Dissipative Structure: 
An Explanation and an Ecological Example

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(Received 27 March 1972)

A physical explanation is given of the fact that diffusion, usually a stabilizing influence which acts with increasing intensity on perturbations of shorter wavelengths, can bring about a finite wavelength instability of a spatially uniform interaction involving two constituents. Such instabilities have been regarded as of importance in biochemical contexts. By presenting an example of their occurrence when cooperating prey interact with predators, this study suggests that diffusive instabilities should also be sought in ecological interactions.

1. Introduction

Dissipative structures are of considerable current interest in modern theoretical biology. Such structures are temporal or spatial inhomogeneities which can arise in purely dissipative systems under suitable conditions. We shall only be concerned with an analysis of spatial dissipative structure. Furthermore, the dissipative terms considered here arise solely from the effects of diffusion so that one could call this paper a study of diffusive structure.

Turing (1952) was the first to present stability calculations which show that the reaction and diffusion of chemicals can give rise to spatial structure, and to suggest that this in turn could be a key event in the formation of biological pattern. Early generalizers of Turing's work were Gmitro & Scriven (1966) and Prigogine & Nicolis (1967). Their theoretical work has

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been supplemented by many other authors. Particularly relevant here is Edelstein (1970). There has been experimental confirmation of some predictions. Surveys of the field have recently been written by Nicolis (1971) and Glansdorff & Prigogine (1971). See also Prigogine & Nicolis (1971).

That structure can "spontaneously" arise has long been well known from the so-called Bénard instability of hydrodynamics (Chandrasekhar, 1961). Here, if a layer of fluid is heated sufficiently from below then the colder denser fluid on top will eventually fall. Circulations ensue which often form extraordinarily regular hexagonal patterns. Instability will commence if destabilizing top-heaviness outweighs the stabilizing diffusive processes associated with viscosity and thermal conductivity. The wavelength of the pattern can be thought of as resulting from a compromise between the infinitely long wavelength which maximizes conversion of gravitational potential energy and the moderate wavelength which minimizes dissipation.

Prigogine & Nicolis (1967) introduced the term dissipative structure to emphasize that in biochemical contexts no driving force such as top-heaviness is present. Although diffusion is normally regarded as a stabilizing factor, and one which acts more intensely on shorter wavelength disturbances, various mathematical calculations show that increasing the effect of diffusion can destabilize an otherwise stable situation, and that the diffusion-induced instability can set in at a positive wavelength. Our first purpose here is to try to explain these results on physical rather than formal mathematical grounds. The effect has been ascribed to "increasing the manifold of perturbations" (Prigogine & Lefever, 1968); our discussion will be more detailed and (we think) more satisfying. (Viscous diffusion can provide destabilizing effects in hydrodynamics (Lin, 1955) but the explanation by means of the hydrodynamical concept of Reynolds stresses is not relevant here.)

The second main purpose of this paper is to call attention to the fact that diffusive structures can appear in an ecological context. We do this by presenting an example of a predator–prey interaction where the addition of random dispersion results in an instability of the "normal" uniform steady state to perturbations of a certain well-defined wavelength.

2. Dissipative Instability in a Two-constituent System

Consider two species of concentrations $C_1$ and $C_2$ whose interaction and two-dimensional diffusion are governed by the equations

\[
\frac{\partial C_1}{\partial t} = R_1(C_1, C_2) + D_1 \nabla^2 C_1,
\]

\[
\frac{\partial C_2}{\partial t} = R_2(C_1, C_2) + D_2 \nabla^2 C_2.
\]

Here $x$ and $y$ are spatial coordinates and $\nabla^2 = \partial^2/\partial x^2 + \partial^2/\partial y^2$. The $R_i$
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Denote interaction terms (e.g. chemical reaction) and the $D_i$ are diffusion coefficients, $i = 1, 2$. We assume the existence of a uniform solution $C_1 = C_1^{(0)}$, $C_2 = C_2^{(0)}$, $C_i^{(0)}$ and $C_2^{(0)}$ constants such that

$$R_i(C_1^{(0)}, C_2^{(0)}) = 0.$$  

(2)

To examine the stability of the uniform solution to perturbations in concentration we write

$$C_i(x, y, t) = C_i(x, y, t).$$  

(3)

