6.337 PROJECT

STABILITY
OF
A NONLINEAR DIFFUSIVE PREDATOR-PREY SYSTEM

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ABSTRACT

The following nonlinear diffusion-reaction predator-prey system is studied.

$$
\left\{
\begin{aligned}
\frac{\partial V}{\partial t} &= \mu \frac{\partial^2 V}{\partial x^2} + V(K-\alpha V-\beta E) \\
\frac{\partial E}{\partial t} &= \mathbb{P} \frac{\partial^2 E}{\partial x^2} + E(\gamma V-\delta E)
\end{aligned}
\right. \tag{10}
$$

where $V = V(x,t)$, the prey population,
$E = E(x,t)$, the predator population,

$\mu, \mathbb{P} > 0,$ (10.1)

$K, \beta, \gamma > 0,$ (10.2)

$\alpha < 0 < \delta\,,$ (10.3)

$\alpha\delta + \beta\gamma > 0,$ (10.4)

$-\alpha - \gamma < 0.$ (10.5)

The system has a spatially uniform equilibrium state. The stability of that equilibrium depends on the diffusive ratio $\mu/\mathbb{P}$. For certain values of that ratio, linear theory predicts that the equilibrium is unstable and the populations increase exponentially, but our nonlinear theory shows that, for certain perturbation, the original spatially uniform state will be succeeded by a new steady state wherein predator and prey are more concentrated in certain regions. The technique used to study the stability is the so-called multiple-scale method in perturbation theory combined with successive approximations.

PART I INTRODUCTION

This paper is mostly based on the paper by Segel and Levin (1976). Segel and Levin gave the mathematical analysis in a very concise fashion. My work is mostly to redo the analysis, to fill in details and to give arguments omitted by Segel and Levin. I follow the notations and equation numbering used by Segel and Levin, although they are sometimes confusing. I number my only appendix as Appendix 4 since Segel and Levin have three appendices for their paper and I don't want to confuse the numbering. An error is found in (54) in Segel and Levin's paper. Fortunately, the error is not fatal.

Diffusion keeps population spreading in space and therefore seems increase the stability of the system. It is not always true. We will see this in PART II by linearizing the system and applying linear theory. We will show further in PART IV that the stability depends on the diffusive ratio of predators and prey. The instability caused by diffusion is called diffusive instability. Diffusive instability is well known and is possible in the model we proposed. Diffusive instability, like other kind of instabilities, usually causes the populations to grow without bound away from the equilibrium point. We will show in PART V that, for certain kind of perturbation and certain diffusivity ratios, although the equilibrium is not stable, the populations do not grow without bound. The populations will reach a new steady state with wave-like spatial distributions. Many arguments in PART V are heuristic as what is often the case in perturbation theory.

The behavior of our model has practical background. In some predator-prey systems, patchiness has been observed even though the environment appears homogeneous. For example, Mimura and Murray (1978) made a reference to a report by Cassie (1963) [*Oceanogr. Mar. Biol. Ann. Reg.*, **1**, 223.] (Remark: I didn't see Cassie's paper since it is not in the science library.) It is said that Cassie reported that, depending on the circumstances, plankton display such patchiness. There are many other examples. We don't study those examples since (i) we don't have data (ii) the real environment is much more complicated than our mathematical model and hence we don't expect the numerical result from our model to fit any sample data. In fact, we don't even know how to estimate the parameters in our model. We will just interpret our mathematical results qualitatively. Our results show that diffusion in a predator-prey system can be a reason for such pathiness to occur.

PART II PRELIMINARY

This part is based on Section 10.6 of A.Okubo (1980). I use the same equation numbering.

Let $S_1=S_1(x,t)$ and $S_2=S_2(x,t)$. Let $D_1, D_2 > 0$ be two constants. Consider the system

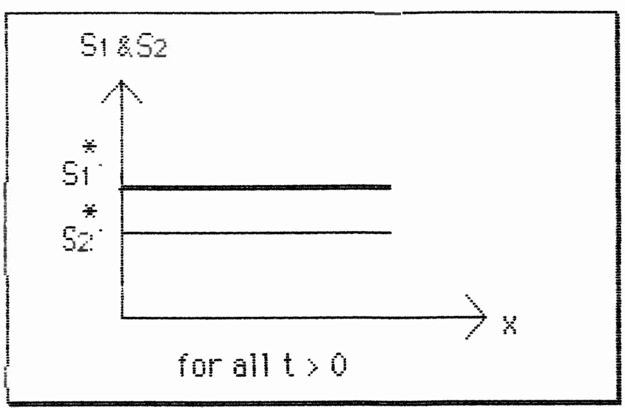
$$\frac{\partial S_1}{\partial t} = D_1 \frac{\partial^2 S_1}{\partial x^2} + F_1(S_1,S_2) \qquad \text{.............................} \qquad (10.95)$$

$$\frac{\partial S_2}{\partial t} = D_2 \frac{\partial^2 S_2}{\partial x^2} + F_2(S_1,S_2) \qquad \text{.............................} \qquad (10.96)$$

D_1 and D_2 are interpreted as diffusivities. Without diffusion (D_1, D_2 = 0), the spatial distribution of S_1 and S_2 are irrelevant and therefore we may regard S_1 and S_2 as functions of t only. Thus the absence of diffusion is equivalent to spatially uniform distribution of S_1 and S_2. We will use this equivalence in our following arguments. ✓

Assume $\begin{cases} S_1(x,t)=S_1^* \\ S_2(x,t)=S_2^* \end{cases}$ is a equilibrium state such that $\begin{cases} F_1(S_1^*,S_2^*)=0 \\ F_2(S_1^*,S_2^*)=0 \end{cases}$.

It's a spatially uniform equilibrium state as shown below.



Suppose there is a spatially homogeneous perturbation to this equilibrium state.

That is, we start at the state $\begin{cases} S_1(x,t_0)=S_1^* + \varepsilon_1 \\ S_2(x,t_0)=S_2^* + \varepsilon_2 \end{cases}$. We assume that the equilibrium is stable to such a perturbation. That is, our system is stable in the absence of diffusion. .... (10.97.1)

We will obtain conditions for such stability in (10.102) and (10.103). To study the effect of diffusion, we consider an arbitrary perturbation S_1 and S_2.

$$S_i(x,t) = S_i^* + S_i'(x,t), \quad i = 1, 2. \qquad \text{............................} \qquad (10.98)$$

Then

$$\frac{\partial S_i}{\partial t} = \frac{\partial S_i'}{\partial t}, \quad \frac{\partial^2 S_i}{\partial x^2} = \frac{\partial^2 S_i'}{\partial x^2}.$$

And we expand $F_1(S_1,S_2)$ around the point (S_1^*, S_2^*) by Taylor's series.

$$F_1(S_1,S_2) = F_1(S_1^* + S_1'(x,t), S_2^* + S_2'(x,t))$$

$$= F_1(S_1^*,S_2^*) + \frac{\partial F_1(S_1^*,S_2^*)}{\partial S_1} S_1'(x,t) + \frac{\partial F_1(S_1^*,S_2^*)}{\partial S_2} S_2'(x,t) + \ldots$$

$$= a_{11}S_1'(x,t) + a_{12}S_2'(x,t) + \ldots$$

Similarly,

$$F_2(S_1,S_2) = F_2(S_1^* + S_1'(x,t), S_2^* + S_2'(x,t))$$

$$= F_2(S_1^*,S_2^*) + \frac{\partial F_2(S_1^*,S_2^*)}{\partial S_1} S_1'(x,t) + \frac{\partial F_2(S_1^*,S_2^*)}{\partial S_2} S_2'(x,t) + \ldots$$

$$= a_{21}S_1'(x,t) + a_{22}S_2'(x,t) + \ldots$$

Substituting those into (10.95) and (10.96), we get the linearized system for the perturbation.

$$\frac{\partial S_1'}{\partial t} = D_1 \frac{\partial^2 S_1'}{\partial x^2} + a_{11}S_1'(x,t) + a_{12}S_2'(x,t) \qquad \text{............................} \qquad (10.99)$$

$$\frac{\partial S_2'}{\partial t} = D_2 \frac{\partial^2 S_2'}{\partial x^2} + a_{21}S_1'(x,t) + a_{22}S_2'(x,t) \qquad \text{............................} \qquad (10.100)$$

Solutions to parabolic differential equations are essentially proportional to $e^{\lambda t+ikx}$ as $t\to\infty$, for some λ and k. λ is interpreted as the frequency and k is wave number. Thus, as what is commonly done to parabolic equations, we assume the solution is of the form

$$S_1^*(x,t) = \alpha\, e^{\lambda t+ikx} \qquad \text{and} \qquad S_2^*(x,t) = \beta\, e^{\lambda t+ikx}$$

Substituting into (10.99) and (10.100), we obtain

$$(\lambda + D_1 k^2 - a_{11})\,\alpha - a_{12}\,\beta = 0$$
$$- a_{21}\,\alpha + (\lambda + D_2 k^2 - a_{22})\,\beta = 0$$

For non-trivial solutions, we require

$$\begin{vmatrix} \lambda + D_1k^2 - a_{11} & -a_{12} \\ -a_{21} & \lambda + D_2k^2 - a_{22} \end{vmatrix} = 0 \qquad \ldots\ldots\ldots\ldots \qquad (10.101)$$

λ is the eigenvalue of the matrix $\begin{pmatrix} -D_1k^2 + a_{11} & +a_{12} \\ +a_{21} & -D_2k^2 + a_{22} \end{pmatrix}$.

