



Analysis of a predator-prey model for exploited fish populations with schooling behavior



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ABSTRACT

In this paper, a predator-prey model for exploited fish populations is considered, where the prey and the predator both show schooling behavior. Due to this coordinated behavior, predator-prey interaction occurs only at the outer edge of the schools formed by the populations. Positivity and boundedness of the model are discussed. Analysis of the equilibria is presented. A criterion for Hopf bifurcation is obtained. The optimal harvest policy is also discussed using Pontryagin's maximum principle, where the effort is used as the control parameter. Numerical simulations are carried out to validate our analytical findings. Implications of our analytical and numerical findings are discussed critically.

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1. Introduction

It is a fact that many fish species live in groups. They enjoy many benefits from living in groups, such as higher success in finding mates, reduction in the risk of predation, increase in the foraging success, protection from bad weather, etc. Such collective behaviors are of two types, one is *shoaling* and the other is *schooling*. When members of a group swim independently in such a way that they stay connected, then this behavior is known as *shoaling*. If all members are swim in the same direction in a coordinated fashion with same speed then such a behavior is called *schooling*. Schooling fishes are usually of the same species and of the same size. Again shoalers and schoolers are of two types. *Obligate* shoalers or schoolers exhibit shoaling or schooling behavior all the time. *Facultative* shoalers or schoolers show collective behavior for finding mates or some other reasons [25]. Schools that are traveling can form thin lines, or squares or ovals or amoeboid shapes.

Usually interactions of different species take several forms, depending on whether the influences are beneficial or detrimental to the species involved. Among these interactions, predator-prey relationship is considered to be an extremely important one. It is true that the preys always try to develop the methods of evasion to avoid being eaten. However, it is certainly not true that a predator-prey relationship is always harmful for the preys, it might be beneficial to both. Further, such a relationship often plays an important role to keep ecological balance in nature. Mathematical modeling of predator-prey interaction was started in the 1920s. Interestingly, the first predator-prey model in the history of theoretical ecology was developed independently by Lotka (a US physical chemist) and Volterra (an Italian mathematician) [17,29]. Subsequently,

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this model has been used as a machine to introduce numerous mathematical and practical concepts in theoretical ecology. Many refinements of the Lotka–Volterra model have also been made to overcome the shortcomings of the model and to get better insights of predator-prey interactions. We notice an important assumption in such modeling. In these models, it is assumed that the individuals of both predator and prey populations live independently so that any predator can interact with any prey. Consequently, the interaction term is proportional to the product of the density of both populations. This concept is used for many decades by many authors.

Many fish species, which are in predator-prey relationship, have economic importance also. Therefore, developing their management strategies is an important area of research. The literature abounds with evidences of many such predator-prey systems. For example, Arctic cod (*Gadus morhua*) and its commercially important prey species: capelin (*Mallotus villosus*) or herring (*Clupea harengus*) [14]. Another example is tuna (*Thunnus spp.*), which feeds mainly on anchovy (e.g. *Engraulis mordax*) and sardine (e.g. *Sardinops sagax*) [5,22].

Most of the above mentioned fishes (both prey and predator) exhibit schooling behavior. For example, adult cods are usually found in dense schools [6]. Schooling behavior of juvenile tuna is well known [24]. On the other hand, small fishes like capelin, herring and sardine are among very spectacular schooling fishes [8,13,23]. Hence consideration of schooling behavior in predator-prey systems of fishes is of utmost importance. Although a number of predator-prey models for fish populations have been cultured in theoretical ecology (see [10,11,18,27] and references there in), but the effect of schooling behavior has remained unuttered. However, there should be no denying that, in case of many fish populations, ignoring schooling behavior is simply ignoring reality.

From the above viewpoint, we consider a predator-prey model for fish populations, where both prey and predator live in schools. A number of interesting results on stability are established. Some results on extinction of the populations are obtained. A criterion for Hopf bifurcation is established. Optimal harvest policy (to be adopted by the fishery management) is discussed and dynamic optimization of the harvest policy is carried out using Pontryagin's Maximum Principle.

The paper is structured as follows. In Section 2, we present the mathematical model with basic considerations. Positivity and boundedness of solutions of the model are established in Section 3. Section 4 contains the detailed analysis of the equilibria, their stability analysis and a criterion for Hopf bifurcation. Bionomic equilibrium points, optimal harvest policy at equilibrium level, and dynamic optimization of the optimal harvest policy are presented in Section 5. To illustrate our analytical findings, computer simulations of variety of solutions of the system are performed; and the results are presented in Section 6. Section 7 contains the general discussion of the paper and biological significance of our analytical findings.

2. The mathematical model

At time t , let $x(t)$ denotes the density of the prey fish, and $y(t)$ denotes the density of the predator fish. In the following, we explain the basic considerations that motivate us to introduce our basic mathematical model.

- (i) So far as the growth of the prey (in the absence of the predator) is concerned, many modelers have suggested the *logistic growth* function to be a logically reliable choice. The function is introduced in 1838 by the Belgian mathematician Verhulst [28]. The logistic growth equation is given by

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{k} \right), \quad (2.1)$$

where r is the intrinsic per capita growth rate and k is the carrying capacity of the environment. The logic behind this is very simple. As the resources (e.g., space, food, essential nutrients) are limited, every population grows into a saturated phase from which it cannot grow further; the ecological habitat of the population can carry just so much of it and no more. This indicates that the per capita growth rate is a decreasing function of the size of the population, and reaches zero as the population achieves a size k (in the saturated phase). Further, any population reaching a size that is above this value will experience a negative growth rate. The term $-rx^2/k$ may also be regarded as the loss due to intraspecific competition.

- (ii) Usually, it is assumed that the individuals of both predator and prey populations live independently so that any predator can interact with any prey. Consequently, the interaction term is proportional to the product of the density of both populations. This concept is used for many decades by many authors. If predators form a school and they attack a prey population which lives independently; then the predators who occupy the edge of the school would get maximum benefit. The idea of such community behaviors of predators had been given by Cosner et al. [12]. According to this idea, the interaction term should be proportional to the product of density of prey and the square root of the predator density. Similarly, when preys form a school and predators live independently, then the most harmed preys during predator hunting are those staying on the boundary of the school; and so the interaction term should be modified in an analogous manner. Unfortunately, such an innovative idea has not been used by the researchers for about a decade. The work of Chattopadhyay et al. [9] may be regarded as a strong recognition of this concept. Then came the works of Ajraldi et al. [1] and Braza [7], which have given such modeling a new dimension. Their works have stimulated developments in the modeling of group behaviors among various populations. The idea is very interesting. Let P be the density of a population that gathers in groups, and suppose that group occupies an area A . The number of individuals staying at outermost positions in the group is proportional to the length of the perimeter of the patch where the group is located. Clearly, its length is proportional to \sqrt{A} . Since P is distributed over a two-dimensional domain, \sqrt{P} would therefore count the

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