If the perturbations $c_i$ are sufficiently small, we can linearize the equations obtained upon substituting equation (3) into equation (1). We obtain

$$\frac{\partial c_1}{\partial t} = a_{11}c_1 + a_{12}c_2 + D_1 \nabla^2 c_1,$$

(4a)

$$\frac{\partial c_2}{\partial t} = a_{21}c_1 + a_{22}c_2 + D_2 \nabla^2 c_2,$$

(4b)

where the constants $a_{ij}$ are given by

$$a_{ij} = \frac{\partial R_i}{\partial C_j} \bigg|_{C_1 = C_1^{(0)}, C_2 = C_2^{(0)}}.$$

To decide whether or not the uniform state (2) is stable it is sufficient to examine the behavior of solutions to equations (4) which have the form

$$q(x, y, t) = \sum \alpha_i \cos (k_1x + k_2y + \theta) \exp (\sigma t),$$

(5)

where $\alpha_i$, $k_1$, $k_2$, $\theta$ and $\sigma$ are constants. The assumption that solutions have this form is not a restrictive one because a wide class of initial conditions can be synthesized by a suitable Fourier superposition of solutions like those of (5). Stability is assured if and only if all these solutions decay with time, i.e. if and only if $\sigma$ is negative (or has a negative real part).

Upon substituting equation (5) into equations (4) one obtains

$$0 = \left[ a_{11}(k) - \sigma \right] \bar{c}_1 + a_{12} \bar{c}_2,$$

$$0 = a_{21} \bar{c}_1 + \left[ a_{22}(k) - \sigma \right] \bar{c}_2,$$

(6)

where

$$a_{ii}(k) \equiv a_{ii} - D_i k^2, \quad k^2 \equiv k_1^2 + k_2^2.$$  

(7)

We see that the effect of diffusion ($D_i \neq 0$) is to decrease the coefficients $a_{11}$ and $a_{22}$ by an amount proportional to $k^2$, the square of the perturbation wavenumber. [It is easily seen that $2\pi/k$ is the spatial period of the perturbation (5). Those unfamiliar with perturbation theory can find this and other such details of the theory discussed in the paper of Keller & Segel (1971).]

The simplest effect of perturbation wavelength occurs when only one chemical is involved, say the first. Then $C_2 = c_2 = \bar{c}_2 = 0$ and $\sigma = a_{11} - D_1 k^2$. Here $a_{11}$ is present because of a (positive or negative) autocatalytic or self-reinforcing effect in which the growth rate of the perturbation $c_1$ is proportional to the instantaneous level of $c_1$. The term $-D_1 k^2$ evidently provides a diffusion-induced reduction of the reinforcement.
Note that more self-reinforcement (larger $a_{11}$) is required to destabilize the more rapidly oscillating disturbances of larger wavenumber $k$. The reason is that perturbations of relatively short spatial period $2\pi/k$ are effaced relatively rapidly by diffusion. In other words, zones of high and low concentration diffuse into uniformity more quickly if they are close together than if they are far apart.

It is helpful to regard instability as occurring when a parameter varies slowly in such a way that a stability condition is suddenly violated. (Although there are subtleties of interpretation, the slow variation essentially insures the relevance of the theoretical analysis in which the parameters are regarded as constants.) In the present simple case, for example, one can regard some mechanism as causing a slow increase of $a_{11}$ from negative values. Instability will set in as soon as $a_{11}$ turns positive, for then randomly introduced disturbances which have wavenumber $k = 0$ will begin to grow. The wavelength $2\pi/k$ of the disturbance which is the first to become capable of growth is called the critical wavelength. As we have just seen, with a single mode present the critical wavelength is infinite. This is what a naive view of the effects of diffusion would lead us to expect; disturbances of infinite wavelength are “most dangerous”, because when regions of high and low concentration are infinitely far apart they are unaffected by the homogenizing process of diffusion. (In finite systems, where because of the geometry there is a maximum wavelength, it is that maximum wavelength which is most dangerous.)

Suppose that two or more species interact and diffuse in such a way that a time-independent spatially uniform state is possible. This state will be said to possess a diffusive instability if a slow parameter change can bring about a situation wherein perturbations of a non-zero (finite) wavelength start growing.

Putting $k = 0$ is tantamount to neglecting diffusion and, by definition, perturbations of zero wavenumber are stable when diffusive instability sets in. Consequently one can say that the instability in question is actually brought about by diffusion.

