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Population Dynamics of sea bass and young sea bass

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1 introduction

The interplay of competition and predation can greatly influence species coexistence or exclusion. A mixture of competition and predation is known as "Intra-guild Predation"(IGP). IGP is a subset of omnivory, which is defined as feeding on resources at different trophic levels. Sea bass is one of an omnivorous fish. In Section 2, we will consider an IGP model composed of a sea bass, a small fish as prey of a sea bass, and plankton as the resource of sea bass and a small fish. Holt and Polis [3] showed that IGP can lead to unstable population dynamics, even when all pairwise interactions are inherently stable and each species can increase when rare. Under the unstable condition of the positive equilibrium point, we discover chaos occurs. Further, we obtain the sufficient and necessary conditions for permanence. Permanence is the property which assures all species in a system of coexistence for a long time. In case chaos occurs, it looks like the trajectory is sticking to the boundary. However, we find it is strictly apart from the boundary if the condition for permanence holds. In Section 3, we incorporate a stage structure of sea bass into the IGP model and consider a time-delayed model.

2 IGP model without young sea bass

2.1 model

First of all we consider a model without young sea bass, that is, without time delay. The model is given as follows:

$$\begin{aligned} \dot{x}(t) &= x(t)(\phi(x(t)) - by(t) - b'Z(t)), \\ \dot{y}(t) &= y(t)(-r_2 + \epsilon bx(t) - cZ(t)), \\ \dot{Z}(t) &= Z(t)(-r_4 + \mu b'x(t) + \theta cy(t)). \end{aligned} \tag{1}$$

The densities of the resource, prey, and sea bass are given by, respectively, $x(t)$, $y(t)$, and $Z(t)$. The quantities $b'x(t)$ and $cy(t)$ are functional responses of the sea bass to the resource and prey, respectively; $bx(t)$ is the functional response of the prey to the resource; and r_2 and r_4 are density-independent mortality rates. The parameters ϵ and μ convert resource consumption into reproduction for the prey and sea bass, respectively; the parameter θ scales the benefit enjoyed by the sea bass from its consumption of prey. Finally, $x(t)\phi(x(t))$ is recruitment of the resource.

Now we introduce the non-dimensional quantities by

$$b = a_{12}, \ b' = a_{14}, \ \epsilon b = a_{21}, \ c = a_{24}, \ \mu b' = \alpha, \ \theta c = \beta.$$

Let $\phi(x(t)) = r_1 - a_{11}x(t)$; the resource when alone grows according to a logisitic model. By substituting these quantites, system (1) becomes

$$\begin{aligned} \dot{x}(t) &= x(t)(r_1 - a_{11}x(t) - a_{12}y(t) - a_{14}Z(t)), \\ \dot{y}(t) &= y(t)(-r_2 + a_{21}x(t) - a_{24}Z(t)), \\ \dot{Z}(t) &= Z(t)(-r_4 + \alpha x(t) + \beta y(t)). \end{aligned} \tag{2}$$

2.2 equilibrium

There exist five equilibria for system (2), namely

1. all species are at zero density: $E_{000} = (0, 0, 0)$ always exists,
2. only the resource is present: $E_{x00} = \left(\frac{r_1}{a_{11}}, 0, 0\right)$ always exists,
3. the resource and prey are present: $E_{xy0} = \left(\frac{r_2}{a_{21}}, \frac{a_{21}r_1 - a_{11}r_2}{a_{12}a_{21}}, 0\right)$ exists if and only if $a_{21}r_1 > a_{11}r_2$,

Table 1: Local stability conditions for non-negative equilibria of system (

Equilibrium point	Local stability conditions
E_{xyZ}	$a_0 = a_{11}x^* > 0,$ $a_1 = a_{12}a_{21}x^*y^* + a_{24}\beta y^* Z^* + a_{14}\alpha x^* Z^* > 0,$ $a_2 = -x^*y^*Z^*\|A\| > 0,$ $a_0a_1 - a_2 > 0$
E_{xy0}	$\tilde{Z} < 0$
E_{x0Z}	$\tilde{y} < 0$
E_{x00}	$a_{21}r_1 < a_{11}r_2, r_1\alpha < a_{11}r_4$
E_{000}	unstable