The solution for λ is

$$\lambda_{1,2} = \frac{1}{2}(\hat{a}_{11} + \hat{a}_{22}) \pm \frac{1}{2}\sqrt{(\hat{a}_{11} + \hat{a}_{22})^2 - 4\,(\hat{a}_{11}\hat{a}_{22} - a_{12}a_{21})}$$

where $\hat{a}_{11} = a_{11} - D_1k^2$, $\hat{a}_{22} = a_{22} - D_2k^2$.

(Remark: The solution for λ given under (10.101) on page 205 of Okubo is wrong.)

For $k=0$, we have $\hat{a}_{11} = a_{11}$ and $\hat{a}_{11} = a_{11}$. Hence

$$\lambda_{1,2} = \frac{1}{2}(a_{11}+a_{22}) \pm \frac{1}{2}\sqrt{(a_{11}+a_{22})^2 - 4(a_{11}a_{22} - a_{12}a_{21})}$$

Since $k=0$ represents a spatially uniform perturbation, the system was required to be stable (see (10.97.1)). Therefore $\lambda_{1,2} < 0$, i.e.,

$$a_{11}+a_{22} < 0 \qquad \ldots\ldots\ldots\ldots \qquad (10.102)$$

and $$a_{11}a_{22} - a_{12}a_{21} > 0 \qquad \ldots\ldots\ldots\ldots \qquad (10.103)$$

Under spatially non-uniform perturbation, we again require $\lambda_{1,2} < 0$ to give a stable system. Thus we require

$$\hat{a}_{11} + \hat{a}_{22} < 0 \qquad \ldots\ldots\ldots\ldots \qquad (10.104)$$

and $$\hat{a}_{11}\hat{a}_{22} - a_{12}a_{21} > 0 \qquad \ldots\ldots\ldots\ldots \qquad (10.105)$$

Recall that $D_1, D_2 > 0$. Hence when (10.102) holds, (10.104) automatically holds. Thus, under the assumption (10.97.1), instability occurs only if (10.105) is violated, i.e.,

$$\begin{aligned} 0 &> \hat{a}_{11}\hat{a}_{22} - a_{12}a_{21} \\ &= (a_{11}-D_1k^2)(a_{22}-D_2k^2) \\ &= D_1D_2k^4 - (D_1a_{22} + D_2a_{11})k^2 + a_{11}a_{22} - a_{12}a_{21} \end{aligned} \qquad \ldots\ldots\ldots \qquad (10.105.5)$$

(10.105.5), along with (10.102) and (10.103), gives the sufficient and necessary condition for diffusive instability to occur in the system (10.99)+(10.100) which is stable in the absence of diffusion.

PART III INTRODUCING OUR MODEL

Let V denote the prey(Victim) population and E the predator(Exploiter) population. Without diffusion, V and E are functions of t only. V=V(t) and E=E(t). A general predator-prey model is usually of the form

$$\begin{cases} \dfrac{dV}{dt} = V\ F(V,E) \\ \dfrac{dE}{dt} = E\ G(V,E) \end{cases}, \text{ for some functions } F(V,E) \text{ and } G(V,E). \qquad \text{.........} \quad (2)$$

(We do not spend time to explain why such a form makes sense.)

Since predators are bad for prey, but prey are good for predators, we assume $\dfrac{\partial F}{\partial E} < 0$ and $\dfrac{\partial G}{\partial V} > 0$. We assume that F and G are some linear functions. So we consider

$$\begin{cases} \dfrac{dV}{dt} = V(K - \alpha V - \beta E) \\ \dfrac{dE}{dt} = E(-L + \gamma V - \delta E) \end{cases}, \text{ where } K, L, \beta \text{ and } \gamma > 0. \qquad \text{.........} \quad (3)$$

We set K, L > 0 so that for small predator and prey populations, prey population (V) increases because of the lack of predators, and predator population decreases because of the lack of prey. The sign of α and δ are important to the stability of the system. We will see this in (15.9).

The non-trivial equilibrium of (3) occurs at $V(t) = \tilde{V}$, $E(t) = \tilde{E}$ such that

$$\begin{cases} K - \alpha\tilde{V} - \beta\tilde{E} = 0 \\ -L - \gamma\tilde{V} - \delta\tilde{E} = 0 \end{cases},$$

$$\text{i.e., } \begin{cases} \tilde{V} = \dfrac{K\delta + L\beta}{\alpha\delta + \beta\gamma} \\ \tilde{E} = \dfrac{K\gamma + L\alpha}{\alpha\delta + \beta\gamma} \end{cases}, \quad \text{where we require } \tilde{V} > 0 \text{ and } \tilde{E} > 0. \qquad \text{............} \quad (4)$$

We will soon find conditions for $\tilde{V}$, $\tilde{E} > 0$.

Now linearize (3) around this equilibrium as we did in PART **II**. Using the notations in PART **II**, we have

$D_1 = D_2 = 0$,

$a_{11} = -\alpha\tilde{V}$, $a_{12} = -\beta\tilde{V}$, $a_{21} = \gamma\tilde{E}$, $a_{22} = -\delta\tilde{E}$

Therefore, like (10.101) ~ (10.105), linear stability of the equilibrium (4) occurs if and only if the two eigenvalues of the matrix

$$M = \begin{pmatrix} -\alpha\tilde{V} & -\beta\tilde{V} \\ \gamma\tilde{E} & -\delta\tilde{E} \end{pmatrix}$$

are both negative(or have negative real parts). This requires (10.103) and (10.102), i.e.,

$$\alpha\tilde{V}\,\delta\tilde{E} + \beta\tilde{V}\,\gamma\tilde{E} > 0; \quad \text{i.e.,} \quad \alpha\delta + \beta\gamma > 0 \quad \text{.........} \quad (6)$$

$$-\alpha\tilde{V} - \delta\tilde{E} < 0; \quad \text{i.e.,} \quad -\alpha(K\delta + L\beta) - \delta(K\gamma - L\alpha) < 0. \quad \text{.........} \quad (8)$$

Now we set

$$K\delta + L\beta > 0, \quad \text{and} \quad K\gamma - L\beta > 0 \quad \text{..........................} \quad (7a,b)$$

to fulfill the requirement in (4) that $\tilde{V}$, $\tilde{E} > 0$.

Since we have assumed that β and $\gamma > 0$ (see (3)), (6) implies that one of α and δ is positive and the other negative. In our model, we now assume that

$$\alpha < 0 < \delta \quad \text{..........................} \quad (15.9)$$

A negative α means that, as the prey population increases, the growth rate of the prey population also increases(or tends to increase). This is called an Allee effect. The practical reasons for the Allee effect are, for example, ease of finding mates and ease of surviving.

A positive δ means the predators are self-damped.

more explanation helpful

Now we add diffusion to our system. We assume a homogeneous environment with regard to habitat conditions, so that (3) describes the local behavior of the system. For the one-dimensional space, our system is of the form

$$\begin{cases} \dfrac{\partial V}{\partial t} = \mu \dfrac{\partial^2 V}{\partial x^2} + V(K - \alpha V - \beta E) \\ \dfrac{\partial E}{\partial t} = \nu \dfrac{\partial^2 E}{\partial x^2} + E(-L + \gamma V - \delta E) \end{cases}, \text{ where } \mu, \nu > 0.$$

(Remark: It's not our intention to explain why $\dfrac{\partial^2}{\partial x^2}$ represents diffusion.)

We still have the same uniform spatial equilibrium (4). We assume our previous conditions still hold, so that the equilibrium is stable in the absence of diffusion. Note that (6) is the same as (10.103) in PART II, (8) is the same as (10.102). For mathematical convenience, we set $L = 0$. This doesn't actually affect our previous conditions.

Therefore, our model is

$$
\left\{
\begin{array}{l}
\dfrac{\partial V}{\partial t} = \mu \dfrac{\partial^2 V}{\partial x^2} + V(K-\alpha V-\beta E) \\[2ex]
\dfrac{\partial E}{\partial t} = \nu \dfrac{\partial^2 E}{\partial x^2} + E(\gamma V-\delta E)
\end{array}
\right.
\qquad \ldots\ldots\ldots\ldots \qquad (10)
$$

where $V = V(x,t)$, the prey population,

$E = E(x,t)$, the predator population,

$\mu, \nu > 0$,		....	(10.1)
$K, \beta, \gamma > 0$,	by (3)	....	(10.2)
$\alpha < 0 < \delta$,	by (15.9)	....	(10.3)
$\alpha\delta + \beta\gamma > 0$,	by (6)	....	(10.4)
$-\alpha - \gamma < 0$.	by (8)	....	(10.5)

Part (IV) NONDMENSIONALIZATION AND STABILITY

We nondimensionalize it as following.

Let $\underline{e} = \frac{\delta}{K} E$, $\underline{v} = \frac{\gamma}{K} V$, $\underline{t} = Kt$, $\underline{x} = \sqrt{\frac{K}{\mu}}\, x$,

$\underline{k} = -\frac{\alpha}{\gamma} > 0$ by (10.2) and (10.3), $a = \frac{\beta}{\delta}$,

$\theta^2 = \frac{\mathbb{P}}{\mu}$, the diffusivity ratio. .... (16) & (21)

(Remark: I didn't use over-barred notations since it is hard to produce them by MS Word 4.0. The following underlined notations correspond to the over-barred notations used by Segel and Levin (1976).)

