A Predator-Prey Model for Two-Species Populations with Nonlinear Interactions and Implications for Fisheries Management

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A predator-prey interaction model is proposed for studying management implications of two fish species populations with nonlinear interactions. Nonlinear interactions seem more plausible than linear ones in natural populations. The present model is built up by adding second order interactive terms to the Lotka-Volterra type linear model proposed by Larkin.

The prey isocline, which is a curve satisfying the equation \( \frac{dN_1}{dt} = 0 \) in the \( N_1 \) (prey population density)-\( N_2 \) (predator population density) plane, is classified into the four types based on the shape of the isocline. The predator isocline is also classified into the four types. The present model with the elliptic predator and prey isoclines, can be used to represent all the types of isoclines and can show the general nature of various nonlinear interactions.

The responses to exploitation of the present nonlinear predator-prey system are qualitatively different from those of the original linear system. The equilibrium catches may suddenly decline from positive levels to zero even if fishing pressure increases continuously. Such a catastrophic phenomenon is caused by the destabilization of the system. If the single-species MSY (maximum sustainable yield) policies are practiced without taking into account the stability of the system, populations may be threatened with sudden collapses. The MSY policies for populations with nonlinear interactions may be quite dangerous.

When two species populations interact with each other, their responses to exploitation cannot be predicted from classical studies of single-species dynamics. The development of predator-prey interaction models1-4 would be of importance in studying the effect of exploitation on these species.

Larkin5, taking the community association of fish species into consideration, proposed the following modified version of the familiar Lotka-Volterra model:

\[
\begin{align*}
\frac{dN_1}{dt} &= N_1 \left( r_1 - a_{11}N_1 - a_{12}N_2 \right) \\
\frac{dN_2}{dt} &= N_2 \left( r_2 + a_{21}N_1 - a_{22}N_2 \right)
\end{align*}
\]

where \( N_1 \): prey population density, \( N_2 \): predator population density, \( t \): time. All the parameters are positive or zero. In equations (1), the per capita rate of increase of the two populations, \( 1/N_1 \cdot dN_1/dt \) and \( 1/N_2 \cdot dN_2/dt \), are expressed in linear terms of \( N_1 \) and \( N_2 \). In other words, this model assumes linear interactions in the two populations.

This simple linear form, however, cannot always represent natural predator-prey interactions. One example is the situation where the Ivlev effect6 on feeding is applicable to a predator population. The amount of food actually utilized by a predator population will be limited even if the prey population density increases infinitely. In this situation, the per capita rate of increase of the predator must be nonlinearly related to the prey population density. When the per capita rate of increase of population \( i \), \( i=1, 2 \), is expressed in nonlinear terms of \( N_i \) and \( N_j \), nonlinear interaction is defined to exist in population \( i \).

Shirakihara and Tanaka7 studied the dynamics of the two competing fish populations with nonlinear interactions and showed that nonlinear systems were more sensitive to exploitation than linear systems. In the present paper, a nonlinear predator-prey interaction model is presented to explore the responses to exploitation of predator and prey populations with nonlinear interactions and to develop insight into fisheries management of such nonlinear predator-prey systems.

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Classification of Isoclines

A predator-prey interaction model might be represented in general form:

\[
\begin{align*}
\frac{dN_1}{dt} &= f_1(N_1, N_2) \\
\frac{dN_2}{dt} &= f_2(N_1, N_2)
\end{align*}
\]  

where \( f_i, (i=1, 2) \) is some function. The prey isocline is given by the locus of points satisfying the equation \( f_1 = 0 \) in the \( N_1 - N_2 \) plane. If linear interaction exist in the prey population, the prey isocline will be a straight line, but nonlinear interaction will result in a curved isocline. The same analysis holds for the predator isocline, which is the locus of points satisfying the equation \( f_2 = 0 \) in the \( N_1 - N_2 \) plane. One of the advantages of making up isoclines is that the nature of various interactions can be judged graphically from the shape of isoclines.

