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# COMMERCIAL FISHING WITH PREDATOR-PREY INTERACTION 

Koji Okuguchi*


#### Abstract

The Smith model of commercial fishing of a single species is generalized, taking into consideration of natural interaction between a prey and a predator. The stability of the non-extinct steady state populations of the two species is proved, and the effects of changes in parameters upon the steady state are examined. Finally, the steady state populations under harvesting and no harvesting are compared.


## 1. INTRODUCTION

A dynamic model of commercial fishing incorporating economic as well as biological aspects of a single species has been formulated and analysed by Smith [4], and the stability of the steady state or bionomic equilibrium has been investigated in great detail by Leung and Wang [3] and Wang and Cheng [6] under the assumptions that the price of the fish is a strictly decreasing function of the total harvest and that the total cost excluding the oppotunity cost per boat or investment is proportional to the square of the harvest per boat or investment and inversely proportional to the stock or population of the fish.

Solow [5], on the other hand, has attempted a comparative dynamical analysis of fishing within a framework of an optimal control theoretical model involving natural predator-prey interaction à la Volterra. Clark [1] also has studied a similar model involving a Gause-type interspecific competition between two species of fishes which feed on a common food supply, each species growing according to a logistic law in the absence of its competing species. Moreover, he has analysed a model with predator-prey interaction à la Larkin. Both Solow and Clark have assumed the constancy of prices of fishes harvested over time. More recently, May, Beddington, Clark, Holt and Laws [4] have analyzed multispecies fisheries assuming intertemporal constancy of fishing efforts. In addition to a prey-preditor (krill-baleen whale) model, they have considered one prey-two preditor (krillwhale and seal) model and a three trophic level (krill, cephalopod and sperm whale) model. They have made some observations on economic aspects of multispecies fisheries, but have not analyzed the optimal determination of fishing efforts from the viewpoint of economic rationality of fishing firms.

The purpose of this paper is to extend the Smith model of commercial fishing of a single species taking into account natural interaction between a predator and a

[^0]prey. In Section 2 we present a commercial fishing model involving predator-prey interaction, and analyze the stability of the steady-state with non-extinct populations of the two species. In Section 3 a comparative statical analysis of the steady state with respect to changes in parameters is given. Further, the populations of the two species in the steady are compared for the case of harvesting and that for no harvesting. Section 4 concludes.

## 2. THE MODEL AND A DYNAMIC ANALYSIS

Let there be two species of fishes in the same territory, one as predator and the other as prey, and let $X_{1}$ and $X_{2}$ denote the populations of the prey and predator, respectively. If uninterrupted by fishing, the two species grow according to

$$
\begin{align*}
& \dot{X}_{1}=X_{1}\left(a_{1}-b_{1} X_{1}-c_{1} X_{2}\right),  \tag{1}\\
& \dot{X}_{2}=-X_{2}\left(a_{2}-b_{2} X_{1}+c_{2} X_{2}\right), \tag{2}
\end{align*}
$$

where the parameters are assumed to satisfy:

$$
\begin{array}{lll}
a_{1}>0, & b_{1}>0, & c_{1}>0 \\
a_{2} \gtrless 0, & b_{2}>0, & c_{2} \geq 0 . \tag{3}
\end{array}
$$

The meanings of these equations and restrictions are as follows. The prey species grows in accordance with a logistic law in the absence of the predator, and the number of prey predated by the predator is proportional to the number of the predator for given number of the prey and to the number of the prey for given number of the predator. The predator, on the other hand, grows according to a logistic law also in the absence of the prey if $a_{2}<0$ and $c_{2}>0$ are satisfied simultaneously. The additional increase in the predator population in the presence of predation is proportional to the number of the prey for given number of the predator and to the number of the predator for given number of the prey.