4. the resource and sea bass are present: $E_{x0Z} = \left(\frac{r_4}{\alpha}, 0, \frac{r_1\alpha - a_{11}r_4}{a_{14}\alpha}\right)$ exists if and only if $r_1\alpha > a_{11}r_4$, and

5. all species are present: $E_{xyZ} = (x^*, y^*, Z^*)$, where

$$
\begin{aligned}
x^* &= -\tilde{x}/|A|, y^* = -\tilde{y}/|A|, Z^* = -\tilde{Z}/|A|, \\
\tilde{x} &= -a_{12}a_{24}r_4 + a_{14}r_2\beta + r_1a_{24}\beta, \\
\tilde{y} &= -r_1a_{24}\alpha + a_{14}a_{21}r_4 - a_{14}r_2\alpha + a_{11}a_{24}r_4, \\
\tilde{Z} &= a_{12}r_2\alpha + r_1a_{21}\beta - a_{12}a_{21}r_4 - a_{11}r_2\beta, \\
|A| &= a_{12}a_{24}\alpha - a_{14}a_{21}\beta - a_{11}a_{24}\beta,
\end{aligned}
$$

exists if and only if
$|A| > 0, \tilde{x} < 0, \tilde{y} < 0$, and $\tilde{Z} < 0$ or $|A| < 0, \tilde{x} > 0, \tilde{y} > 0$, and $\tilde{Z} > 0$.

2.3 local stability

Conditions for local stability of equilibria are summarized in Table 1.

2.4 permanence

We consider the following differential equation:

$$\dot{x}_i = x_i f_i(\mathbf{x}),\ i = 1, \cdots, n \tag{3}$$

on $\mathbb{R}^n_+$. We are interested in whether all species in the system can survive or not. There are several mathematical concepts dealing with this aspect. In particular, a system of type (3) is said to be *permanent* if there exists a compact set K in the interior of the state space such that all orbits in the interior end up in K.

Equivalently, permanence means for (3) that there exists a $\delta > 0$ such that

$$\delta < \liminf_{t\to\infty} x_i(t) \tag{4}$$

for all i, whenever $x_i(0) > 0$ for all i. In addition permanence requires that there exists a d such that

$$\limsup_{t\to\infty} x_i(t) \leq d \tag{5}$$

for all i, whenever $\mathbf{x}(0) \in$ int $\mathbb{R}^n_+$. If (5) holds for all $\mathbf{x}(0) \in \mathbb{R}^n_+$, we shall say that the orbits of (3) are *uniformly bounded.* Condition (4) means that if all species are initially present, the dynamics will not lead to extinction. The threshold δ is a uniform one, independent of the initial condition (see Hofbauer and Sigmund [2]).

For most examples, the terms f_i in (3) are linear. This yields the Lotka-Volterra equation

$$\dot{x}_i = x_i(r_i + (A\mathbf{x})_i) \tag{6}$$

on $\mathbb{R}^n_+$. Sufficient conditions for permanence of system (6) are given by the following Lemma 2.1, which is used to obtain a sufficient condition for permanence of system (2).

Lemma 2.1 *(Hofbauer and Sigmund [2]) A Lotka-Volterra equation (6) with uniformly bounded orbits is permanent if there exists a positive solution* $\mathbf{p}$ *for*

$$\sum_{i:x_i=0} p_i[r_i + (A\mathbf{x})_i] > 0 \tag{7}$$

(where $\mathbf{x}$ *runs through the boundary rest points).*

By using Lemma 2.1, we obtain the following theorem:

Theorem 2.1 *System (2) with uniformly bounded orbits is permanent if the following conditions hold:*

$$\begin{aligned} &\tilde{y} > 0, \tilde{Z} > 0, \textit{and} \\ (a_{21}r_1 - a_{11}r_2)(\alpha r_1 - a_{11}r_4) < 0 \ &\textit{or} \ a_{21}r_1 - a_{11}r_2 > 0, \alpha r_1 - a_{11}r_4 > 0. \end{aligned} \tag{8}$$