Hereby we will classify the prey isocline by the following method. Let us define \( G_{11} \) and \( G_{12} \) as

\[
G_{11} = \left( \frac{\partial f_1}{\partial N_1} \right) \quad \text{and} \quad G_{12} = \left( \frac{\partial f_1}{\partial N_2} \right)
\]

at the point \( (N_{1I}, N_{2I}) \), where \( (N_{1I}, N_{2I}) \) is the co-ordinates of an arbitrary point on the prey isocline. The information required for the classification of the prey isocline is not the values of \( G_{11} \) and \( G_{12} \) but the signs of them. We will first explain how to determine these signs by examining the example in Fig. 1. The region near the point \( (N_{1I}, N_{2I}) \) can be divided into two regions bounded by the prey isocline \( f_1 = 0 \), i.e. one where the prey population will increase \( (f_1 > 0) \) and another where the prey population will decrease \( (f_1 < 0) \). In this example, an increase in \( N_1 \) from a level smaller than \( N_{1I} \) to a level larger than \( N_{1I} \), under a constant \( N_2 \) level equal to \( N_{2I} \), changes the sign of \( f_1 \) from positive to negative. It is judged that \( G_{11} \) is negative and a negative intraspecific effect exists for the prey population at the point shown in Fig. 1. An increase in \( N_2 \) from a level smaller than \( N_{2I} \) to a level larger than \( N_{2I} \), under a constant \( N_1 \) level equal to \( N_{1I} \), also changes the sign of \( f_1 \) from positive to negative. It is judged that \( G_{12} \) is negative and the predator population has a negative interspecific effect on the prey population.

In general, the prey isocline can be classified into the four types shown in Fig. 2, based on the combination of the signs of \( G_{11} \) and \( G_{12} \).

Fig. 1. The prey isocline. This figure is shown as the example of examining the signs of \( G_{11} \) and \( G_{12} \). Arrows indicate the direction of change in the prey population density.

Fig. 2. Classification of the prey isocline. Shaded area indicates the region where the prey population will increase.

The predator isocline can be also classified similarly. Let us define \( G_{21} \) and \( G_{22} \) as

\[
G_{21} = \left( \frac{\partial f_2}{\partial N_1} \right) \quad \text{and} \quad G_{22} = \left( \frac{\partial f_2}{\partial N_2} \right)
\]

at the point \( (N_{1II}, N_{2II}) \), where \( (N_{1II}, N_{2II}) \) is the co-ordinates of an arbitrary point on the predator isocline. The sign of \( G_{22} \) represents the intraspecific effect of the predator on its own population and the sign of \( G_{21} \) represents the interspecific effect of the prey population on the predator population. The predator isocline can be classified into the four types shown in Fig. 3, based on the combination of the signs of \( G_{22} \) and \( G_{21} \).

**TYPE 1:** (prey) \( G_{11} \) negative or zero and \( G_{12} \) negative or zero
Fig. 3. Classification of the predator isocline.
The shaded area indicates the region where the predator population will increase.

(predator) $G_{22}$ negative or zero and
$G_{21}$ positive or zero

Negative or zero intraspecific effects exist at all points on each isocline. Negative or zero interspecific effects of the predator on the prey exist at all points on the prey isocline. Positive or zero interspecific effects of the prey on the predator exists at all points on the predator isocline.

TYPE 2: (prey) $G_{11}$ positive at some points and
$G_{12}$ negative or zero at all points

(predator) $G_{22}$ positive at some point and
$G_{21}$ positive or zero at all points

This type includes positive intraspecific effects which correspond to the depensatory density-dependent process, over a certain range of population levels. In the examples of Fig. 2 and Fig. 3, the range from the point A to the point B is applicable to this condition.

TYPE 3: (prey) $G_{11}$ negative or zero at all points and
$G_{12}$ positive at some points

(predator) $G_{22}$ negative or zero at all points and
$G_{21}$ negative at some points

This type of the prey isocline includes positive interspecific effects of the predator on the prey over a certain range of prey population levels. When such effects exist, an increase in the predator population density does not inhibit the growth of the prey population but rather promote it. This type of the predator isocline includes negative interspecific effects of the prey on the predator over a certain range of predator population levels. In Fig. 2 and Fig. 3, the range from the point C to the point D is applicable to this condition.