We have seen that dissipative instability is impossible when only one species is present. Returning to the case of two species, we note from equation (6) that for a non-zero perturbation the determinant of coefficients must vanish, so

$$
\sigma = \frac{1}{2}(\hat{a}_{11} + \hat{a}_{22}) \pm \frac{1}{2}[(\hat{a}_{11} + \hat{a}_{22})^2 - 4(\hat{a}_{11}\hat{a}_{22} - a_{12}a_{21})]^{1/2}.
$$

Inspection of this equation shows that decay with time of solutions proportional to $\exp(\sigma t)$ takes place if and only if

$$
\hat{a}_{11}(k) + \hat{a}_{22}(k) < 0 \quad (8a)
$$
and
\[ \hat{a}_{11}(k) \hat{a}_{22}(k) - a_{12}a_{21} > 0. \] (8b)

In diffusive instability, perturbations of zero wavenumber are required to be stable so the inequalities (8) must hold when \( k = 0 \). Thus, necessary conditions for diffusive instability are
\[
\begin{align*}
  a_{11} + a_{22} &< 0, \quad (9a) \\
  a_{11}a_{22} - a_{12}a_{21} &> 0. \quad (9b)
\end{align*}
\]

If inequality (9a) holds, then (8a) will remain valid for positive \( k \), for the left side of the latter inequality is decreased when \( k \) increases. Dissipative instability is brought about, therefore, by a reversal of inequality (8b) for at least one value of \( k \).

It is worth deriving some further necessary conditions for dissipative instability. To do this, we first note that \( a_{11} \) and \( a_{22} \) cannot both be positive, by inequality (9a). If both these coefficients are negative then inequality (8b) cannot be reversed by increasing \( k \). Necessarily, then
\[ a_{11}a_{22} < 0. \] (10)

From this and inequality (9b) it follows that
\[ a_{12}a_{21} < 0. \] (11)

Often useful is the fact that a dissipative instability can immediately be ruled out in the absence of the opposition of signs required by inequalities (10) and (11).

Reversal of inequality (8b) is equivalent to
\[ Q(k^2) < 0; \quad Q(k^2) = D_1D_2k^4 - (D_1a_{22} + D_2a_{11})k^2 + a_{11}a_{22} - a_{12}a_{21}. \]

For the case of interest \( Q(0) > 0 \), by inequality (9b). If \( Q < 0 \) for positive \( k^2 \) then it is clearly necessary that
\[ D_1a_{22} + D_2a_{11} > 0. \] (12)

In what follows we assume \( D_1D_2 \neq 0 \). Otherwise \( Q \) is linear in \( k^2 \) and instability would set in as soon as inequality (12) becomes valid, at \( k = \infty \). The definition of diffusive instability excludes this relatively uninteresting case.

For instability it is sufficient that \( Q \) be negative at its minimum. This minimum is assumed at \( k^2 = k_m^2 \) where
\[ k_m^2 = (D_1a_{22} + D_2a_{11})/2D_1D_2. \] (13)

The condition \( Q(k_m^2) < 0 \) is
\[ (a_{11}a_{22} - a_{12}a_{21}) - (D_1a_{22} + D_2a_{11})^2/4D_1D_2 < 0. \] (14)
Because of inequalities (9b) and (12) we may take a square root to find the following final form for the instability condition:

\[ D_1 a_{22} + D_2 a_{11} > 2(D_1 D_2)^{\frac{1}{4}} (a_{11} a_{22} - a_{12} a_{21})^{\frac{1}{2}}. \]

(15)

When inequality (15) is fulfilled then inequality (12) is automatically fulfilled as well.

Suppose that one or several of the parameters vary slowly in such a way that inequality (9) always holds (stability at zero wavenumber), and that inequality (15) is initially violated (stability at non-zero wavenumbers). When inequality (15) is first obeyed, we have the onset of dissipative instability. The critical conditions for the occurrence of this instability occur when inequality (15) is an equality. The critical wave-number \( k_c \) of the first perturbations to grow is found by evaluating the \( k_m \) of equation (13) under the supposition that critical conditions hold.

3. An Explanation of the Mathematical Results

We have presented a mathematical demonstration that if the inequalities of (9) hold then dissipative instability will set in when inequality (15) is satisfied. [In any particular case, unequivocal demonstration of the instability requires a proof that inequality (15) does not conflict with inequalities (9a) and (9b).] Inequalities (10) and (11) have been shown to be a necessary condition for the appearance of this instability.

We explain these results in two steps. (i) We explain why the system is stable in the absence of diffusion, provided that the opposition of signs required by inequalities (10) and (11) prevails in the self-reinforcing and cross-coupling terms. (ii) We explain why diffusion destabilizes the situation described in (i) by effectively decreasing self-reinforcement.