Solow has analysed the Volterra case where $a_{2}>0, b_{2}>0$ and $c_{2}=0$. In this case the predator decreases exponentially without predation. The case where $a_{2}<0$, $b_{2}>0$ and $c_{2}>0$ has been considered by Larkin (see Clark [1, Chap. 9]), and the case where $a_{2}>0, b_{2}>0$ and $c_{2}>0$ has been treated by Hirsch and Smale [2, Chap. 12]. May, Beddington, Clark, Holt and Laws [4] have assumed the following differential equation for the growth of the predator, instead of (2):

$$
\begin{equation*}
\dot{X}_{2}=r_{2} X_{2}\left(1-X_{2} / \alpha X_{1}\right), \tag{2}
\end{equation*}
$$

where $r_{2}>0$ is the intrinsic growth rate of the predator and $\alpha>0$ is a proportionality constant relating the carrying capacity of the predator to the stock of the prey when the predator is not harvested.

Let us now introduce selective harvesting of the two species of fishes. In contrast to Smith [5], Leung and Wang [3], and Wang and Cheng [7], we assume à la Solow [6] and Clark [1] that both species of fishes are sold at constant prices, $p_{1}$ and $p_{2}$,
over time. Let $Y_{1}$ and $Y_{2}$ be the amounts of harvest of the prey and predator, respectively. The selective harvesting cost per boat or investment are given by $\gamma_{1} Y_{1}^{2} / X_{1}$ and $\gamma_{2} Y_{2}^{2} / X_{2}$, respectively, for the prey and predator. Profit per boat or investment for fishing the $i$-th species (the prey for $i=1$ and the predator for $i=2$ ) is given by

$$
\begin{equation*}
\pi_{i}=p_{i} Y_{i}-\gamma_{i} Y_{i}^{2} / X_{i}-\pi_{i}^{0}, \quad i=1,2, \tag{4}
\end{equation*}
$$

where $\pi_{i}^{0}$ is the opportunity cost per unit of investment in fishing the $i$-th species.
Maximising $\pi_{i}$ with respect to $Y_{i}$, we get ${ }^{1}$

$$
\begin{equation*}
Y_{i}=p_{i} X_{i} / 2 \gamma_{i}, \quad i=1,2 \tag{5}
\end{equation*}
$$

which substituted into (4) yields

$$
\begin{equation*}
\pi_{i}=p_{i}^{2} X_{i} / 4 \gamma_{i}-\pi_{i}^{0}, \quad i=1,2 .^{2} \tag{6}
\end{equation*}
$$

Let $K_{i}$ be the number of boats engaged in fishing the $i$-th species. In the presence of fishing the natural growth equations (1) and (2) have to be modified as:

$$
\begin{align*}
& d X_{1} / d t=X_{1}\left(a_{1}-b_{1} X_{1}-c_{1} X_{2}\right)-K_{1} Y_{1}  \tag{7}\\
& d X_{2} / d t=-X_{2}\left(a_{2}-b_{2} X_{1}+c_{2} X_{2}\right)-K_{2} Y_{2}, \tag{8}
\end{align*}
$$

or in view of (5), as

$$
\begin{align*}
& d X_{1} / d t=X_{1}\left(a_{1}-b_{1} X_{1}-c_{1} X_{2}-p_{1} K_{1} / 2 \gamma_{1}\right)  \tag{9}\\
& d X_{2} / d t=-X_{2}\left(a_{2}-b_{2} X_{1}+c_{2} X_{2}+p_{2} K_{2} / 2 \gamma_{2}\right) .
\end{align*}
$$

We assume that the number of boats engaged in fishing increases or decreases in
${ }^{1}$ It might be more faithful to current practice to consider maximization of the integral of discounted profit than to consider current profit maximization. Technical difficulties associated with the former maximization, however, forces us to be satisfied with the latter maximization as a first approximation. Moreover, this approximation is valid if the discount factor is sufficiently large, or if future is very uncertain.
${ }^{2}$ Let the demand function and the harvesting cost per boat be given by $p_{i}=f^{i}\left(Y_{i}\right)$ and $C^{i}=$ $C^{i}\left(Y_{i}, X_{i}\right)$, respectively, where $f_{Y_{i}}^{i}<0, C_{Y_{i}}^{i}>0$ and $C_{X_{i}}^{i}<0, i=1,2$. The profit per boat for fishing the $i$ th species is
(a)

$$
\pi_{i}=x_{i} f^{i}\left(Y_{i}\right)-C^{i}\left(Y_{i}, X_{i}\right)-\pi_{i}^{0}, \quad i=1,2 .
$$