Proof Let us apply Lemma 2.1 to system (2):
For $\mathbf{x} = (E_{xy0})$, (7) becomes

$$p_3\left(-r_4 + \alpha\frac{r_2}{a_{21}} + \beta\frac{a_{21}r_1 - a_{11}r_2}{a_{12}a_{21}}\right) > 0. \tag{9}$$

If $a_{12}r_2\alpha + r_1a_{21}\beta - a_{12}a_{21}r_4 - a_{11}r_2\beta > 0$ which is equivalent to $\tilde{Z} > 0$, (9) holds for any $\mathbf{p} > 0$.
For $\mathbf{x} = (E_{x0Z})$, (7) becomes

$$p_2\left(-r_2 + a_{21}\frac{r_4}{\alpha} - a_{24}\frac{r_1\alpha - a_{11}r_4}{a_{14}\alpha}\right) > 0. \tag{10}$$

If $-r_1a_{24}\alpha + a_{14}a_{21}r_4 - a_{14}r_2\alpha + a_{11}a_{24}r_4 > 0$ which is equivalent to $\tilde{y} > 0$, (10) holds for any $\mathbf{p} > 0$.
For $\mathbf{x} = (E_{x00})$, we have

$$p_2(-r_2 + a_{21}\frac{r_1}{a_{11}}) + p_3(-r_4 + \alpha\frac{r_1}{a_{11}}) > 0. \tag{11}$$

If

$$\begin{aligned} &(a_{21}r_1 - a_{11}r_2)(\alpha r_1 - a_{11}r_4) < 0 \\ \text{or } &a_{21}r_1 - a_{11}r_2 > 0, \alpha r_1 - a_{11}r_4 > 0, \end{aligned}$$

there exists $p_2 > 0$, $p_3 > 0$ such that (11) holds.
For $\mathbf{x} = (E_{000})$,

$$p_1r_1 + p_2(-r_2) + p_3(-r_4) > 0.$$

This inequality holds for sufficiently large $p_1 > 0$.
This shows that system (2) is permanent if (8) hold.

Next, necessary conditions for permanence of system (6) are given by the following Lemma 2.2 and 2.3, which are used to obtain a necessary condition for permanence of system (2).

Lemma 2.2 *(Hofbauer and Sigmund [2]) If (6) is permanent, then there exists a unique interior rest point* $\hat{\mathbf{x}}$.

Lemma 2.3 *(Hofbauer and Sigmund [2]) Let (6) be permanent and denote the Jacobian at the unique interior rest point* $\hat{\mathbf{x}}$ *by* J. *Then*

$$\begin{aligned} (-1)^n \det J &> 0, & (12)\\ \mathrm{tr} J &< 0, & (13)\\ (-1)^n \det A &> 0. & (14) \end{aligned}$$

By using Lemma 2.2 and 2.3, we obtain the following theorem:

Theorem 2.2 *If (2) is permanent,* $|A| < 0$.

Proof In system (2),

$$A = \begin{pmatrix} -a_{11} & -a_{12} & -a_{14} \\ a_{21} & 0 & -a_{24} \\ \alpha & \beta & 0 \end{pmatrix}.$$

It is easy to check that we have $|A| < 0$ by (14).

3 IGP model with young sea bass

We consider a model with a stage structure for sea bass. Sea bass breeds young sea bass and some time later young sea bass grows up into sea bass. By incorporating this phenomenon into system (2), the model becomes

$$\begin{aligned} \dot{x}(t) &= x(t)(r_1 - a_{11}x(t) - a_{12}y(t) - a_{13}z(t) - a_{14}Z(t)), \\ \dot{y}(t) &= y(t)(-r_2 + a_{21}x(t) - a_{24}Z(t)), \\ \dot{z}(t) &= -r_3 z(t) + \alpha x(t)Z(t) + \beta y(t)Z(t) - e^{-r_3\tau}(\alpha x(t-\tau) + \beta y(t-\tau))Z(t-\tau), \\ \dot{Z}(t) &= -r_4 Z(t) + e^{-r_3\tau}(\alpha x(t-\tau) + \beta y(t-\tau))Z(t-\tau), \end{aligned} \qquad (15)$$

where $z(t)$ is the density of the young sea bass and r_3 is its density-independent mortality rate. A constant τ is the length of time from birth of the young sea bass to grow up into the sea bass. Since the mortality rate of the young sea bass is r_3, the density of the sea bass at time t is given by $e^{-r_3\tau}(\alpha x(t-\tau) + \beta y(t-\tau))Z(t-\tau)$. Here we suppose that a young sea bass eats only the resource. Further, note that (15) becomes (2) if τ is neglected(when $\tau = 0$, $\dot{z}(t) = -r_3 z(t)$).

