), Shigesada and Terramoto (1978), Shegesada *et al.* (1979), Shigesada (1980) among others. In particular Gurney and Nisbet (1975) investigated the effect of density-dependent diffusion on the spatial distribution of population undergoing spatially varying growth and death. For purely density-dependent diffusion their model equation reads

$$\frac{\partial S}{\partial t} = \frac{\partial}{\partial x}(\gamma S \frac{\partial S}{\partial x}) + \alpha_o\{1 - (x/x_o)^2\}S \tag{37}$$

where diffusivity is assumed to depend linearly on the population density S, $D = \gamma S$. Gurney and Nisbet (1975) then show that regardless of the size of favorable region there always exists a non-trivial, non-negative, stable steady-state solution to (29), i.e., there is no minimum size of habitat for population survival.

The density-dependent diffusion plays an important role in animal dispersal (Morishita, 1971). Shigesada (1980) compared her mathematical model of density-dependent dispersal favorably with experimental data on ant lion dispersion by Morishita. Zooplankton might as well exhibit density-dependent dispersal. Even though phytoplankton are considered to be passive in their movement, many dinoflagellates are able to migrate vertically by phototactic responses (Blasco, 1978; Heaney and Eppley, 1981; Forward, 1976). Whether or not any density-dependence operates in the dinoflagellate movement is unclear. However, an analysis of the self-shading effect on algal vertical distribution by Shigesada and Okubo (1981) suggests that the self shading may give rise to some density dependence in the advective flow of dinoflagellates, so that the dispersal of dinoflagellates can be modelled by a Burgers' type equation (Levin and Okubo, 1983).

The critical size problem has also been extended to more general population growth processes such as logistic growth (Skellam, 1951; Levandowsky and White, 1977; Ludwig *et al.*, 1979) and asocial population growth (Bradford and Philip, 1970 a, b).

For a population undergoing logistic growth and diffusion the KISS scale is still a minimum size of habitat required for survival. More individuals to accommodate, larger the critical habitat size, and to maintain the level of population at the carrying capacity of the resources, the habitat size must be infinitely large. An asocial population is characterized by negative growth at small population densities, positive growth at intermediate densities, and negative growth at large densities. The critical habitat size is obtained as $c(D/\alpha_1)^{\frac{1}{2}}$, where α_1 is a growth rate at an intermediate population density and c is a numerical constant of order unity. Again a formula similar to the KISS scale is applied to the critical size for asocial populations.

4. Vertical-horizontal coupling in phytoplankton patchiness

Though fairly robust, the KISS model is by no means immune to flaws. A particular weakness of the model is found in its arbitrary boundary conditions, i.e., two distinct water masses, one favorable and the other unfavorable for organisms. Even the improved models which can relax this boundary condition are still unable to interpret the occurrence of plankton patches in the sea where the oceanographical conditions are seemingly uniform in the horizontal direction.

The previously mentioned models including the KISS are concerned primarily with the horizontal diffusion of plankton patches by horizontal turbulence. This is the main reason why the model needs the arbitrary boundary conditions. In the sea the vertical and horizontal processes are strongly coupled in such a manner that the combined action of vertical shear in horizontal currents and transverse vertical mixing can produce an effective dispersion in the horizontal direction (Bowden, 1965). This "shear effect" claims that the vertical and horizontal processes of dispersion cannot be treated independently, but rather the advection-diffusion in the vertical direction is responsible for the dispersion of plankton in the horizontal direction.

Analyzing chlorophyll-a data obtained in central Long Island Sound, Wilson and Okubo (1980) demonstrated that the horizontal distribution of phytoplankton was generated by the interaction of the vertical structure with a vertical shear in horizontal currents at semi-diurnal and lower frequencies and possibly by short period internal waves. In short, horizontal patchiness is a manifestation of vertical patchiness.

Steele (1976, 1978), Evans, Steele and Kullenberg (1977), Evans (1978) and Kullenberg (1978) attempted to couple the vertical and horizontal processes in interpretation of plankton patchiness. Yet a unified mathematical model has not been developed to evaluate the critical size of phytoplankton in the sea. In this article I will outline a simple model of vertical-horizontal coupling; a full exploration of the model will be presented elsewhere.

The concept of a *critical depth* for phytoplankton blooming is relatively old (Gran and Bracrud, 1935). Sverdrup (1953) first presented a mathematical model dealing with conditions for the vernal blooming of phytoplankton: coincidentally in the same year as Kierstead and Slobodkin's work. Sverdrup's approach is based on a comparison between the depth of upper mixed layer and the "critical depth" at which the total production of plant beneath a unit surface is equal to the total respiration.