TYPE 4: (prey) $G_{11}$ positive at some points and
$G_{12}$ positive at some points

(predator) $G_{22}$ positive at some points and
$G_{21}$ negative at some points

This type incorporates both TYPE 2 and TYPE 3 effects.

Predator-Prey Interaction Model

We will propose the following model to examine the dynamic behavior of the predator-prey system with nonlinear interactions:

$$
\begin{align*}
\frac{dN_1}{dt} &= N_1 \left[ r_1 - a_{11}N_1 - a_{12}N_2 - b_{11}N_1(N_1 - c_{11}) - b_{12}N_2(N_2 - c_{12}) \right] \\
\frac{dN_2}{dt} &= N_2 \left[ r_2 + a_{21}N_1 - b_{21}N_1(N_1 - d_{21}) - b_{22}N_2(N_2 - d_{22}) \right]
\end{align*}
$$

Equations (3) can be rewritten as:

$$
\begin{align*}
\frac{dN_1}{dt} &= N_1 \left[ a_1 - b_{11}(N_1 - d_1)^2 - b_{12}(N_2 - d_2)^2 \right] \\
\frac{dN_2}{dt} &= N_2 \left[ a_2 - b_{21}(N_1 - d_2)^2 - b_{22}(N_2 - d_2)^2 \right]
\end{align*}
$$

In equations (4), the prey isocline is an ellipse as
shown in Fig. 4. If the center of the ellipse at $(d_{11}, d_{12})$ is in the first, second, third and fourth quadrants of the $N_1-N_2$ plane, the prey isocline corresponds to TYPE 4, 2, 1 and 3 respectively. The predator isocline is also an ellipse with the center at $(d_{21}, d_{22})$. The parameter $d_{21}$ is always positive and therefore equations (4) can show only predator isoclines of TYPE 3 and TYPE 4. But if $d_{21}$ increases infinitely keeping $(d_{21}-(a_2/b_{21})^{1/2})$ at a finite value, the isocline approaches to a parabola as shown by the dotted line in Fig. 5. And TYPE 3 and TYPE 4 could be converted to TYPE 1 and TYPE 2 respectively.

Thus, all the types of isoclines can be represented by choosing the values of the various parameters. Therefore, this model can show the general nature of various nonlinear interactions, though it is built up simply by assuming hypothetical second order interactions.

When fishing pressure on population $i$ is added at strength $F_i$ (instantaneous fishing mortality coefficient), equations (4) will be:

$$\frac{dN_1}{dt} = N_1[a_1 - b_{11}(N_1 - d_{11})^2 - b_{12}(N_2 - d_{12})^2] - F_1 N_1$$

$$\frac{dN_2}{dt} = N_2[a_2 - b_{21}(N_1 - d_{21})^2 - b_{22}(N_2 - d_{22})^2] - F_2 N_2$$

and equations for the prey and predator isoclines are:

$$b_{11}(N_1 - d_{11})^2 + b_{12}(N_1 - d_{12})^2 = a_1 - F_1$$

$$b_{21}(N_1 - d_{21})^2 + b_{22}(N_2 - d_{22})^2 = a_2 - F_2$$

The intersections of two isoclines are the equilibrium points of both populations ($dN_i/dt = dN_j/dt = 0$). The equilibrium points can be classified into the stable and unstable equilibrium points by examining the local stability at the points. It is only at a stable equilibrium point that the two populations can maintain a steady state against perturbation, e.g. a sudden change of fishing pressure. In the present paper, the local stability is analysed by the method of VANDERMEER.

The stable equilibrium population of population $i$ under fishing pressure, denoted as $N_{ieq}$, can be obtained by solving equations (6) and checking the local stability. Thus, the equilibrium catch obtained from population $i$, $C_{ieq}$ is:

$$C_{ieq} = F_i N_{ieq}$$

The values of $C_{ieq}$ and $C_{2eq}$ can be calculated for various combinations of $F_1$ and $F_2$ when all the parameters of equations (5) are given.