To accomplish (i), let us consider a representative case wherein inequalities (10) and (11) are satisfied. Let

\[ a_{11} = -\bar{a}_{11}, a_{21} = -\bar{a}_{21}; \bar{a}_{11} > 0, \bar{a}_{21} > 0, a_{12} > 0, a_{22} > 0; \]

(16)

so that in the absence of diffusion the equations (4) are

\[ \frac{dc_1}{dt} = -\bar{a}_{11} c_1 + a_{12} c_2, \quad \frac{dc_2}{dt} = -\bar{a}_{21} c_1 + a_{22} c_2. \]

(17)

Because of our assumptions concerning signs, the perturbation \( c_2 \) would grow if left by itself but \( c_1 \) would decay. The coupled perturbations decay when

\[ \bar{a}_{11} > a_{22}, \]

(18a)

\[ \bar{a}_{21} a_{12} > \bar{a}_{11} a_{22}. \]

(18b)
The reason must be that $c_1$—which decays, faster than $c_2$ grows—is strongly enough coupled to $c_2$ to quench the latter fluctuation. Indeed an increase in $c_2$ causes a growth in $c_1(a_{12} > 0)$ which in turn causes decay of $c_2(-\bar{a}_{21} < 0)$. Note that if species one decays too rapidly ($\bar{a}_{11}$ too large) the stability condition (18b) is violated. Too rapid decay of the stable species destabilizes the system. The reason is that the first species can decay so fast that it does not have sufficient time to exert its stabilizing influence on the second species. When written in the form $\bar{a}_{11} < (\bar{a}_{21} a_{12})/a_{22}$ the stability condition (18b) shows this quite clearly, for the critical size of $\bar{a}_{11}$ increases with the magnitude of the coupling coefficients $\bar{a}_{21}$ and $a_{12}$.

With the understanding summarized in the italicized sentence of the previous paragraph, we can now appreciate why it is that by selecting a disturbance of an appropriate wavenumber we can effectively cause a relative decrease of $a_{11}$ which brings about instability. Explanation is facilitated if we rewrite the full perturbation equations (4) using inequalities (16) and the fact [from equation (5)] that $\nabla^2 c_i = -k^2 c_i$. We have

$$\frac{\partial c_1}{\partial t} = -\alpha_{11} c_1 + \alpha_{12} c_2, \quad \frac{\partial c_2}{\partial t} = -\alpha_{21} c_1 + \alpha_{22} c_2,$$

(19)

where

$$\alpha_{11} = \bar{a}_{11} + D_1 k^2, \quad \alpha_{12} = a_{12}, \quad \alpha_{21} = \bar{a}_{21}, \quad \alpha_{22} = a_{22} - D_2 k^2.$$  

(20)

There is a complete analogy between equations (17) and (19), but in the latter case, with diffusion taken into account, the coefficients are functions of the wavenumber $k$.

For a given set of parameters, let us now scan disturbances of increasing wavenumber $k$, beginning at $k = 0$. We see that $\alpha_{11}$ will increase but $\alpha_{22}$ will decrease. Now the stability condition (8b) in the present notation is

$$\alpha_{21} \alpha_{12} > \alpha_{11} \alpha_{22}.$$  

(21)

When $k = 0$ this condition holds, because we assume inequality (18b) to avoid instability at zero wavenumber. But there is a chance that the instability condition will be violated at positive $k$ if the above-mentioned increase in $\alpha_{11}$ sufficiently outweighs the decrease in $\alpha_{22}$. Indeed, inequality (15) is the condition that the stability condition is violated.

If our explanation is correct, one would expect that (with $a_{11} = -\bar{a}_{11} < 0$, $a_{22} > 0$) a necessary condition for instability at finite wavelength is $D_1 > D_2$, for then there is a chance that the increase with $k^2$ of $\alpha_{11} = \bar{a}_{11} + D_1 k^2$ can outweigh the decrease in $\alpha_{22} = a_{22} - D_2 k^2$. Indeed, from inequalities (18a) and (12) we have

$$1 < (\bar{a}_{11}/a_{22}) \text{ and } (\bar{a}_{11}/a_{22}) < (D_1/D_2),$$
so \( D_1 \) indeed must exceed \( D_2 \). This inequality would be reversed if \( a_{11} \) were positive and \( a_{22} \) negative.