In the upper layer of the ocean the photosynthesis exceeds the destruction by respiration, while in the lower layer the loss exceeds the production. The two layers are separated by the depth of compensation at which the rate of production exactly balances the rate of loss. In this sense the modified KISS model with relaxed boundary conditions can be applied to determine the critical depth of compensation for phytoplankton blooming. Note that this critical depth of compensation is not the same as Sverdrup's critical depth. To this end let a and b be respectively the net growth rate in the upper layer and net loss rate in the lower layer, and K_z be vertical diffusivity. Then the same argument as before leads to the following result for the critical depth of compensation

$$H_{cr} = (K_z/a)^{\frac{1}{2}} \tan^{-1}(b/a)^{\frac{1}{2}} \tag{38}$$

If the observed depth of compensation z_c is shallower than H_{cr}, phytoplankton population tends to decay. On the other hand, if z_c is deeper than H_{cr}, phytoplankton blooming may occur.

To make only an order of magnitude estimate for H_{cr}, we take $K_z = 10\ \text{cm}^2/\text{sec}$, $a = 10^{-5} \sim 10^{-6}/\text{sec}$, $b/a \sim 1$, as typical

for the open ocean. These values yield

$$H_{cr} = \begin{cases} 10\ \text{m for 1 cell division per day} \\ 30\ \text{m for 1 cell division per 10 days} \end{cases} \tag{39}$$

As a result of the shear effect this critical depth can manifest itself into the horizontal patch scale. A simple model will explain the process (Okubo, 1980). Consider a small patch of phytoplankton starting to diffuse in a layer where exists a uniform vertical shear given by the velocity profile $u = \Omega z$. In time t the patch will diffuse vertically a distance of the order of $(K_z t)^{\frac{1}{2}}$. Accordingly the effective shear, i.e., vertical velocity difference, acting on the patch amounts to $\Omega(K_z t)^{\frac{1}{2}}$, and the patch will disperse horizontally, in time t, a distance equal to $\Omega(K_z t)^{\frac{1}{2}} t$. In other words the horizontal scale of the patch L increases with time as $L \sim \Omega K_2^{\frac{1}{2}} t^{3/2}$, while the vertical scale grows with time as $H \sim K_z^{\frac{1}{2}} t^{\frac{1}{2}}$, so that we find the relationship between L and H by eliminating t from both expressions,

$$L = \Omega K_z^{-1} H^3 \tag{40}$$

so far as the order of magnitude is concerned.

The critical horizontal scale L_{cr} is obtained when $H = H_{cr}$, i.e.,

$$L_{cr} = \Omega K^{-1} H_{cr}^3 \tag{41}$$

Using (38) for H_{cr}, we can rewrite (41) as

$$L_{cr}/H_{cr} = \Omega/a\ (\tan^{-1}(b/a)^{\frac{1}{2}}) \sim \Omega/a \tag{42}$$

since usually $\tan^{-1}(b/a)^{\frac{1}{2}}$ is order unity.

The above expression indicates that the horizontal critical scale is proportional to the (vertical) critical depth of compensation; the proportionality constant is the ratio of the vertical current shear (physical parameter) to the net growth rate (biological parameter) in the upper layer. Typically $\Omega = 10^{-3}$/sec. For $a = 10^{-5}$/sec (1 div/day), $L_{cr}/H_{cr} \sim 100$, and for $a = 10^{-6}$/sec (1 div/10 days), $L_{cr}/H_{cr} \sim 1000$. Thus the magnification factor ranges from 100 to 1000. Using (39) for H_{cr} we estimate

$$\begin{aligned} L_{cr} &\sim 1 \text{ km for } a = 1 \text{ div/day} \\ L_{cr} &\sim 30 \text{ km for } a = 1 \text{ div/10 days} \end{aligned} \tag{43}$$

Hence this coupling model predicts minimum scales of horizontal patchiness of roughly the right order of magnitude.

A more rigorous mathematical analysis of the vertical-horizontal coupling in patchiness depends on the following shear diffusion equation with population growth

$$\frac{\partial S}{\partial t} = -u(z)\frac{\partial S}{\partial x} + K_x\frac{\partial^2 S}{\partial x^2} + K_z\frac{\partial^2 S}{\partial z^2} + r(z)S \;, \quad \begin{matrix} t > 0 \\ -\infty < x < \infty \\ 0 \le z \end{matrix} \tag{44}$$

where $u(z)$ is the horizontal velocity varying with depth, K_x and K_z are horizontal and vertical diffusivities, respectively, $r(z)$ is the depth variable net growth rate. (44) is subject to

$$\begin{aligned} &\text{at } t = 0, \quad S = \delta(x)\delta(z) \\ &\text{at } z = 0, \quad \partial S/\partial z = 0 \\ &\text{at } |x| \to \infty, \text{ or } z \to \infty, \; S \to 0 \end{aligned} \tag{45}$$