The numerical analysis of the model is executed by the computer, FACOM M-160S, at the Ocean Research Institute of the University of Tokyo.
Effects of Exploitation on Prey and Predator Fish Populations and Their Equilibrium Catches

The dynamics of the two populations will show different behaviors according to the number of the stable equilibrium points occurring, and the number will vary depending on the combination of the previously classified two population isoclines. The model to be discussed here possesses no more than two equilibrium points. In the case where both prey and predator isoclines are either TYPE 3 or TYPE 4, the two stable equilibrium points will be obtained. This case, however, is the same as Example 1 of Shirakihara and Tanaka(7), and will not be discussed further here.

We will examine the example shown in Fig. 6, with parameters \(a_1=a_2=2.0, b_{11}=0.4, b_{12}=3.0, b_{21}=0.025, b_{22}=3.0, d_{11}=4.0, d_{12}=0.0, d_{21}=10.0, d_{22}=0.0\). These parameters result in prey and predator isoclines of TYPE 2 and TYPE 1 respectively. The point A is a single stable equilibrium point and the point B is an unstable equilibrium point. The reasons we choose this case are as follows. First, a prey isocline of TYPE 2 is plausible, for Rosenzweig(10), and Maly(11,12) have demonstrated prey isoclines similar to this type for experimental animals. Secondly, a predator isocline of TYPE 1 represents negative intra-

Fig. 6. An example to show the effect of exploitation of prey and predator populations. Prey and predator isoclines are curves I and II respectively. As the fishing mortality coefficient \(F_1\) increases from zero, the prey isocline changes from I, through I', to I". The trajectory for the two population densities is also indicated when the prey isocline changes suddenly from I' to I".

specific effects and positive interspecific effects. This type seems the most likely and realistic of the four predator types.

Larkin's model(5), equations (1), has a predator isocline of TYPE 1.

We will first consider the effect of exploitation on the prey. An equilibrium catch diagram for the prey, which plots the equilibrium catch \(C_{1\text{eq}}\) in relation to the instantaneous fishing mortality coefficient \(F_1\) for various constant levels of \(F_2\), is shown in Fig. 7. As \(F_1\) increases, the equilibrium catch \(C_{1\text{eq}}\) increases until \(F_1\) approaches a specific level \(a\) for the curve with \(F_2=0.0\) and when \(F_1\) exceeds this level, the equilibrium catch begins to decrease smoothly. Note that once \(F_1\) becomes larger than some specific level \(b\) with \(F_2=0.0\), the equilibrium catch suddenly declines to zero. This phenomenon is caused by the following mechanism. When heavy fishing pressure is applied to the prey population at level larger than \(b\), the prey isocline changes from I to I", as shown in Fig. 6. The stable equilibrium point A disappears and the two population densities then decrease to zero. The extinction of the two populations is also possible if a stable equilibrium point turns into an unstable one, owing to a change in fishing pressure. Such a phenomenon due to the destabilization of the system is a catastrophic one, for a continuous change in \(F_1\) causes a sudden irreversible reduction of each population density from a positive level to zero.

Fig. 7. The prey equilibrium catch diagram. Numerals indicate the level of \(F_2\) applied. The dotted line is the prey equilibrium catch diagram with linear interactions, which will be discussed later in the section on management implications.
Fig. 8. The isopleth diagram of the prey equilibrium catch. Numerals indicate the prey equilibrium catch $C_{eq}$. The catch $C_{eq}$ is zero in the area to the right of the catastrophic line. The isopleth diagram above the predator extinction line is shown by the dotted line, because the increase of $F_2$ is meaningless in this region.

Fig. 9. The isopleth diagram of the predator equilibrium catch. Numerals indicate the predator equilibrium catch $C_{eq}$. The catch $C_{eq}$ is zero in the area to the right of the catastrophic line and in the area above the predator extinction line.