From inequality (10), a necessary condition for dissipative instability is that one of the coefficients \( a_{11} \) and \( a_{22} \) be positive and the other negative. If \( a_{11} > 0 \) and \( a_{22} < 0 \) we shall speak of the first substance as the destabilizer and the second substance as the stabilizer. The terminology will of course be reversed when the inequalities are reversed. Using this terminology, the result of the previous paragraph, in words, is as follows:

a necessary condition for instability at positive wavelength is the faster diffusion of the stabilizer. (22)

Instability occurs when diffusion increases the effective decay of the stabilizer to such an extent that it disappears before it can damp the destabilizer to which it is coupled. Because of condition (22), this can happen even though diffusion also decreases the growth rate of the destabilizer, making it less dangerous.

4. A Chemical Example

A useful point can be made by considering an example discussed by Prigogine & Lefever (1968). A certain (artificial) scheme of chemical reactions leads to the equations

\[
\begin{align*}
\frac{\partial C_1}{\partial t} &= k_1 A + k_2 C_1^2 C_2 - k_3 B C_1 - k_4 C_1 + D_1 \nabla^2 C_1, \\
\frac{\partial C_2}{\partial t} &= k_3 B C_1 - k_4 C_2 + D_2 \nabla^2 C_2.
\end{align*}
\]

(23)

Here the \( k \)'s are various kinetic constants, while \( A \) and \( B \) are the fixed concentrations of two initial products. There is an equilibrium state \( (C_1^{(0)}, C_2^{(0)}) \) whose stability is governed by the equations (4) when

\[
\begin{align*}
a_{11} &= k_3 B - k_4, \quad a_{12} = k_2 \frac{k_1}{k_2^2} k_4^2, \quad a_{21} = -k_3 B, \\
a_{22} &= -k_2 \frac{k_1}{k_2^2} A^2. 
\end{align*}
\]

(24)

It is convenient to regard \( B \) as a controllable parameter. Instability will set in at wavelength \( \lambda_c = 2\pi/k_c \) when \( B \) exceeds a certain value \( B_c \), where

\[
k_c = \left(\frac{k_4}{k_2^2 k_1^2}\right)^{\frac{1}{4}} (D_1 D_2)^{-\frac{1}{4}} A^{\frac{1}{4}},
\]

(25)

\[
B_c = \left[ \frac{k_1}{k_4} \left( \frac{k_2}{k_3} \right)^{\frac{1}{4}} A + \left( \frac{k_4}{k_3} \right)^{\frac{1}{4}} \right]^2.
\]

(26)

Note that when a parameter like \( B \) is singled out as controlling the situation, formula (15) is implicit.

It is a natural goal to explain in general terms the variation of \( B_c \) and \( k_c \) with the various parameters. But this example illustrates the fact that in general such explanations will not be forthcoming, because variation of a
parameter of interest will cause coordinated variation of the coefficients $a_{11}$, $a_{12}$, $a_{21}$, and $a_{22}$. If variation of a parameter changes just one of the four coefficients, it is not difficult to provide a qualitative explanation of the effect of this parameter. But if parameter variation changes more than one coefficient it is almost a hopeless task to summarize the various contradictory influences: one must be content with the mathematical predictions.

5. Dissipative Instability in a Predator–Prey Interaction

The nature of equations which describe ecological interactions does not seem fundamentally different from the nature of those which describe chemical interactions, so it is natural to conjecture that dissipative structures will be found in ecological situations. In a sense, these have already been demonstrated in Keller & Segel's (1971) study of the initiation of slime mold aggregation. Although this study predicted that instability would commence at infinite wavelength, an extension by Segel & Stoeckly (1972) shows that, under certain conditions at least, a uniform distribution of chemotactic cells, attractant, and attractant-destroying enzyme will break up at a well-defined finite wavelength. Yet this work does not provide an example of a purely dissipative structure, since chemotaxis provides a non-dissipative driving force.

We attempted to find a purely dissipative structure by tinkering with the standard type of predator–prey equations, modified by the addition of diffusive terms to represent the effect of random motion. We were unsuccessful at first, so we tried to discern the characteristics of a situation where uneven geographic distribution of predator and prey would be mutually advantageous. It occurred to us that such a situation would result if the prey were capable of some sort of cooperation so that the number of offspring per prey individual was an increasing function of prey density at first. (Of course, one would expect that the birth rate would be a decreasing function of prey density at higher density levels.) It would appear to be mutually beneficial if the predators concentrated in certain areas, letting the prey population rise outside the areas of predator concentration. At higher population levels, the prey’s ability to cooperate would allow them to reproduce faster. The predators would partially benefit from this, since some of the larger prey population would “diffuse” into the concentrations of predator.