Then

$$\frac{\partial V}{\partial t} = \frac{K^2}{\gamma}\frac{\partial \underline{v}}{\partial \underline{t}}, \qquad \frac{\partial^2 V}{\partial x^2} = \frac{K^2}{\gamma\mu}\frac{\partial^2 \underline{v}}{\partial \underline{x}^2},$$

$$\frac{\partial E}{\partial t} = \frac{K^2}{\delta}\frac{\partial \underline{e}}{\partial \underline{t}}, \qquad \frac{\partial^2 E}{\partial x^2} = \frac{K^2}{\delta\mu}\frac{\partial^2 \underline{e}}{\partial \underline{x}^2}.$$

Therefore, (10) becomes

$$\begin{cases} \dfrac{\partial \underline{v}}{\partial \underline{t}} = \dfrac{\partial^2 \underline{v}}{\partial \underline{x}^2} + (1+\underline{k}\ \underline{v})\underline{v} - a\ \underline{e}\ \underline{v} \\ \dfrac{\partial \underline{e}}{\partial \underline{t}} = \theta^2 \dfrac{\partial^2 \underline{e}}{\partial \underline{x}^2} + \underline{e}\ \underline{v} - \underline{e}^2 \end{cases} \qquad \text{......................} \quad (19)$$

To find a spatially uniform equilibrium, set

$$(1+\underline{k}\ \underline{v})\,\underline{v} - a\,\underline{e}\,\underline{v} = 0$$

and

$$\underline{e}\,\underline{v} - \underline{e}^2 = 0$$

For non-trivial cases, $\underline{v} \neq 0 \neq \underline{e}$. Therefore,

$$1+\underline{k}\ \underline{v} - a\,\underline{e} = 0$$

$$\underline{v} - \underline{e} = 0$$

i.e., $\underline{v} = \dfrac{1}{a - \underline{k}}$

$\underline{e} = \dfrac{1}{a - \underline{k}}$

By (16), $a = \frac{\beta}{\delta}$ and $\underline{k} = -\frac{\alpha}{\gamma}$. We have

$$a - \underline{k} = \frac{\beta\gamma + \alpha\delta}{\delta\gamma} > 0 \text{ by (10.2), (10.3) and (10.4).}$$

Therefore we may assume that

$$a - \underline{k} = p^2 \quad (p > 0) \qquad \text{.......... (24)}$$

With the above substitution, the spatially uniform equilibrium is

$$\underline{v}(\underline{x}, \underline{t}) = \underline{e}(\underline{x}, \underline{t}) = p^{-2} \qquad \text{.......... (22)}$$

To study the stability of this equilibrium, assume we have some perturbation v and e:

$$v(\underline{x}, \underline{t}) = \underline{v}(\underline{x}, \underline{t}) - p^{-2}$$
$$e(\underline{x}, \underline{t}) = \underline{e}(\underline{x}, \underline{t}) - p^{-2}.$$

Substituting $v(\underline{x}, \underline{t})$ and $e(\underline{x}, \underline{t})$ into (19), using the relation (24), we get

$$\begin{aligned}
\frac{\partial v}{\partial \underline{t}} &= \frac{\partial^2 v}{\partial \underline{x}^2} + [1+\underline{k}(v+p^{-2})]\,(v+p^{-2}) - a(e+p^{-2})(v+p^{-2}) \\
&= \frac{\partial^2 v}{\partial \underline{x}^2} + (v+p^{-2}) + \underline{k}v^2 + 2\underline{k}vp^{-2} + \underline{k}p^{-4} - aev - ap^{-2}e - avp^{-2} - ap^{-4} \\
&= \frac{\partial^2 v}{\partial \underline{x}^2} + \underline{k}v^2 - ap^{-2}e - aev + 2\underline{k}vp^{-2} - (a-\underline{k})p^{-4} + v + p^{-2} - (\underline{k} + p^2)vp^{-2} \\
&= \frac{\partial^2 v}{\partial \underline{x}^2} + \underline{k}v^2 - ap^{-2}e - aev + 2\underline{k}vp^{-2} - p^2p^{-4} + v + p^{-2} - \underline{k}vp^{-2} - v \\
&= \frac{\partial^2 v}{\partial \underline{x}^2} + \underline{k}v^2 - ap^{-2}e - aev + \underline{k}vp^{-2}.
\end{aligned}$$

Similarly,

$$\frac{\partial e}{\partial \underline{t}} = \theta^2 \frac{\partial^2 e}{\partial \underline{x}^2} + p^{-2}v - p^{-2}e - e^2 + ev.$$

Our equations for perturbation is therefore

$$\begin{cases} -\dfrac{\partial v}{\partial \underline{t}} + \dfrac{\partial^2 v}{\partial \underline{x}^2} + \underline{k}p^{-2}v^2 - ap^{-2}e = aev - \underline{k}v^2 \\[2ex] -\dfrac{\partial e}{\partial \underline{t}} + \theta^2 \dfrac{\partial^2 e}{\partial \underline{x}^2} + p^{-2}v - p^{-2}e = e^2 - ev \end{cases} \qquad \text{.......... (27)}$$

Or, in matrix notation,

$$-\frac{\partial}{\partial \underline{t}}\begin{pmatrix} v \\ e \end{pmatrix} + \begin{pmatrix} k\ p^{-2} + \dfrac{\partial^2}{\partial \underline{x}^2} & -ap^{-2} \\ p^{-2} & -p^{-2} + \theta^2\dfrac{\partial^2}{\partial \underline{x}^2} \end{pmatrix}\begin{pmatrix} v \\ e \end{pmatrix} = \begin{pmatrix} aev-\underline{k}v^2 \\ e^2-ev \end{pmatrix} \qquad \text{.......... (27)}$$

Since it is too tedious to produce the underlined symbols, we will just use x , t and k instead of $\underline{x}$, $\underline{t}$ and $\underline{k}$ from now on. The x and t are not the same as those in (16). To study small perturbation, we linearize (27) around the equilibrium v=0, e=0. Using the notations in PART II, we have

$$F_1(v,e) = kp^{-2}v + kv^2 - aev - ap^{-2}e$$
$$F_2(v,e) = p^{-2}v + ev - p^{-2}e - e^2$$

Note that the equilibrium point is $(v^*, e^*) = (0,0)$. Then

$$a_{11} = \frac{\partial F_1(v^*, e^*)}{\partial v} = kp^{-2} + 2kv^* - ae^* = kp^{-2}$$

$$a_{12} = \frac{\partial F_1(v^*, e^*)}{\partial e} = -av^* - ap^{-2} = -ap^{-2}$$

$$a_{21} = \frac{\partial F_2(v^*, e^*)}{\partial v} = p^{-2} + e^* = p^{-2}$$

$$a_{22} = \frac{\partial F_2(v^*, e^*)}{\partial e} = v^* - p^{-2} - 2e^* = -p^{-2}$$

$D_1 = 1$

$D_2 = \theta^2$.

The linearized version of (27) is

$$-\frac{\partial}{\partial \underline{t}}\begin{pmatrix} v \\ e \end{pmatrix} + \begin{pmatrix} k\ p^{-2} + \frac{\partial^2}{\partial \underline{x}^2} & -ap^{-2} \\ p^{-2} & -p^{-2} + \theta^2 \frac{\partial^2}{\partial \underline{x}^2} \end{pmatrix}\begin{pmatrix} v \\ e \end{pmatrix} = 0 . \qquad \text{......................} \quad (27^*)$$

It's parabolic. As explained in PART II, we may assume the solution is of the form

$$\begin{cases} v(x,t) = \text{Const}_1\ e^{\sigma t + iqx} \\ e(x,t) = \text{Const}_2\ e^{\sigma t + iqx} \end{cases} \qquad \text{....................} \quad (30)$$

where Const_1 and Const_2 are some constants. If $\text{Const}_{1,2} = 0$, it is the equilibrium. If not, we have a perturbation, and (30), which is the solution to the linearized version of (27), gives an approximation to the future of predator and prey populations.

For convenience, we introduce a new parameter $m = \sqrt{a}$ . ... (31.5)

(Note: By (16)&(21), (10.2) and (10.3), $a > 0$.)

By (24), the parameters have the following relations.

$$a = m^2 , \qquad k = m^2 - p^2 \qquad \text{.......................} \quad (32)$$

By the condition (10.105.5), we get

$$\begin{aligned} &\theta^2 q^4 - (a_{22} + \theta^2 a_{11}) q^2 + a_{11}a_{22} - a_{12}a_{21} \\ &= \theta^2 q^4 - (-p^{-2} + \theta^2 kp^{-2})q^2 + kp^{-2}(-p^{-2}) - (-ap^{-2})(p^{-2}) \\ &= \theta^2 q^4 + p^{-2}(1-k\theta^2)q^2 + (a-k)p^{-4} \\ &= \theta^2 q^4 + p^{-2}(1-k\theta^2)q^2 + p^{-2} && \text{(by (24))} \\ &> 0 \quad \text{required to give stability.} \end{aligned}$$

Note that (10.102) is satisfied because of (10.5) and that (10.103) is satisfied because of (10.4). Thus, the equilibrium is stable if and only if

$$\theta^2 q^4 + p^{-2}(1-k\theta^2)q^2 + p^{-2} > 0 \qquad \text{..} \quad (31)$$

The region for (31) is the region **below** the shaded area in Figure 3. (Note: It's not interesting to explain why the region is like that in Figure 3. For a quick verification, note that θ=0 satisfies (31) and therefore stability occurs below the shaded area.)

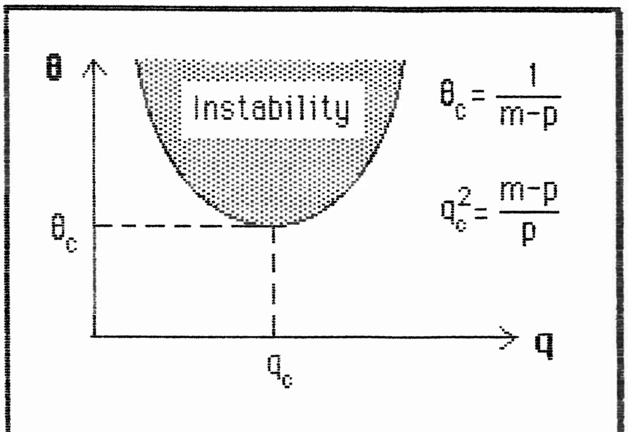


Figure 3. Stability Diagram

When $\theta < \theta_c$, our system is stable to all wave number q. θ_c is the smallest diffusivity ratio for which instability can possibly occur. To study diffusive instability, we will from now on restrict ourselves to the critical wave number q_c and study the behavior of our system for $\theta \approx \theta_c$.