4 equilibrium

There exist five equilibria for system (15), namely

1. all species are at zero density: E_{0000}=(0,0,0,0) always exists,
2. only the resource is present: $E_{x000}=\left(\frac{r_1}{a_{11}},0,0,0\right)$ always exists,
3. the resource and prey are present:
   $E_{xy00}=\left(\frac{r_2}{a_{21}},\frac{1}{a_{12}}(r_1-\frac{a_{11}}{a_{21}}r_2),0,0\right)$ exists if and only if $r_1a_{21}>a_{11}r_2$,
4. the resource, young sea bass, and sea bass are present:
   $E_{x0zZ}=\left(\frac{r_4}{\alpha}e^{r_3\tau},0,\frac{r_4}{r_3}e^{r_3\tau}(1-e^{-r_3\tau})\hat{Z},\hat{Z}\right)$
   where $\hat{Z}\equiv\left(a_{14}+a_{13}\frac{r_4}{r_3}e^{r_3\tau}(1-e^{-r_3\tau})\right)^{-1}\left(r_1-a_{11}\frac{r_4}{\alpha}e^{r_3\tau}\right)$ exists if and only if $r_1\alpha>a_{11}r_4e^{r_3\tau}$, and
5. all species are present: $E_{xyzZ}=(x^*,y^*,z^*,Z^*)$ exists if and only if
   $\left(r_1-\frac{a_{11}}{a_{21}}r_2-\frac{a_{12}}{\beta}\left(r_4e^{r_3\tau}-\frac{\alpha}{a_{21}}r_2\right)\right)\left(\frac{a_{11}a_{24}}{a_{21}}-\frac{\alpha}{\beta}\frac{a_{12}a_{24}}{a_{21}}+\frac{r_4(e^{r_3\tau}-1)}{r_3}a_{13}+a_{14}\right)^{-1}$ $(\equiv Z^*)>0$ and $r_4e^{r_3\tau}>\alpha\frac{r_2+a_{24}Z^*}{a_{21}}$.

5 local stability

In this section, we will discuss the local stability of the equilibiria. Denote a nonnegative equilibrium point of (15) as $\bar{\mathbf{x}}=(\bar{x},\bar{y},\bar{z},\bar{Z})$. Let define

$$\mathbf{x}(t)=(x(t)-\bar{x},y(t)-\bar{y},z(t)-\bar{z},Z(t)-\bar{Z}).$$

Then the linearzied equation of (15) at $\bar{\mathbf{x}}$ is described by

$$\dot{\mathbf{x}}(t)=C\mathbf{x}(t)+D\mathbf{x}(t-\tau)$$

where C and D are 4×4 matrices given by

$$C=\begin{pmatrix} r_1-2a_{11}\bar{x}-a_{12}\bar{y}-a_{13}\bar{z}-a_{14}\bar{Z} & -a_{12}\bar{x} & -a_{13}\bar{x} & -a_{14}\bar{x} \\ a_{21}\bar{y} & -r_2+a_{21}\bar{x}-a_{24}\bar{Z} & 0 & -a_{24}\bar{y} \\ \alpha\bar{Z} & \beta\bar{Z} & -r_3 & \alpha\bar{x}+\beta\bar{y} \\ 0 & 0 & 0 & -r_4 \end{pmatrix},$$

$$D = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ -e^{-r_3\tau}\alpha\bar{Z} & -e^{-r_3\tau}\beta\bar{Z} & 0 & -e^{-r_3\tau}(\alpha\bar{x}+\beta\bar{y}) \\ e^{-r_3\tau}\alpha\bar{Z} & e^{-r_3\tau}\beta\bar{Z} & 0 & e^{-r_3\tau}(\alpha\bar{x}+\beta\bar{y}) \end{pmatrix}.$$

The characteristic equation of (15) at $\bar{\mathbf{x}}$ is given by

$$\Delta(\bar{\mathbf{x}}) \equiv \det[C + De^{-\lambda\tau} - \lambda I] = 0$$

where I is an identity matrix and λ denotes the characteristic roots.