We prefer to use the terminology “exploiters” and “victims” rather than “predators” and “prey” since we can then employ the mnemonic notation $E^*(x^*, y^*, t^*)$ and $V^*(x^*, y^*, t^*)$ to denote population densities at points $(x^*, y^*)$, at time $t^*$. With the previous qualitative thoughts in mind, we
search for dissipative structure in a situation described by the following equations:

\[
\begin{align*}
\frac{\partial V}{\partial t} &= VR(V) - \bar{a}VE + \mu_1 \left[ \frac{\partial^2 V}{\partial x^2} + \frac{\partial^2 V}{\partial y^2} \right], \\
\frac{\partial E}{\partial t} &= bVE - dE - \bar{c}E^2 + \mu_2 \left[ \frac{\partial^2 E}{\partial x^2} + \frac{\partial^2 E}{\partial y^2} \right].
\end{align*}
\] (27)

Here the victim's reproduction rate \( R \) is a function to be specified below, while \( \bar{a}, \bar{b}, \bar{c}, \bar{d}, \mu_1 \) and \( \mu_2 \) are all positive constants.

The consumption of victims by exploiters, and the consequent enhancement of exploiter population growth, has been assumed to be simply proportional to the product of the population densities. (More realistic assumptions here should not affect the qualitative conclusions.) The exploiters are imagined as requiring the consumption of victims for their existence. Their numbers are limited not only by the simple death rate term \(-dE\) but also by the higher order term \(-\bar{c}E^2\). Finally, the random dispersal of the two classes of organisms is represented by diffusion-like terms proportional to the motility constants \( \mu_1 \) and \( \mu_2 \).

A simple reproduction rate exhibiting cooperativity is \( R(V) = \kappa_0 + \kappa_1 V - \kappa_2 V^2; \) \( \kappa_0, \kappa_1 \) and \( \kappa_2 \) positive constants. We will simplify still further by taking \( \kappa_2 = 0 \). Intuitively, this final simplification should not cause difficulty providing victim population levels are not so high that crowding dominates cooperativity. Indeed, we have carried out the calculations when \( \kappa_2 \neq 0 \) and find the same qualitative conclusions as we shall present below. We shall not give the results of these calculations, for the simplest possible example best makes our point that diffusive instability can occur in an ecological context.

The higher-order exploiter death term, \(-\bar{c}E^2\), was initially included in equations (27) almost accidentally. But if \( \bar{c} \) is set equal to zero, the model will not yield a diffusive instability. The instability remains, however, if we set \( \bar{d} = 0 \), and this we shall do because we wish the model to be as simple as possible. Neglect of the random death term \(-dE\) should be justified in situations where exploiter mortality is due primarily to the "combat" term \(-\bar{c}E^2\). Moreover, when the random death term is retained, our formulae below hold if \( \kappa \) and \( \bar{a} \) are replaced by \( R\kappa \) and \( Ra \) respectively, where \( R = (1 + \bar{a}d)/(1 + \kappa d), \) \( \bar{d} = d/\kappa_0 \).

It might be thought that exploiter cooperativity would also give rise to diffusive instability. This may well be. But it did not in the only case we tried, namely equations identical to (27) (with no prey cooperativity), except that \( \bar{a} \) and \( \bar{b} \) were multiplied by the factor \( 1+\bar{q}E \).
For reasons we have stated, then, in equations (27) we assume that \( R(V) = \kappa_0 V \) and that \( \bar{d} = 0 \). To reduce the number of parameters we introduce the dimensionless variables, \( e, v, x, y, \) and \( t \) where
\[
e = E\bar{c}/\kappa_0, \quad v = V\bar{b}/\kappa_0, \quad x = \bar{x}(\mu_2/\kappa_0)^{-\frac{1}{2}}, \quad y = \bar{y}(\mu_2/\kappa_0)^{-\frac{1}{2}}, \quad t = \kappa_0\bar{t}.
\]
With these, the dimensionless exploiter and victim population levels \( e(x, y, t) \) and \( v(x, y, t) \) are governed by
\[
\frac{\partial v}{\partial t} = (1 + \kappa_0)v - aev + \delta^2 \nabla^2 v, \quad \frac{\partial e}{\partial t} = ev - e^2 + \nabla^2 e.
\]
In its original form, the interaction was governed by the seven parameters \( \bar{a}, \bar{b}, \bar{c}, \mu_1, \mu_2, \kappa_0, \) and \( \kappa_1 \). Now we see that the phenomenon is governed by three dimensionless groups, defined by
\[
\kappa = \kappa_1\bar{b}, \quad a = \bar{a}/\bar{c}, \quad \delta^2 = \mu_1/\mu_2.
\]
There is a trivial uniform steady-state solution \( e = v = 0 \). This solution is unstable. For example, if a small uniform level of victims is introduced, the victim population grows exponentially at first, according to the law \( \frac{dv}{dt} = v \).