Applying the results in PART II, we know that $\begin{pmatrix} Const_1 \\ Const_2 \end{pmatrix}$ is required to be an eigenvector associated with the eigenvalue σ of the matrix $\begin{pmatrix} k\ p^{-2} - q^2 & -ap^{-2} \\ p^{-2} & -p^{-2} - \theta^2 q^2 \end{pmatrix}$. σ is given by the following equation.

$$\begin{vmatrix} k\ p^{-2} - q^2 - \sigma & -ap^{-2} \\ p^{-2} & -p^{-2} - \theta^2 q^2 - \sigma \end{vmatrix} = 0,$$

i.e.,

$$\sigma^2 + (p^{-2} - kp^{-2} + \theta^2 q^2 + q^2)\sigma + ap^{-4} - kp^{-4} - p^{-2}k\theta^2 q^2 + p^{-2}q^2 + \theta^2 q^4 = 0.$$

Use the new parameters in (32), we can write the equation for σ as

$$\sigma^2 + (p^{-2} - kp^{-2} + \theta^2 q^2 + q^2)\sigma + (p^{-2} - p^{-2}k\theta^2 q^2 + p^{-2}q^2 + \theta^2 q^4) = 0. \qquad (34.5)$$

This is a quadratic equation in σ. With constant k, p and a, the solution σ depends on q and θ. As mentioned before, we are interested in the critical wave number $q=q_c$. Set $q=q_c$, then σ depends on θ only. As θ approaches its critical value θ_c, the two eigenvalues are given by

$$\sigma_1 = \frac{2(m-p)^2(\theta-\theta_c)}{p[1-(m-p)^2]} + O(\theta-\theta_c)^2,$$

$$\sigma_2 = -q_c^2(1+\theta_c^2) - p^{-2}(1-m^2+p^2) + O(\theta-\theta_c). \qquad (36)$$

The detail of this calculation is in Appendix 4.

The corresponding eigenvectors are

$$\underline{C}_1 = \begin{pmatrix} C_1 \\ K_1 \end{pmatrix} = \begin{pmatrix} m\theta_c \\ 1 \end{pmatrix} + O(\theta-\theta_c), \qquad \underline{k}_1 = \begin{pmatrix} m/\theta_c \\ 1 \end{pmatrix} + O(\theta-\theta_c). \qquad \text{............} \qquad (37a)$$

(Remark: I didn't derive (37a) myself since we can easily verify it directly.)

By (10.2), (10.3) and (16)&(21), $k > 0$. (Recall that we dropped the underline of k for convenience.) So $m > p$. .... (31.6)

By (10.5) and (16)&(21), $k = -\frac{\alpha}{\gamma} < 1$. In summary,

$$0 < k < 1; \quad \text{i.e.,} \quad 0 < m^2 - p^2 < 1 \,. \qquad \text{......................} \qquad (33)$$

Since both m and p are positive(by (31.5) and (24)) and $m > p$ (by (31.6)), we see, from (33), that $0 < m - p < 1$. Therefore, for $q=q_c$ and θ slightly greater than θ_c, we have, from (36), $\sigma_1 > 0$. .... (36.1)
By (36) and (33), $\sigma_2 < 0$ for $\theta \approx \theta_c$ . ... (36.2)

Consider (34.5) again. For $q \neq q_c$, the two roots σ_1 and σ_2 are certainly not given by (36). Let's see what we can say about σ_1 and σ_2 in this case. The region below the shaded area is for stability. This means the two eigenvalues σ_1 and σ_1 are negative. For $\theta_c \approx \theta$, unless $q \approx q_c$, the point (q_c,θ_c) does lie below the shaded area. Thus σ_1, $\sigma_2 < 0$. .... (37b)

We now discuss boundary conditions. For any bounded region $0 \leq x \leq L$ and some boundary conditions, (say, the zero flux boundary conditions $\left.\frac{\partial V}{\partial x}\right|_{(o,t)} = \left.\frac{\partial V}{\partial x}\right|_{(L,t)} = \left.\frac{\partial E}{\partial x}\right|_{(o,t)} = \left.\frac{\partial E}{\partial x}\right|_{(L,t)} = 0$,) the possible values for q are discrete (in fact, $\frac{n\pi}{L}$, for n = 0, 1, 2, 3, ...). Those values are determined by the Fourier expansion in x of any function on the interval [0, L]. Thus q is not always possible to reach q_c. In our following analysis, we assume that the region for x is such that q_c **is** a possible value for q. We further assume zero flux boundary conditions (or some other boundary conditions that give periodic solutions), so that the Fourier expansion of the solution contains $\cos(\frac{n\pi}{L}x)$'s, for which q_c is one of the $\frac{n\pi}{L}$'s (for some integer n). And therefore $\cos(q_c x)$ is one of the terms in the Fourier expansion.

(Remark: Since q can take many different values, (30) actually gives a kind of "eigenfunctions" of (27*). The general solution to (27*) is the sum of those "eigenfunctions". We will use this idea soon.)

Part (V) SUCCESSIVE APPROXIMATIONS

When $\theta > \theta_c$ (but $\approx \theta_c$) and $q=q_c$, the system is unstable. We will consider some perturbation. Any arbitrary perturbation function (i.e., a solution which starts near the equilibrium point) can be expanded in Fourier series. We are interested in $q=q_c$. Therefore, we only pick up the $\cos(q_c x)$ term in the Fourier expansion (thus our solution to the linearized system will consist of only one "eigenfunction", not a sum of many "eigenfunctions".) That's why Segel and Levin call such thing "the most dangerous sinusoidal mode." Therefore, our work is to find an approximate solution to (27) with the initial condition (a small perturbation to the equilibrium $v = e = 0$):

$$v(x,0) = \varepsilon C_1 \cos(q_c x)$$
$$e(x,0) = \varepsilon K_1 \cos(q_c x) \qquad \text{......} \qquad (42)$$

where $\begin{pmatrix} C_1 \\ K_1 \end{pmatrix}$ is the eigenvector associated with the eigenvalue σ_1. The coefficients C_1 and K_1 are not artificial since we knew from linear theory that a solution to the linearized system has to have such coefficients.

The linearized system (27*) is valid as long as the linear approximation is valid. It can only approximate v and e near the equilibrium 0. For θ slightly greater than θ_c, the solution to (27*) was seen to grow exponentially without bound. Therefore it is an approximation to the solution to (27) for only a short period of time. So far, we don't know the behavior of (27) for large t. Now we use iteration method to approximate the solution to (27). We try to obtain $v_1, v_2, v_3, \ldots \rightarrow v$, and $e_1, e_2, e_3, \ldots \rightarrow e$. We want to see if it is possible for the solution to the nonlinear system (27) **<u>not</u>** to grow without bound. In particular, we seek a solution that is of order $O(\varepsilon)$ (the same order of the initial state) <u>uniformly in t</u>. If such a solution exists, we can set up the iteration to be (from (27)):

$$-\frac{\partial v_1}{\partial t} + \frac{\partial^2 v_1}{\partial x^2} + kp^{-2}v_1 - ap^{-2}e_1 = O(\varepsilon^2)$$
$$-\frac{\partial e_1}{\partial t} + \theta^2 \frac{\partial^2 e_1}{\partial x^2} + p^{-2}v_1 - p^{-2}e_1 = O(\varepsilon^2) \qquad \text{......} \qquad (40)$$

and, for $i = 2, 3, 4, \ldots$,

$$-\frac{\partial v_i}{\partial t} + \frac{\partial^2 v_i}{\partial x^2} + kp^{-2}v_i - ap^{-2}e_i = av_{i-1}e_{i-1} - kv_{i-1}^2 + O(\varepsilon^{i+1})$$

$$-\frac{\partial e_i}{\partial t} + \theta^2 \frac{\partial^2 e_i}{\partial x^2} + p^{-2} v_i - p^{-2} e_i = e_{i-1}^2 - e_{i-1} v_{i-1} + O(\varepsilon^{i+1}) \qquad \text{.......... (41)}$$

We stress this point again that we may write those big-O notations in (40) and (41) because of the assumption that the solution will be of order $O(\varepsilon)$ uniformly in t. Thus any approximation will be valid only when the approximation is $O(\varepsilon)$. When the approximating function gets large, it is not valid anymore.

The Fourier expansion of the solution to the (almost) linear system (40) will consist of the $\cos(q_c x)$ term only. (That's why the initial value (42) is like that.) We also know that the coefficients of the solution to a linear system should give an eigenvector. Therefore, with our initial condition, the solution to (40) is of the form

$$v_1(x,t) = \varepsilon C_1 A(t) \cos(q_c x)$$
$$e_1(x,t) = \varepsilon K_1 A(t) \cos(q_c x) \qquad \text{.......... (44)}$$

where $\begin{pmatrix} C_1 \\ K_1 \end{pmatrix} = \begin{pmatrix} m\theta \\ 1 \end{pmatrix}$ is the eigenvector associated with the eigenvalue σ_1.(See 37a)

(Note: If we omit the $O(\varepsilon^2)$ at the right hand side of (40), we get a linear system as (27*) and A(t) is in fact $e^{\sigma_1 t}$.)