In order to examine the combined effects of $F_1$ and $F_2$ on $C_{eq}$, an isopleth diagram for the prey equilibrium catch is shown in Fig. 8. The effect of $F_1$ on $C_{eq}$ under constant $F_1$ is the same as explained before in Fig. 7, for $F_2$ less than or equal to $d$ in Fig. 8. If $F_2$ exceeds this level, a catastrophe is not observed. Next let us examine the effect of $F_2$ on $C_{eq}$. An increase in $F_2$ under constant $F_1$ always results in an increase in $C_{eq}$ until the increase in $F_2$ brings about the extinction of the predator.

Now, the effect of exploitation on the predator will be considered. An isopleth diagram for the predator equilibrium catch is shown in Fig. 9. An increase in $F_2$ under constant $F_1$ always decreases the predator equilibrium catch $C_{eq}$ until the increase in $F_2$ brings about a catastrophe. Two outcomes are possible as to the effect of an increase in $F_1$ on $C_{eq}$, depending on the magnitude of $F_2$. For lower levels of $F_2$ (e.g. $F_2$ less than 1.0 under $F_1$ equal to 1.0), an increase in $F_2$ increases $C_{eq}$, but for higher levels of $F_2$, an increase in $F_1$ decreases $C_{eq}$.

Management Implications

Conventional theories of fisheries management have considered only the steady state of the system. Recently the importance of the stability of the system to fisheries management has begun to be discussed. Here it will be pointed out that the MSY (maximum sustainable yield) policy is inappropriate for the present nonlinear predator-prey system from the viewpoint of the stability of the system.

In Larkin's linear model, the local stability of the equilibrium points is not affected by each population's fishing pressure and therefore the stability of the system need not be considered. In this case, the prey equilibrium catch diagram follows the general shape of a parabola, shown by the dotted line in Fig. 7. The maximum level of $C_{eq}$ is obtained at the $F_1$ level of $c$. Even if a change in $F_1$ from this level decreases $C_{eq}$, the maximum level of $C_{eq}$ is readily recovered by setting $F_1$ back to the original level of $c$. Thus the MSY level of the prey catch can be successfully achieved and maintained.

In the present model, the local stability can be affected by fishing pressure and there is a possibility that a change in fishing pressure can cause the sudden destabilization of the system. Now let us examine the response of the nonlinear system under the MSY policy for managing the prey. It should be noted that $F_{1,MSY}$ ($F_1$ level yielding the maximum prey equilibrium catch) lies close to the $F_1$ level causing a catastrophe due to the destabilization of the system, for the three curves of the prey equilibrium catch diagram in Fig. 7.
Certainly the prey maximum catch may be maintained as long as $F_1$ can be fixed at $F_{1,MY}$. In practice, however, it is nearly impossible to maintain the level of $F_{1,MY}$ for a long time, for the following reason. The level of the prey fishing mortality $F_1$ depends on catchability coefficient of the prey $q_1$ and fishing effort for the prey $X_1$. A fisheries manager may control $X_1$ but not $q_1$, for $q_1$ may vary with unpredictable environmental fluctuations. Thus even if he tries to approximate $F_1$ to the desired level of $F_{1,MY}$, $F_1$ will inevitably fluctuate around this level over time. And once $F_1$ happens to exceed the catastrophic level, the prey population will collapse. In this sense the MSY policy is quite a dangerous one. The prey catch should be restricted to a level considerably lower than the maximum catch level in order to avoid the catastrophic collapse of the population.

Another aspect accounting for the inappropriateness of the MSY policy is that there is a conflict between a policy exploiting the maximum prey catch and a policy exploiting the maximum predator catch. Though such a viewpoint has already been pointed out\textsuperscript{21,22}, we can discuss it in a more concrete way by comparing the two isopleth diagrams in Fig.8 and Fig.9. The allocation of fishing pressure to each population to yield the maximum prey catch is quite different from the allocation to yield the maximum predator catch. It is clear that independent realization of the MSY policies for each of the two interacting populations is impossible.

References