Since we shall assume that
\[
a > \kappa,
\]
there is a single non-trivial uniform steady solution given by
\[
e \equiv L, \quad v \equiv L; \quad L \equiv (a - \kappa)^{-1}.
\]
The stability of this solution is governed by equations of the form (4) where
\[
a_{11} = \kappa L, \quad a_{12} = -aL, \quad a_{21} = L, \quad a_{22} = -L, \quad D_1 \equiv \delta^2, \quad D_2 \equiv 1.
\]
To guarantee stability at zero wavenumber, inequality (9b) requires \( L^2(a - \kappa) > 0 \), which is assured by inequality (31). Condition (9a) requires
\[
L(\kappa - 1) < 0 \text{ or } \kappa < 1.
\]
Applied to the present case, the instability condition (15) is
\[
\kappa - \delta^2 > 2\delta(a - \kappa)^\frac{1}{2}.
\]
At the onset of instability
\[
\kappa - \delta^2 = 2\delta(a - \kappa)^\frac{1}{2}.
\]
From equation (13), using equation (36), the critical wavenumber of the growing disturbances is found to be
\[
k_c^2 = \delta^{-1}(a - \kappa)^{-\frac{1}{2}}.
\]
To gain some appreciation of how the dissipative instability can arise, we shall consider in turn the possibilities that its onset is due to a slow change in \( \delta \), in \( a \), or in \( \kappa \). (It could also arise by appropriate simultaneous changes in two of the parameters, or of all three.)
I: Change in $\delta$. Suppose the parameters $a$ and $\kappa$ are fixed. Suppose further that $\kappa < a$ and $\kappa < 1$ as is required by inequalities (31) and (34). Let us find the range of $\delta$ for which inequality (35) holds. This inequality certainly is valid at $\delta = 0$. The upper limit of the interval in which inequality (35) holds is $\delta_c$ where

$$\kappa - \delta_c^2 = 2\delta_c(a - \kappa) \quad \text{or} \quad \delta_c = a + (a - \kappa)^{1/2}.$$  \hspace{1cm} (38)

It is easy to verify that $\delta_c > 0$ and $\delta_c < \kappa$ so the situation is as depicted in Fig. 1(a). The uniform state will break up in a diffusive instability when

$$\delta \equiv (\mu_1/\mu_2)^{1/3} \text{ drops below } \delta_c.$$  \hspace{1cm} 

It is perhaps simplest to regard the instability as “caused” by a slow increase in the motility $\mu_2$ of the exploiter. If $\mu_2$ becomes sufficiently large compared to $\mu_1$, inhomogeneities in the exploiter population disappear so quickly that a concentration of victims will intensify itself. Since $\delta_c < \kappa$ it is necessary (in this model) that cooperativity be present ($\kappa > 0$) but not in too intense a form ($\kappa < 1$). The mechanism of instability is precisely that which we have already discussed. Since $a_{11} > 0$ and $a_{22} < 0$ the predators are the “stabilizers”, using our earlier terminology.

We now give an expression for $\lambda_c$, the dimensional critical wavelength of the growing perturbation. Since $k_c$ is the dimensionless wavenumber, from equations (28) we see that $k_c(\kappa_0/\mu_2)^{1/2}$ is the dimensional wavenumber, so in general

$$\lambda_c = 2\pi(\mu_2/\kappa_0)^{1/2}k_c^{-1}.$$  \hspace{1cm} (39)
In providing a formula for $\lambda_c$, we will always use equation (36) to express the (slowly changing) governing parameter in terms of the remaining (fixed) parameters. In the present case we find from equations (37) and (38) that

$$\lambda_c = 2\pi (\mu_1/\kappa_0)^{1/2} (1 - a^{-1}\kappa)^{-1/2}. \quad (40)$$

It can be shown that $\lambda_c > 0$ when $\delta > \delta_c$. Note that $\lambda_c$ is small when $\kappa \approx a$.