Substituting (44) into (40) with $\begin{pmatrix} C_1 \\ K_1 \end{pmatrix}$ being the eigenvector, we obtain

$$-\varepsilon C_1 \cos(q_c x) A'(t) + \varepsilon \sigma_1 C_1 \cos(q_c x) A(t) = O(\varepsilon^2),$$
$$-\varepsilon K_1 \cos(q_c x) A'(t) + \varepsilon \sigma_1 K_1 \cos(q_c x) A(t) = O(\varepsilon^2).$$

Therefore,

$$-A'(t) + \sigma_1 A(t) = O(\varepsilon) \qquad \text{.......... (45.5)}$$

where $\sigma_1 > 0$ since $\theta > \theta_c$. (See (36.1))

The general solution to (45.5) is

$$A(t) = [\int_0^t -O(\varepsilon)\ e^{-\sigma_1 t}\ dt + \text{Const.}]\ e^{\sigma_1 t}.$$

where Const. is determined by the initial condition. In general, with the particular Const. and arbitrary $O(\varepsilon)$,

$[\int_0^t -O(\varepsilon)\ e^{-\sigma_1 t}\ dt + \text{Const.}]$ does not go to 0 or is greater than $O(e^{-\sigma_1 t})$ as $t \to \infty$.

This implies that A(t) is essentially proportional to $e^{\sigma t}$ for some $\sigma > 0$ as $t \to \infty$. Since (40) is only valid for v and e of order $O(\varepsilon)$, our first approximation is valid, within an error of $O(\varepsilon)$, for only some finite time interval [0,T]. For the 2nd approximation, the right hand side of (41) will contain terms proportional to $e^{\sigma t}e^{\sigma t} = e^{2\sigma t}$, corresponding to $v_1 e_1$, v_1^2 and e_1^2. The solution A(t) will then contain terms proportional to $e^{2\sigma t}$. We see that the "higher" approximations would be valid within the same limited time period as the first approximation. We conclude that either there is no bounded solution (in which case our iteration scheme (40)+(41) cannot possibly give an approximation anyway,) or our assumed solution (44) is not appropriate to fit the iteration scheme (in which case the solution (44) does not tell us anything about the real solution for large t.) Let's change the form of (44). If we can find approximations that do not grow without bound (or, specifically, approximations that are of order $O(\varepsilon)$ uniformly in time,) then we can say that a solution to (27) of order $O(\varepsilon)$ uniformly in time **exists**. If we still can not find such approximations, we still don't know what the real solution looks like.

Anyway, we will change the assumption (44). The difficulty of our previous approximation is that we always assume the solution is a polynomial of ε and therefore it can not possibly suppress an exponential growth. It is a common problem in perturbation theory. One of the techniques to deal with this problem is called Multiple-Scale Method. Now assume

$$A = A(t_0, t_1, t_2, \ldots), \text{ where } t_i = \varepsilon^i\, t. \qquad \ldots\ldots\ldots\ldots \quad (45)$$

t_0 is the usual time scale. t_1 is a slower time scale. t_2 is an even slower time scale than t_1. Or, we can say that t_0 is the fast time, t_2 is the intermediate time, t_3 is the slow time, and so on.

Then

$$\frac{\partial A}{\partial t} = \frac{\partial A}{\partial t_0} + \varepsilon^1 \frac{\partial A}{\partial t_1} + \varepsilon^2 \frac{\partial A}{\partial t_2} + \ldots$$

We shall require A to be such that the successive approximations are all of order O(1) <u>uniformly in time</u> so that our approximated solutions to (27) are of order $O(\varepsilon)$ and are thus valid for all t.

Therefore, (40) becomes

$$-\varepsilon\, C_1 \cos(q_c x) \frac{\partial A}{\partial t_0} + \varepsilon\, \sigma_1\, C_1 \cos(q_c x)\, A = O(\varepsilon^2)$$

$$-\varepsilon\, K_1 \cos(q_c x) \frac{\partial A}{\partial t_0} + \varepsilon\, \sigma_1 K_1 \cos(q_c x)\, A = O(\varepsilon^2)$$

i.e.,

$$-\frac{\partial A}{\partial t_0} + \sigma_1\, A = O(\varepsilon) \qquad \ldots\ldots\ldots \quad (45.6)$$

To avoid terms with exponential growth (like that in (45.5)) in the solution , we set

$$\frac{\partial A}{\partial t_0} = 0, \qquad \sigma_1 = O(\varepsilon).$$

Note that this satisfies the equation (45.6). And A is O(1) on the fast time scale.

Our first approximation is therefore

$$v_1(x,t) = \varepsilon\, C_1\, A(t_1, t_2, \ldots) \cos(q_c x)$$

$$e_1(x,t) = \varepsilon\, K_1\, A(t_1, t_2, \ldots) \cos(q_c x) \qquad \ldots\ldots\ldots\ldots\ldots\ldots \quad (44)$$

where $\dfrac{\partial A}{\partial t_0} = 0$ and $\sigma_1 = O(\varepsilon)$. $\qquad \ldots\ldots\ldots\ldots\ldots\ldots \quad$ (46a,b)

Now we do the 2nd approximation. We solve, from (41), the system

$$-\frac{\partial v_2}{\partial t} + \frac{\partial^2 v_2}{\partial x^2} + kp^{-2}v_2 - ap^{-2}e_2 = av_1e_1 - kv_1{}^2 + O(\varepsilon^3)$$

$$-\frac{\partial e_2}{\partial t} + \theta^2 \frac{\partial^2 e_2}{\partial x^2} + p^{-2}v_2 - p^{-2}e_2 = e_1{}^2 - e_1v_1 + O(\varepsilon^3)$$

We have, from our first approximation (44),

$$av_1e_1 - kv_1{}^2 = a\varepsilon m\theta\, A\cos(q_c x)\, \varepsilon\, 1\, A\cos(q_c x) - k\,\varepsilon^2 m^2\theta^2 A^2\cos^2(q_c x)$$

$$= m\theta\,(a-km\theta)\varepsilon^2A^2\cos^2(q_c x)$$

$$= m\theta\,(a-km\theta)\varepsilon^2A^2\,\frac{1}{2}\,(1+\cos(2q_c x))\,.$$

Similarly,

$$e_1{}^2 - e_1v_1 \quad = (1-m\theta)\varepsilon^2A^2\,\frac{1}{2}\,(1+\cos(2q_c x))\,.$$

Thus the system (41) becomes

$$-\frac{\partial v_2}{\partial t} + \frac{\partial^2 v_2}{\partial x^2} + kp^{-2}v_2 - ap^{-2}e_2 = \frac{1}{2}\,\hat{v}_2\varepsilon^2A^2\,(1+\cos(2q_c x)) + O(\varepsilon^3)$$

$$-\frac{\partial e_2}{\partial t} + \theta^2 \frac{\partial^2 e_2}{\partial x^2} + p^{-2}v_2 - p^{-2}e_2 = \frac{1}{2}\,\hat{e}_2\,\varepsilon^2A^2\,(1+\cos(2q_c x)) + O(\varepsilon^3)$$

$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (47)$

where $\hat{v}_2 = m\theta\,(a-km\theta)$ and $\hat{e}_2 = 1-m\theta$. $\qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (48)$

Since (47) is a particular case of (40), the solution to (47) will contain the solution to (40), i.e.,

$$v_2(x,t) = \varepsilon\, C_1\, A(t_1, t_2, \ldots) \cos(q_c x) + \ldots$$

$$e_2(x,t) = \varepsilon\, K_1\, A(t_1, t_2, \ldots) \cos(q_c x) + \ldots$$

The right hand side of (47) contains ε^2A^2 and $\varepsilon^2A^2\cos(2q_c x)$. Those terms introduce ε^2A^2 and $\varepsilon^2A^2\cos(2q_c x)$ to the solution. Therefore, the solution is of the form

$$v_2(x,t) = \varepsilon C_1 A\cos(q_c x) + \varepsilon^2A^2\,(C_0+C_2\cos(2q_c x)) + O(\varepsilon^2),$$

$$e_2(x,t) = \varepsilon K_1 A\cos(q_c x) + \varepsilon^2A^2\,(K_0+K_2\cos(2q_c x)) + O(\varepsilon^2),$$

where C_0, K_0, C_1 and K_1 should be chosen such that those new terms satisfy (47). Note that we have to set the error to be $O(\varepsilon^2)$ in stead of $O(\varepsilon^3)$ to satisfy the initial condition. By the argument in Appendix 2 of Segel and Levin (1976), we can say

$$v_2(x,t) = \varepsilon C_1 A\cos(q_c x) + \varepsilon^2A^2\,(C_0+C_2\cos(2q_c x)) + O(\varepsilon^2A^2e^{-\sigma t})$$

$e_2(x,t) = \varepsilon K_1 A \cos(q_c x) + \varepsilon^2 A^2 (K_0 + K_2 \cos(2q_c x)) + O(\varepsilon^2 A^2 e^{-\sigma t})$,

for some $\sigma > 0$. .... (49)

(Remark: Appendix 2 of Segel and Levin is not hard to understand, but the notations are hard to follow. To be concise, I will not explain that appendix. I will just use the above result in (49).)