Maximizing $\pi_{i}$ with respect to $Y_{i}$, we get

$$
\begin{equation*}
Y_{i} \equiv h^{i}\left(X_{i}\right), \quad i=1,2, \tag{b}
\end{equation*}
$$

where
(c) $\quad d h^{i} / d X_{i} \gtreqless 0$ according as $C_{Y_{i} X_{i}}^{i} \leqq 0, \quad i=1,2$.

Substituting (b) into (a),
(d)

$$
\pi_{i}=h^{i}\left(X_{i}\right) f^{i}\left(h^{i}\left(X_{i}\right)\right)-C^{i}\left(h^{i}\left(X_{i}\right), X_{i}\right)-\pi_{i}^{0}, \quad i=1,2 .
$$

More generally, the demand function should be formulated as
(e)

$$
p_{i}=f^{i}\left(Y_{i}, Y_{j}\right), \quad i \neq 1,2 .
$$

proportion to profit or loss per boat. Hence

$$
\begin{equation*}
d K_{i} / d t=\delta_{i}\left(p_{i}^{2} X_{i} / 4 \gamma_{i}-\pi_{i}^{0}\right), \quad i=1,2, \tag{11}
\end{equation*}
$$

where $\delta_{i}$ 's are positive constants.
Equations (9)-(11) constitute our fundamental system of differential equations, the stability of which steady state being our main concern in this section. If $d K_{i} / d t$ approaches zero independently of (9) and (10), the stability may be proved by appealing to the results already obtained by others. However, (9), (10) and (11) are interdependent, making our stability analysis rather complex.

Let $X_{i}^{*}$ and $K_{i}^{*}$ be the steady state values of $X_{i}$ and $K_{i}$, respectively, where we assume that $X_{i}^{*}$ and $K_{i}^{*}$ are both positive. Expand (9)-(11) in the neighbourhood of $X_{i}^{*}$ and $K_{i}^{*}$ to derive the following system of linear differential equations in four variables.

$$
\begin{align*}
\left(\begin{array}{l}
d Z_{1} / d t \\
d Z_{2} / d t \\
d N_{1} / d t \\
d N_{2} / d t
\end{array}\right) & =\left(\begin{array}{cccc}
-b_{1} X_{1}^{*} & -c_{1} X_{1}^{*} & -p_{1} X_{1}^{*} / 2 \gamma_{1} & 0 \\
b_{2} X_{2}^{*} & -c_{2} X_{2}^{*} & 0 & -p_{2} X_{2}^{*} / 2 \gamma_{2} \\
\delta_{1} p_{1}^{2} / 4 \gamma_{1} & 0 & 0 & 0 \\
0 & \delta_{2} p_{2}^{2} / 4 \gamma_{2} & 0 & 0
\end{array}\right)\left(\begin{array}{c}
Z_{1} \\
Z_{2} \\
N_{1} \\
N_{2}
\end{array}\right)  \tag{12}\\
& \equiv\left(\begin{array}{cccc}
-a_{11} & -a_{12} & -a_{13} & 0 \\
a_{21} & -a_{22} & 0 & -a_{23} \\
a_{31} & 0 & 0 & 0 \\
0 & a_{42} & 0 & 0
\end{array}\right)\left(\begin{array}{l}
Z_{1} \\
Z_{2} \\
N_{1} \\
N_{2}
\end{array}\right),
\end{align*}
$$

where

$$
\begin{equation*}
Z_{i} \equiv X_{i}-X_{i}^{*}, \quad N_{i} \equiv K_{i}-K_{i}^{*}, \quad i=1,2, \tag{13}
\end{equation*}
$$

and

$$
\begin{equation*}
a_{11}, a_{12}, a_{13}, a_{21}, a_{23}, a_{31}, a_{42}>0, \quad a_{22} \geq 0 \tag{14}
\end{equation*}
$$