II: Change in $a$. Now imagine $\kappa$ and $\delta$ to be fixed with $\kappa > 1$. By solving equation (36) for $a$ and determining the relative magnitudes of various quantities we arrive at Fig. 1(b). The uniform state becomes unstable when the limitation of victims by predation becomes sufficiently small, compared to the extraneous limitation of the predators themselves, that $a - \bar{a}/\bar{c}$ drops below $a_c$, where

$$a_c = (\kappa + \delta^2)^2/4\delta^2. \quad (41)$$

The wavelength of the instability in this case is expressed by

$$\lambda_c = 2\pi (\mu_1/2\kappa_0)^{1/2} (\kappa \delta^{-2} - 1)^{1/2}. \quad (42)$$

III: Change in $\kappa$. Finally, imagine $a$ and $\delta$ to be fixed. From equation (35) we then find diffusive instability when $\kappa$ drops below $\kappa_c$, where

$$\kappa_c = \delta(2a^\frac{1}{2} - \delta). \quad (43)$$

But if requirement (34) is applied to $\kappa_c$ then one obtains the condition

$$a < (1 + \delta^2)^2/4\delta^2. \quad (44)$$

If this inequality is not satisfied, there can be no dissipative instability, regardless of the value of $\kappa$. Given inequality (44) the situation is summed up in Fig. 1(c). Structure appears when victim cooperativity, afforded by higher population density, is sufficiently large compared to the benefit which the victims afford the exploiters so that $\kappa_1/b \equiv \kappa > \kappa_c$. The wavelength of the instability is

$$\lambda_c = 2\pi (\mu_1/\kappa_0)^{1/2} (a^{1/2} \delta^{-1} - 1)^{1/2}. \quad (45)$$

6. Summary and Conclusions

Suppose that two constituents interact in such a way that a uniform steady state obtains. In the presence of diffusion, it is possible that slow variation of the parameters will bring about a breakdown of the steady state and the development of spatial inhomogeneities at a certain well-defined “critical wavelength”. In starting from the essentially known theory of this phenomenon, we have emphasized that certain conditions must necessarily hold if the above-described “diffusive instability” is to take place. In the linearized perturbation equations, the self-reinforcement of one species (the “destabilizer”) must be positive. The self-reinforcement of the other (the “stabilizer”) must be negative. Moreover, the coupling terms must be of opposite sign.
The diffusion constant of the destabilizer must be larger than the (non-zero) diffusion constant of the stabilizer.

If the various necessary conditions are satisfied, a slow change in parameters can bring about diffusive instability. We have given a detailed discussion of the mechanism which brings about this instability. The essence of the matter is that diffusion may cause too rapid a decay of the stabilizer, so that it no longer has time to bring the system to stability through its coupling with the destabilizer.

We have shown, using a previously studied biochemical example, that one cannot expect to understand the variation of such features as the critical wavelength with the various underlying parameters of the problem. These parameters are too intertwined in the self-reinforcement and coupling coefficients to permit unravelling of their individual effects.

From a formal point of view, diffusive instabilities should sometimes occur in ecology when two (or more) species interact in a uniform domain of sufficiently wide extent. In this paper, we have sought to open discussion of this possibility by presenting as simple an example as we could find where diffusive instability occurs. Our example involves an exploiter-victim interaction in which (i) cooperativity among victims is assumed to cause an increase of their birth rate with population level; (ii) combat among exploiters is assumed to cause an increase of their death rate with population level; (iii) both exploiter and victim disperse randomly. Concerning (iii), we remark that the prediction of patterned spatial inhomogeneity which we make is not relevant to cat–mouse interactions where the movement of the exploiters is affected by the distribution of victims. [Studies involving chemotaxis, e.g. Keller & Segel (1971), can easily be adapted to handle such situations.] Here, as in some host–parasite interactions, the dispersal of each constituent is independent of the concentration of the other constituent.

It is hoped that a forthcoming non-linear analysis will establish the connection between diffusive instability and steady, spatially inhomogeneous, dissipative structure; and will further illuminate the role of cooperativity in the present ecological example.

We acknowledge with thanks the hospitality and stimulation afforded to us at the Weizmann Institute. One of us (LAS) was supported by a John Simon Guggenheim Fellowship and by National Science Foundation Grant GU2605 to Rensselaer. One of us (JLJ) was supported by a Weizmann Fellowship.

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