Now we determine C_0, K_0, C_1 and K_1. As just said, we require

$$\begin{cases} v(x,t) = \varepsilon^2 A^2 \,(C_0 + C_2 \cos(2q_c x)) \\ e(x,t) = \varepsilon^2 A^2 \,(K_0 + K_2 \cos(2q_c x)) \end{cases}$$

to be a particular solution to (47). To equate the coefficients of likely powers of $\cos(q_c x)$, we divide it into two parts. We require

$$\begin{cases} v(x,t) = \varepsilon^2 A^2 C_0 \\ e(x,t) = \varepsilon^2 A^2 K_0 \end{cases} \qquad \text{.. (49.5)}$$

be a solution to

$$\begin{cases} -\dfrac{\partial v}{\partial t} + \dfrac{\partial^2 v}{\partial x^2} + kp^{-2}v - ap^{-2}e = \dfrac{1}{2}\hat{v}_2 \;\varepsilon^2 A^2 \\ -\dfrac{\partial e}{\partial t} + \theta^2 \dfrac{\partial^2 e}{\partial x^2} + p^{-2}v - p^{-2}e = \dfrac{1}{2}\hat{e}_2 \,\varepsilon^2 A^2 \end{cases} \qquad \text{.................... (49.6)}$$

and $\begin{cases} v(x,t) = \varepsilon^2 A^2 C_2 \cos(2q_c x) \\ e(x,t) = \varepsilon^2 A^2 K_2 \cos(2q_c x) \end{cases}$ be a solution to

$$\begin{cases} -\dfrac{\partial v}{\partial t} + \dfrac{\partial^2 v}{\partial x^2} + kp^{-2}v - ap^{-2}e = \dfrac{1}{2}\hat{v}_2 \,\varepsilon^2 A^2 \cos(2q_c x) \\ -\dfrac{\partial e}{\partial t} + \theta^2 \dfrac{\partial^2 e}{\partial x^2} + p^{-2}v - p^{-2}e = \dfrac{1}{2}\hat{e}_2 \,\varepsilon^2 A^2 \cos(2q_c x) \end{cases}$$

Substituting (49.5) into (49.6), we obtain

$$-\varepsilon^2\, 2A \frac{\partial A}{\partial t} C_0 + kp^{-2}C_0 \varepsilon^2 A^2 - ap^{-2}K_0 \varepsilon^2 A^2 = \frac{1}{2}\hat{v}_2 \varepsilon^2 A^2$$

Equating the coefficients of A and A^2, we get

$$C_0 = 0,$$

$$K_0 = \frac{-\dfrac{1}{2}\overset{+}{v}_2 \,\varepsilon^2 A^2}{ap^{-2}\,\varepsilon^2 A^2} = -\frac{1}{2}\frac{m\theta(a-km\theta)}{ap^{-2}} = -\frac{1}{2}\frac{m\theta\left(m^2-(m^2-p^2)m\,\dfrac{1}{m-p}\right)}{m^2p^{-2}}$$

$$= \frac{1}{2}\theta\, p^3 \qquad \text{................................ (50a)}$$

Similarly,

$$C_2 = \frac{p^3}{18(m-p)} 4\theta^2 q_c{}^2 m^2$$

$$K_2 = \frac{p^3}{18(m-p)}(1+4q_c{}^2) \qquad \text{................................ (50b)}$$

With C_0, C_2, K_0 and K_2 given by (50a,b), we are going to substitute (49) into (47). Since C_0, C_2, K_0 and K_2 are chosen such that the middle term of (49) is a particular solution to (47) already, we only need to take care of the first term of (49) and, for the right hand side of (47), the error $O(\varepsilon^3)$. We easily obtain

$$-\varepsilon[\varepsilon^1 \frac{\partial A}{\partial t_1} + \varepsilon^2 \frac{\partial A}{\partial t_2} + \ldots] C_1 \cos(q_c x) + \varepsilon A \sigma_1 C_1 \cos(q_c x) = O(\varepsilon^3)$$
$$-\varepsilon[\varepsilon^1 \frac{\partial A}{\partial t_1} + \varepsilon^2 \frac{\partial A}{\partial t_2} + \ldots] K_1 \cos(q_c x) + \varepsilon A \sigma_1 K_1 \cos(q_c x) = O(\varepsilon^3)$$

where we used the assumption that $\begin{pmatrix} C_1 \\ K_1 \end{pmatrix}$ is the eigenvector associated with the eigenvalue σ_1. (See 44)
Rearranging the terms, we obtain

$$(-\varepsilon^2 \frac{\partial A}{\partial t_1} + \varepsilon \sigma_1 A) C_1 \cos(q_c x) = O(\varepsilon^3)$$
$$(-\varepsilon^2 \frac{\partial A}{\partial t_1} + \varepsilon \sigma_1 A) K_1 \cos(q_c x) = O(\varepsilon^3) \quad \ldots\ldots\ldots\ldots \quad (51)$$

Therefore,

$$-\varepsilon \frac{\partial A}{\partial t_1} + \sigma_1 A = O(\varepsilon^2) \quad \ldots\ldots\ldots\ldots \quad (51b)$$

The solution will contain terms that grows exponentially like that in (45.5). To suppress these terms, we set

$$\frac{\partial A}{\partial t_1} = 0, \qquad \sigma_1 = O(\varepsilon^2) \quad \ldots\ldots\ldots\ldots \quad (52ab)$$

This satisfies the equation (51b) and A is O(1) on the intermediate time scale t_1.

Our second approximation therefore gives (49):

$$v_2(x,t) = \varepsilon C_1 A \cos(q_c x) + \varepsilon^2 A^2 (C_0 + C_2 \cos(2q_c x)) + O(\varepsilon^2 A^2 e^{-\sigma t})$$
$$e_2(x,t) = \varepsilon K_1 A \cos(q_c x) + \varepsilon^2 A^2 (K_0 + K_2 \cos(2q_c x)) + O(\varepsilon^2 A^2 e^{-\sigma t}))$$

where

$$\frac{\partial A}{\partial t_1} = 0, \qquad \sigma_1 = O(\varepsilon^2) \qquad \text{by(52ab)}$$
$$C_0 = 0, \qquad \text{by(50a)}$$
$$K_0 = \frac{1}{2} \theta p^3 \qquad \text{by(50a)}$$
$$C_2 = \frac{p^3}{18(m-p)} 4\theta^2 q_c^2 m^2 \qquad \text{by(50b)}$$
$$K_2 = \frac{p^3}{18(m-p)} (1+4q_c^2) \qquad \text{by(50b)}$$

We now do the third approximation.

We need to solve, from (41),

$$-\frac{\partial v_3}{\partial t}+\frac{\partial^2 v_3}{\partial x^2}+kp^{-2}v_3-ap^{-2}e_3=av_2e_2-kv_2^2+O(\varepsilon^4) \quad \text{.......... (53.1)}$$

$$-\frac{\partial e_3}{\partial t}+\theta^2\,\frac{\partial^2 e_3}{\partial x^2}+p^{-2}v_3-p^{-2}e_3=e_2^2-e_2v_2+O(\varepsilon^4) \quad \text{.......... (53.2)}$$

By (49),

$av_2e_2 - kv_2^2$

$=a\,[\,\varepsilon C_1A\cos(q_cx)+\varepsilon^2A^2(C_0+C_2\cos(2q_cx))\,]\,[\,\varepsilon K_1A\cos(q_cx)+\varepsilon^2A^2(K_0+K_2\cos(2q_cx)\,]$

$\quad -k[\,\varepsilon C_1A\cos(q_cx)+\varepsilon^2A^2(C_0+C_2\cos(2q_cx))\,]^2$

$=a\,[\,\varepsilon^3A^3C_1K_0\cos(q_cx)+\varepsilon^3A^3C_1K_2\cos(q_cx)\cos(2q_cx)+\varepsilon^3A^3C_0K_1\cos(q_cx)$

$\qquad +\varepsilon^3A^3C_2K_1\cos(q_cx)\cos(2q_cx)\,]$

$\quad -k[\,2\varepsilon^3A^3C_1C_0\cos(q_cx)+2\varepsilon^3A^3C_1C_2\cos(q_cx)\cos(2q_cx)\,]$

$\quad$ + terms not proportional to $\cos(q_cx)$.

$=\varepsilon^3A^3\cos(q_cx)\,[\,a\,(\,C_1K_0+\frac{1}{2}C_1K_2+C_0K_1+\frac{1}{2}C_2K_1)-k\,(\,2C_0C_1+C_1C_2)\,]$

$\quad$ + terms not proportional to $\cos(q_cx)$.

$=\varepsilon^3A^3\cos(q_cx)\,[\,a\,(\,m\theta K_0+\frac{1}{2}m\theta K_2+C_0+\frac{1}{2}C_2)-k\,(\,2m\theta C_0+m\theta C_2)$

$\quad$ + terms not proportional to $\cos(q_cx)$. (by(37a))

Let $\quad \hat{v}_3=a\,(\,m\theta K_0+\frac{1}{2}m\theta K_2+C_0+\frac{1}{2}C_2)-k\,(\,2C_0C_1+C_1C_2)$.

Now we can write (53.1) as

$$-\frac{\partial v_3}{\partial t}+\frac{\partial^2 v_3}{\partial x^2}+kp^{-2}v_3-ap^{-2}e_3=\varepsilon^3A^3\cos(q_cx)\,\hat{v}_3$$

+ terms not proportional to $\cos(q_cx)$.
$+\,O(\varepsilon^4)$ ....(53)

Similarly, we can write (53.2) as

$$-\frac{\partial e_3}{\partial t}+\theta^2\,\frac{\partial^2 e_3}{\partial x^2}+p^{-2}v_3-p^{-2}e_3=\varepsilon^3A^3\cos(q_cx)\,\hat{e}_3$$

+ terms not proportional to $\cos(q_cx)$.
$+\,O(\varepsilon^4)$ ....(53)

where

$$\hat{e}_3=(2K_0+K_2)-(m\theta K_0+\frac{1}{2}m\theta K_2+C_0+\frac{1}{2}C_2)\,.$$

(Remark: The $\hat{v}_3$ and $\hat{e}_3$ given under (54) on page 139 in Segel and Levin's paper are wrong. Some terms are mistakenly interchanged.)