If the steady value of either $X_{1}$ or $X_{2}$ is zero, then $\pi_{1}^{0}$ or $\pi_{2}^{0}$ has to be zero because of (11). We therefore assume away the possibility of extinction of both species of fishes, as the opportunity cost of investment in fishing can, in general, be considered to be positive. Note also that in deriving (12), use has been made of the following two equations relevant to the steady state.

$$
\begin{align*}
& a_{1}-b_{1} X_{1}^{*}-c_{1} X_{2}^{*}-p_{1} K_{1}^{*} / 2 \gamma_{1}=0,  \tag{15}\\
& a_{2}-b_{2} X_{1}^{*}+c_{2} X_{2}^{*}+p_{2} K_{2}^{*} / 2 \gamma_{2}=0 \tag{16}
\end{align*}
$$

The characteristic equation for the coefficient matrix of (12) is shown to be

$$
\begin{align*}
\lambda^{4}+\left(a_{11}+a_{22}\right) \lambda^{3}+\left(a_{11} a_{22}\right. & \left.+a_{12} a_{21}+a_{13} a_{31}+a_{24} a_{42}\right) \lambda^{2}  \tag{17}\\
+ & \left(a_{11} a_{24} a_{42}+a_{13} a_{22} a_{31}\right) \lambda+a_{13} a_{24} a_{31} a_{42} \\
& \equiv \lambda^{4}+\alpha_{1} \lambda^{3}+\alpha_{2} \lambda^{2}+\alpha_{3} \lambda+\alpha_{4} \\
& =0
\end{align*}
$$

In view of the definition of $\alpha_{1}, \alpha_{2}, \alpha_{3}$ and $\alpha_{4}$, a simple calculation shows that all of the upper left-hand corner principal minors of the matrix

$$
\left(\begin{array}{cccc}
\alpha_{1} & \alpha_{2} & 0 & 0 \\
1 & \alpha_{2} & \alpha_{4} & 0 \\
0 & \alpha_{1} & \alpha_{3} & 0 \\
0 & 1 & \alpha_{2} & \alpha_{4}
\end{array}\right)
$$

are positive. Hence by the Routh-Hurwitz stability criterion, the real parts of all characteristic roots of (17) are negative, establishing the local stability of the steady state for the system of differential equations (9)-(11). We should note here that we have been able to establish the stability independently of the sign of $a_{2}$ which may be of any sign.

## 3. COMParative statics

We now conduct a comparative statical analysis of the steady state with respect to changes in the values of the parameters. From (11) we have

$$
\begin{equation*}
X_{i}^{*}=4 \gamma_{i} \pi_{i}^{0} / p_{i}^{2}, \quad i=1,2 \tag{18}
\end{equation*}
$$

This coupled with (15) and (16) yields:

$$
\begin{align*}
& K_{1}^{*}=\left(a_{1}-4 \gamma_{1} b_{1} \pi_{1}^{0} / p_{1}^{2}-4 \gamma_{2} c_{1} \pi_{2}^{0} / p_{2}^{2}\right) 2 \gamma_{1} / p_{1}  \tag{19}\\
& K_{2}^{*}=\left(-a_{2}+4 \gamma_{1} b_{2} \pi_{1}^{0} / p_{1}^{2}-4 \gamma_{2} c_{2} \pi_{2}^{0} / p_{2}^{2}\right) 2 \gamma_{2} / p_{2} \tag{20}
\end{align*}
$$

By simple calculations we get the following Table 1. ${ }^{3}$

[^1]TABLE 1. Comparative Statics

|  | $X_{1}^{*}$ | $X_{2}^{*}$ | $K_{1}^{*}$ | $K_{2}^{*}$ |
| :---: | :---: | :---: | :---: | :---: |
| $p_{1}$ | - | 0 | $?$ | - |
| $p_{2}$ | 0 | - | + | $?$ |
| $\pi_{1}^{0}$ | + | 0 | - | + |
| $\pi_{2}^{0}$ | 0 | + | - | - |
| $c_{1}$ | 0 | 0 | - | 0 |
| $b_{2}$ | 0 | 0 | 0 | + |