Theorem 5.1 *(i) E_{0000} is always unstable.*
(ii) E_{x000} is locally asymptotically stable if $r_1 a_{21} < a_{11} r_2$ and $r_1\alpha < a_{11} r_4 e^{r_3\tau}$.
(iii) E_{xy00} is locally asymptotically stable if $r_4 > e^{-r_3\tau}\left(\frac{r_2}{a_{21}}\alpha - \frac{a_{11}}{a_{12}a_{21}} r_2\beta + \frac{r_1}{a_{12}}\beta\right)$.

Proof (i) Since

$$\Delta(E_{0000}) = (r_1 - \lambda)(-r_2 - \lambda)(-r_3 - \lambda)(-r_4 - \lambda),$$

the characteristic roots are given by

$$\lambda = r_1, -r_2, -r_3, -r_4.$$

Since one characteristic root r_1 is positive, E_{0000} is always unstable.
(ii) Since

$$\begin{aligned} \Delta(E_{x000}) &= (-a_{11}\bar{x} - \lambda)(-r_2 + a_{21}\bar{x} - \lambda)(-r_3 - \lambda)(-r_4 + e^{-\tau(r_3+\lambda)}\alpha\bar{x} - \lambda) \\ &= 0, \end{aligned}$$

its solutions are given by $\lambda = -r_3 < 0$, $\lambda = -a_{11}\bar{x} < 0$, and $\lambda = -r_2 + a_{21}\bar{x} < 0$ if $r_1 a_{21} < a_{11} r_2$. Now we consider the fourth factor and define

$$h(\lambda) = \lambda + r_4 - e^{-\tau(r_3+\lambda)}\alpha\bar{x}.$$

Then $h(\lambda) = 0$ implies that

$$\lambda + r_4 = \alpha\bar{x}e^{-\tau(r_3+\lambda)}$$

If Re $\lambda \geq 0$, then

$$r_4 \leq |\lambda + r_4| = \alpha\bar{x}e^{-r_3\tau}|e^{-\lambda\tau}| \leq \alpha\bar{x}e^{-r_3\tau},$$

which gives a contradiction to $r_1\alpha < a_{11}r_4e^{r_3\tau}$. This shows that all roots of $h(\lambda) = 0$ have negative real parts and E_{x000} is locally asymptotically stable.
(iii) Since

$$\Delta(E_{xy00}) = (-r_3 - \lambda)(\lambda^2 + a_{11}\bar{x}\lambda + a_{12}a_{21}\bar{x}\bar{y})(-r_4 + e^{-\tau(r_3+\lambda)}(\alpha\bar{x} + \beta\bar{y}) - \lambda) = 0,$$

we have $\lambda = -r_3 < 0$. The solutions λ obtained from the second factor have negative real parts by Routh-Hurwitz criterion. Like (ii) we consider the third factor and define

$$h(\lambda) = \lambda + r_4 - e^{-\tau(r_3+\lambda)}(\alpha\bar{x} + \beta\bar{y}).$$

If the solution λ of $h(\lambda) = 0$ has nonnegative real parts, then we have

$$r_4 \leq |\lambda + r_4| = (\alpha\bar{x} + \beta\bar{y})e^{-r_3\tau}|e^{-\lambda\tau}| \leq (\alpha\bar{x} + \beta\bar{y})e^{-r_3\tau},$$

which gives a contradiction. This shows that E_{xy00} is locally asymptotically stable.

Remark 5.1 : Theorem 5.1(ii) implies that E_{x000} is locally asymptotically stable if neither E_{xy00} nor E_{x0zZ} exists.

6 discussion

We only obtain the local stability conditions of E_{x000} and E_{xy00}. With respect to E_{x0zZ} and E_{xyzZ}, it is not easy to analyze the local stability rigorously. Furthermore, global stability, permanence, and boundedness of the model with a stage structure are also future problems.

References

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