Now recall that $\underline{C}_1 = \begin{pmatrix} C_1 \\ K_1 \end{pmatrix} = \begin{pmatrix} m\theta \\ 1 \end{pmatrix}$ is the eigenvector associated with the eigenvalue σ_1, and $\underline{K}_1 = \begin{pmatrix} m/\theta \\ 1 \end{pmatrix}$ is the eigenvector associated with the eigenvalue σ_2.(See 44)
(Remark: Do not confuse $\underline{C}_1$ and $\underline{K}_1$ with C_0, C_1, C_2, K_0, K_1 and K_2. This is one place where Segel and Levin used confusing notations.)

Also recall that, when $\theta \approx \theta_c$ and $\theta > \theta_c$, $\sigma_1 > 0$ and $\sigma_2 < 0$ (see (36.1) and (36.2)). We expand $\begin{pmatrix} \hat{v}_3 \\ \hat{e}_3 \end{pmatrix}$ in terms of the two eigenvectors.

$$\begin{pmatrix} \hat{v}_3 \\ \hat{e}_3 \end{pmatrix} = \gamma\underline{C}_1 + \delta\underline{K}_1 = \gamma\begin{pmatrix} C_1 \\ K_1 \end{pmatrix} + \delta\begin{pmatrix} m/\theta \\ 1 \end{pmatrix},$$

for some real numbers γ and δ. .... (55)

By superposition principle, the solution to (53) is the sum of the solutions to the following two systems of equations.

$$\begin{cases} -\dfrac{\partial v_3}{\partial t} + \dfrac{\partial^2 v_3}{\partial x^2} + kp^{-2}v_3 - ap^{-2}e_3 = \varepsilon^3 A^3 \cos(q_c x)\ \delta\dfrac{m}{\theta} \\ -\dfrac{\partial e_3}{\partial t} + \theta^2\dfrac{\partial^2 e_3}{\partial x^2} + p^{-2}v_3 - p^{-2}e_3 = \varepsilon^3 A^3 \cos(q_c x)\ \delta \end{cases}$$

.... (53.1)

$$\begin{cases} -\dfrac{\partial v_3}{\partial t} + \dfrac{\partial^2 v_3}{\partial x^2} + kp^{-2}v_3 - ap^{-2}e_3 = \varepsilon^3 A^3 \cos(q_c x)\ \gamma C_1 + \ldots + O(\varepsilon^4) \\ -\dfrac{\partial e_3}{\partial t} + \theta^2\dfrac{\partial^2 e_3}{\partial x^2} + p^{-2}v_3 - p^{-2}e_3 = \varepsilon^3 A^3 \cos(q_c x)\ \gamma K_1 + \ldots + O(\varepsilon^4) \end{cases}$$

.... (53.2)

where "..." denotes the terms (which is of order $O(\varepsilon^3)$) not proportional to $\cos(q_c x)$.

We solve (53.1) first. The form of (53.1) suggests we try eigenvalue method. Assume the solution is of the form

$$v(x,t) = \varepsilon^3 B(t)\,\frac{m}{\theta}\cos(q_c x)$$

$$e(x,t) = \varepsilon^3 B(t)\ 1\ \cos(q_c x),$$

for some function $B(t)$. Again, recall that $\underline{K}_1 = \begin{pmatrix} m/\theta \\ 1 \end{pmatrix}$ is the eigenvector associated with the eigenvalue σ_2. Substituting the above $v(x,t)$ and $e(x,t)$ into (53.2), we obtain

$$\begin{cases} (-\varepsilon^3 \dfrac{\partial B}{\partial t} + \varepsilon^3\sigma_2 B)\ \dfrac{m}{\theta}\ \cos(q_c x) = \varepsilon^3 B^3 \cos(q_c x)\ \delta \dfrac{m}{\theta} \\ (-\varepsilon^3 \dfrac{\partial B}{\partial t} + \varepsilon^3\sigma_2 B)\ \cos(q_c x) = \varepsilon^3 B^3 \cos(q_c x)\ \delta \end{cases}$$

Therefore,

$$-\frac{\partial B}{\partial t} + \sigma_2 B = B^3\,\delta$$

The solution is $B(t) = \sqrt{\dfrac{\sigma_2}{\delta - C\ e^{-2\sigma_2 t}}}$, where C is an arbitrary constant.

We see that when $t > O(1)$, $e^{-2\sigma_2 t}$ becomes the dominant term in $B(t)$ since $\sigma_2 = O(1)$ and < 0 (see (36) and (36.2)). Thus the solution, $\begin{cases} v(x,t) = \varepsilon^3 B(t)\ \dfrac{m}{\theta}\ \cos(q_c x) \\ e(x,t) = \varepsilon^3 B(t)\ 1\ \cos(q_c x) \end{cases}$, to (53.1) is essentially proportional to $e^{\sigma_2 t}$ ($= \sqrt{e^{-2\sigma_2 t}}$) when $t > O(1)$. Therefore we will omit this rapidly decaying solution to (53.1).

(**Remark**: Since we may omit the solution to (53.1), we say that the δ contribution in (55) is not central. **"The δ contribution ..." is what was meant to say under (56) on page 140 of the paper, not "the γ contribution"!)**

Therefore, our third approximation is essentially given by (53.2) only. Our second approximation (49) (along with (50a), (50b) and (52ab)) should be a solution to (53.1) within an error of $O(\varepsilon^3)$. Substituting (49) into (53.1) and omitting that exponentially decaying error $O(\varepsilon^2 A^2 e^{-\sigma t})$ in our second approximation, we obtain

$$\begin{aligned} &(-\varepsilon^3 \frac{\partial A}{\partial t_2} + \varepsilon\sigma_1 A)\ C_1 \cos(q_c x) = \varepsilon^3 A^3 \cos(q_c x)\ \gamma C_1 + \ldots + O(\varepsilon^4) \\ &(-\varepsilon^3 \frac{\partial A}{\partial t_2} + \varepsilon\sigma_1 A)\ K_1 \cos(q_c x) = \varepsilon^3 A^3 \cos(q_c x)\ \gamma K_1 + \ldots + O(\varepsilon^4) \qquad \ldots\ldots \quad (58) \end{aligned}$$

where "..." denotes some terms (which is of order $O(\varepsilon^3)$) not proportional to $\cos(q_c x)$. We need to equate the corresponding coefficients of $\cos(q_c x)$ and possibly $\cos(2q_c x)$, $\cos(3q_c x)$, etc., in "...". To do the latter part, we have to assume some additional quantity into our second approximation, like we did when we move from the first approximation to the second approximation (see my argument between (48) and (49)). We don't do it here (and hence we are not going to get a higher order approximation than the second one, but we will get more information about A.) We will just equate the coefficients of $\cos(q_c x)$ in (58) and obtain an equation for A. Therefore,

$$-\varepsilon^2 \frac{\partial A}{\partial t_2} + \sigma_1 A = \varepsilon^2 A^3 \gamma \qquad \ldots\ldots\ldots\ldots \quad (58.1)$$

Solve for $\frac{\partial A}{\partial t_2}$, we get

$$\frac{\partial A}{\partial t_2} = \frac{\sigma_1}{\varepsilon^2} A - A^3 \qquad \text{..................} \quad (58.2)$$

By (52b). $\sigma_1 = O(\varepsilon^2)$. By (36), $\sigma_1 = O(\theta - \theta_c) + O(\theta - \theta_c)^2$. .... (59)

Thus $\theta - \theta_c = O(\varepsilon^2)$ .... (60)

and $\sigma_1 = O(\varepsilon^2) + O(\varepsilon^4) = \sigma^* \varepsilon^2 + O(\varepsilon^4)$, for some $\sigma^* = O(1)$. .... (61)

By (36), $\mathrm{sgn}(\sigma^*) = \mathrm{sgn}(\theta - \theta_c)$.

Substituting (61) into (58.2), we get

$$\frac{\partial A}{\partial t_2} = \sigma^* A - A^3 \gamma \qquad \text{....................} \quad (62)$$

Either by phase plane analysis or by solving (62) directly as an o.d.e. in t_2 (the solution is $A = \sqrt{\frac{\sigma^*}{\gamma - C\ e^{-2\sigma^* t_2}}}$ where C is any arbitrary quantity not depending on t_2 ,) we see that $A \to \sqrt{\frac{\sigma^*}{\gamma}}$ as $t_2 \to \infty$ for $\sigma^* > 0$ (i.e., θ slightly greater than θ_c.)

> Thus our third approximation tells us
>
> $$A \to \sqrt{\frac{\sigma^*}{\gamma}} \text{ as } t_2 \to \infty \qquad \text{......................} \quad (63)$$

For a summary, recall the assumption when we set up (40) and (41) that (40) and (41) are valid only when the solutions are $O(\varepsilon)$. We see that our approximations indeed give an approximated solution of order $O(\varepsilon)$ uniformly in t in the following fashion.

(0) The approximated solution is of the form (49), which gives a wave-like spatial distribution. (See the 2nd approximation.)

(i) Equation (46a) shows that A does not change on the fast $O(1)$ time scale.

(ii) Equation (52) shows that A also does not change on the intermediate $O(\varepsilon^{-1})$ time scale.

(iii) (63) shows that on the slow $O(\varepsilon^{-2})$ time scale A approaches to an $O(1)$ equilibrium value $\sqrt{\frac{\sigma^*}{\gamma}}$. Thus the amplitude of the solution is $O(\varepsilon)$ uniformly in time. This is illustrated in the following Fig. 4(a).