Table 1 is not exhaustive, as we are interested only in the effects of changes in the values of some parameters. From Table 1 we can read, for examples, $\partial X_{1}^{*} / \partial p_{1}<0$, $\partial X_{2}^{*} / \partial p_{1}=0, \partial K_{1}^{*} / \partial p_{1} \gtreqless 0, \partial K_{1}^{*} / \partial p_{2}>0$, etc. We should note especially the asymmetrical sign patterns pertaining to changes in $K_{1}^{*}$ and $K_{2}^{*}$. These asymmetries reflect the effects of the predator-prey interaction.

The populations in the steady state with and without harvesting can be compared on the basis of Figs. 1-5 as follows.


Fig. 1. Harvesting of both species.


Fig. 2. Harvesting of both species.


Fig. 3. Harvesting of both species.


Fig. 4. Only prey is harvested.


Fig. 5. Only preditor is harvested.

Consider first the case where two species are both harvested. Let $a_{2}<0,{ }^{4}$ and let $X^{* *}=\left(X_{1}^{* *}, X_{2}^{* *}\right)$ be the pair of the steady state values of $X_{1}$ and $X_{2}$ in the absence of harvesting, and $X^{*}=\left(X_{1}^{*}, X_{2}^{*}\right)$ be that in the presence of harvesting. Three cases are possible (see Figs. $1-3$ ). In these cases, we have unambiguously $X_{2}^{*}<X_{2}^{* *}$. However, for the prey we may have $X_{1}^{*}<X_{1}^{* *}$ (Fig. 1), or $X_{1}^{*}=X_{1}^{* *}$ (Fig. 2), or $X_{1}^{*}>X_{1}^{* *}$ (Fig. 3). If only the prey is harvested (Fig. 4), the steady state shifts from $X^{* *}$ to $A$, and the steady state populations of both species are decreased. If, on the other hand, only the preditor is harvested (Fig. 5), the steady shifts from $X^{* *}$ to $B$. In this case, the prey population increases and the preditor population decreases.

## 4. CONCLUSION

We have formulated a dynamic model of commercial fishing, as distinct from recreational fishing, allowing for existence of natural interaction between the predator and prey, and assuming that the prices of both species will remain constant over time during which fishes are harvested. Our model is different from that of May et al. [4] mainly in that economic rationality of fishing firms is taken into account. It has been found that the steady state or bionomic equilibrium with non-extinct populations of both species is locally stable, regradless of the signs of a parameter pertaining to the intrinsic growth rate of the predator. We have also given a comparative statical analysis of the steady state with respect to changes in exogeneous parameters. The steady state population of the predator in the presence of harvesting is smaller than that in the absence of harvesting, while the prey population in the presence of harvesting may be of any size compared with that in the presence of harvesting. The above comparison holds when both species are simultaneously harvested. Figures 4 and 5 are concerned with similar comparison when only one species is harvested.

Tokyo Metropolitan University

[^2]
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[^0]:    * Thanks are due to a referee who has suggested a simple proof of our stability result.

[^1]:    ${ }^{3}$ If the demand function and the harvesting cost are given as in the footnote 2 , the steady state value of $X_{i}$ is determined by

    $$
    \begin{equation*}
    h^{i}\left(X_{i}^{*}\right) f^{i}\left(h^{i}\left(X_{i}^{*}\right)\right)-C^{i}\left(h^{i}\left(X_{i}^{*}\right), X_{i}^{*}\right)-\pi_{i}^{0}=0, \quad i=1,2 \tag{f}
    \end{equation*}
    $$

    Totally differentiating ( f ), and taking into account the first order condition for maximization of (d), we have

    $$
    \begin{equation*}
    d X_{i}^{*} / d \pi_{i}^{0}=-1 / C_{X_{i}}^{i}>0, \quad i=1,2 \tag{g}
    \end{equation*}
    $$

    However, comparative statics for other variables and parameters are not as straightforward as for the table given above.

[^2]:    ${ }^{4}$ The case where $a_{2}>0$ may be similarly analyzed.