Since our concern is primarily with the relationship between vertical and horizontal scales associated with a patch of plankton, we transform (44) into a set of moment equations. Define the jth moments ($j \ge 0$)

$$m_j(z,t) \equiv \int_{-\infty}^{\infty} x^j S(x,z,t)\,dx \tag{46}$$

Multiplying (44) by x^j and integrating over x, we obtain

$$\frac{\partial m_j}{\partial t} = j\,u(z)\,m_{j-1} + j(j-1)K_x m_{j-2} + K_z\frac{\partial^2 m_j}{\partial z^2} + r(z)\,m_j \tag{47}$$

subject to

$$\begin{aligned} &\text{at } t = 0, \; m_j = \delta(z)\delta_{jo} \quad (\delta_{jo}\text{: Kronecker delta}) \\ &\text{at } z = 0, \; \partial m_j/\partial z = 0 \\ &\text{at } z \to \infty, \; m_j \to 0 \end{aligned} \tag{48}$$

The set of equations (47) subject to (48) can be solved successively starting with the zero-order moment equation

$$\frac{\partial m_o}{\partial t} = K_z\frac{\partial^2 m_o}{\partial z^2} + r(z)\,m_o \tag{49}$$

$$\begin{aligned} &\text{at } t = 0, \; m_o = \delta(z) \\ &\text{at } z = 0, \; \partial m_o/\partial z = 0 \\ &\text{at } z \to \infty, \; m_o \to 0 \end{aligned} \tag{50}$$

The vertical variance σ_z^2 associated with m_o is obtained from

$$\sigma_z^2(t) = \int_0^\infty z^2 m_o(z,t)\,dz \tag{51}$$

and the horizontal variance σ_x^2 from

$$\sigma_x^2(t) = \int_0^\infty m_2(z,t)\,dz - \left\{ \int_0^\infty m_1(z,t)\,dz \right\}^2 \qquad (52)$$

The square root of the variance gives us the scale of the patch in the corresponding direction.

5. Further extensions

For proper modeling of an ecosystem it is often necessary to deal with interacting populations of two or more species. Thus Dubois (1975) attempted to explain the horizontal structure of zooplankton-phytoplankton populations in environments containing a patch of physiologically suitable water surrounded by hostile conditions, although he did not pay attention to the critical size problem. Armstrong (personal communication) has made an attempt to remove the arbitrary boundary conditions of the KISS model by coupling phytoplankton and nutrient dynamics. Armstrong's model allows both patch expansion by diffusion and limitation of growth by nutrient exhaustion.

Levin and Segel (1976) and Okubo (1974, 1978) suggest that plankton patchiness may arise from diffusive instability, in which initially stable uniform distributions of predator and prey populations, e.g., zooplankton and phytoplankton, are destabilized by the differential dispersal rates of the species. The basic idea derives from the celebrated work by Turing (1952) on morphogenesis and first advanced in an ecological context by Segel and Jackson (1972) and Levin (1974).

Levin and Segel's model (1976) is based on the system

$$\begin{aligned} \frac{\partial S}{\partial t} &= S(a_1 + c_1 S - b_1 Z) + D_1 \frac{\partial^2 S}{\partial x^2} \\ \frac{\partial Z}{\partial t} &= Z(-c_2 Z + b_2 S) + D_2 \frac{\partial^2 Z}{\partial x^2} \end{aligned} \qquad (53)$$

where S and Z are respectively phytoplankton and zooplankton population densities, D_1 and D_2 are respective diffusivities, and a_1, b_1, b_2, c_1, c_2 are all positive constants. This predator-prey system admits a spatially uniform stable equilibrium (S^*, Z^*) in the absence of diffusion:

$$S^* = a_1 c_2/(b_1 b_2 - c_1 c_2)$$

$$Z^* = a_1 b_2/(b_1 b_2 - c_1 c_2)$$

provided $1 > \frac{c_1}{b_2} < \frac{b_1}{c_2}$.

We now impose to the stable state small perturbations of the initial form

$$S' = p \cos kx, \quad Z' = q \cos kx$$

The diffusive instability of Turing's sense arises when

$$D_2/D_1 > \left\{ (b_1/c_2)^{1/2} - (b_1/c_2 - c_1/b_2)^{1/2} \right\}^{-2} \equiv R_{cr} \qquad (54)$$

For R slightly greater than R_{cr}, a perturbation will destabilize the system and start to growth if its initial wavelength is approximately equal to L_{cr}:

$$L_{cr} = 2\pi (D_1/a_1)^{1/2} \left\{ (b_1/c_2)^{1/2} - (b_1/c_2 - c_1/b_2)^{1/2} - 1 \right\}^{-1} \qquad (55)$$

It is important to remark that the above expression for the critical wavelength is very much analogous to the KISS scale, although in Levin and Segel's model no such assumption is made that a viable water is surrounded by totally hostile environments. As a matter of fact the original state is spatially uniform and the initial perturbation is assumed to be periodic in space.

Segel and Levin (1976) also developed a nonlinear analysis for the system (52) and have shown that the destabilized equilibrium is replaced by a spatially non-uniform steady state. Thus a pattern of patchiness can arise from a uniform pattern of phytoplankton-zooplankton system due to the effects of diffusivity-driven instability.

Mimura (1978), Mimura and Murray (1979) and Mimura *et al.* (1979) considered a generalized predator-prey model with dispersal to study in detail the development of patchiness.

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