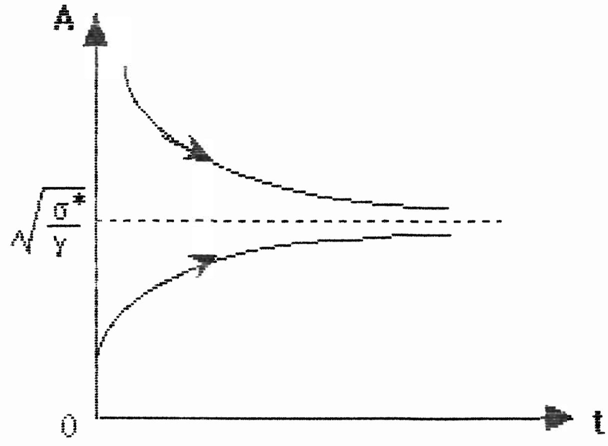


Fig. 4(a). Possible curves A(t)

Now we can see the difference between linear and nonlinear theory. Recall that the linear theory predicts that the solution is of the form (30) where σ was seen to be the eigenvalue and A(t) is the $e^{\sigma t}$ part of (30). (30) is the solution of the linearized system (27*). For $q=q_c$ and θ slightly greater than θ_c, we have $\sigma_1 > 0$ and $\sigma_2 < 0$ (see (36.1) and (36.2)). Therefore the A(t) part in the solution is essentially $e^{\sigma_1 t}$ as $t->\infty$. If we require the ε in our initial condition to satisfy (59)~(61), then A(t) is essentially $e^{\sigma_1 t} = e^{\sigma^* \varepsilon^2 t}$ as $t->\infty$. We *knew* that this would not be valid since it is too far away form the equilibrium and therefore the linearized system no longer gives an approximation to the nonlinear system.

Part (VI) NUMERICAL EXAMPLE

Mimura and Murray (1978) gave a numerical example for an initial and boundary value problem which is diffusionally unstable. In our notations, the problem is

$$\begin{cases} \dfrac{\partial V}{\partial t} = \beta \dfrac{\partial^2 V}{\partial x^2} + V\ [f(V)-E] \\ \dfrac{\partial E}{\partial t} = \dfrac{\partial^2 E}{\partial x^2} + E\ [V-a\ g(E)] \end{cases}$$

where

$$f(V) = \frac{35+16V-V^2}{9},$$

$$g(E) = 1 + \frac{2}{5}E,$$

$$\beta = 0.0125,$$

$$a = 1.$$

And we require zero flux boundary conditions:

$$\left.\frac{\partial V}{\partial x}\right|_{(o,t)} = \left.\frac{\partial V}{\partial x}\right|_{(L,t)} = \left.\frac{\partial E}{\partial x}\right|_{(o,t)} = \left.\frac{\partial E}{\partial x}\right|_{(L,t)} = 0$$

Initial values are give as the dashed lines in the following Figure 3*. Note that the initial value has a small deviation from the spatially uniform equilibrium V=5 and E=10.

This model has more terms than our model (10). It has a V^2 term in f(V) and a constant term in g(E) which we don't have in (10). We can easily check that the corresponding parameters in this model satisfies the requirements (10.1) ~ (10.4) in our model. But (10.5) is not satisfied. Recall that (10.5) comes from the requirement that the equilibrium point should be positive. In this example, the equilibrium would be negative if we don't have the V^2 term in f(V). So it is natural that (10.5) is not satisfied. With the V^2 term in f(V), the equilibrium is positive. So this particular numerical example is in a more general form than (10). The solution is graphed in the following Figure 3*.

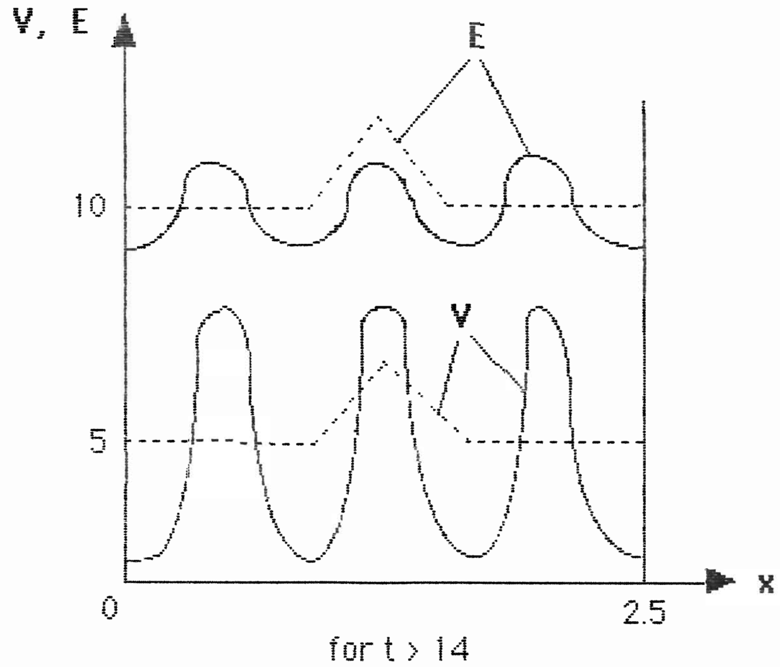


Figure 3* a=1, β=0.0125
"---" Initial Distribution
"___" Final Distribuion For Large t

We see that the populations will reach a new stable state with wave-like spatial distributions.

In this example, the diffusivity ratio β is not the critical value. Therefore I don't know why Okubo (1980) quoted this example at the end of section 10.7 in his book. What I can see is that Segel and Levin's result showed that the populations may reach a new steady state, although it does not apply to Mimura and Murray's numerical example directly.

PART (VII) CONCLUSIONS

Our analysis shows that, under certain conditions (i.e., an Allee effect in the prey, predators are self damped, etc.) diffusion can cause perturbation to a spatially uniform equilibrium to grow and reach a new steady state with wave-like population distributions. The diffusivity ration (θ^2) of predators and prey has to be high enough (for $q=q_c$, it is required that $\theta \approx \theta_c$, for other values of q, the smallest value for θ is $> \theta_c$.). We can explain such a behavior intuitively as following.

An Allee effect in the prey means that, as the prey population grows, the growth rate of the prey population also increases. We explained this point in PART III. When we have some perturbation (like that in PART VI) to the spatially uniform equilibrium state, it causes the predators and prey population distributions to change. The prey population in certain regions will grow. As it grows, the Allee effect causes it to grow even faster. This further concentrates the prey population in those regions. The low diffusivity of prey does not discourage this process. Since the prey population grows in those regions, the predators population will also grow in the same regions. But predators are self damped and have a high diffusivity. Therefore there are not enough predators to suppress the prey population back to previous level. That's why the system is destabilized. On the other hand, prey do have a diffusivity and the overall population of predators can grow. Therefore prey cannot increase their concentration forever. Thus it is possible that both population distributions will stabilize eventually.

As indicated by Segel and Levin in their conclusions, our nonlinear analysis stops at the third approximation for the slow time $t_2 = \varepsilon^2 t$ and therefore we don't know the ultimate fate of our model (No one knows it for sure, anyway.) The analysis just shows that a new steady state in which V and E are $O(\varepsilon)$ uniformly in time is possible and can be approximated.

Part (VIII) REFERENCES

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Appendix 4
Details of the Calculation of (36)

We may get the analytic solution for σ from (34.5) and expand it around θ_c by Taylor's series to obtain (36). I did this by *Mathematica* and indeed got the same result as (36); however, the expressions are long. Or, we may use the method of undetermined coefficients to get the expansion. At last I decided to verify (36) instead of deriving it here.

In our following calculations, we use t instead of θ, s instead of σ and e instead of ε. The eigenvalue σ is the root of the determinant of the following boxed matrix.

In[1]:=

```
MatrixForm[M={{k p^-2 -q^2 -s, -a p^-2},{p^-2,-p^-2 -t^2 q^2 -s}}]
```

Out[1]//MatrixForm=

$$\boxed{\begin{matrix} \frac{k}{p^2} - q^2 - s & -(\frac{a}{p^2}) \\ p^{-2} & -p^{-2} - s - q^2\ t^2 \end{matrix}}$$

Now assign values to the parameters as following.

t (standing for θ) is assigned a value with a deviation e (standing for ε) away from the critical value $\theta_c = 1/(m-p)$ given by (34).

k and a are given by (32).

q is assigned the critical value given by (34).

s (standing for σ) is assumed to be in Taylor's series form $d_1 + d_2\ \varepsilon + O(\varepsilon^2)$ where d1 and d2 are unknown.

The following bold faced *Mathematica commands do the job.*

In[5]:=

```
t = 1/(m-p)+e;
k = m^2-p^2;
a = m^2;
q = Sqrt[(m-p)/p];
```

Now we are going to verify (36). For the first eigenvalue, (36) tells us that

$$s = d\ \varepsilon + O(\varepsilon^2),$$

where $d = 2(m-p)^2/[p(1-(m-p)^2)]$.

The following *Mathematica* commands assign the values.

In[7]:=

```
s = d e  + O[e]^2;
d = 2(m-p)^2 / (p(1-(m-p)^2));
```

Substituting those values into the determinant, we obtain the following boxed value.

In[8]:=

```
Det[M]  //Simplify
```

Out[8]=

$$\boxed{O[e]^2}$$

We see that the solution given by (36) therefore **is** a root of the determinant, within an error of $O(\varepsilon^2)$. Thus we verified the first eigenvalue.

(36) tells us the second eigenvalue is

$$s = d + O(\varepsilon),$$

where $d = -q_c^2(1+\theta_c^2) - p^{-2}(1-m^2+p^2)$.
This is done by the following commands.

In[10]:=

```
d = -q^2(1+1/(m-p)^2) -p^-2(1-m^2+p^2);
s = d + O[e];
```

Substituting those values into the determinant, we obtain

In[11]:=

```
Det[M]  //Simplify
```

Out[11]=

$$\boxed{O[e]^1}$$

We see that the solution given by (36) therefore **is** a root of the determinant, within an error of $O(\varepsilon)$. Thus we verified the second eigenvalue.