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Existence and global stability of positive periodic solution of tri-trophic food chain with middle predator migratory in nature

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A B S T R A C T

Predator avoidance is the most important factor inducing vertical migration among zooplankton. Light intensity at the surface water also plays an important role to shape the predation pressure on zooplankton as most of the fishes show visually oriented predation. In the present paper, we assume that zooplankton can switch between vulnerable and invulnerable state through vertical migration. This switching is regulated by light intensity, predator abundance and food abundance in surface water. We propose a tri-trophic food chain model incorporating migratory behavior of middle predator. Further, we study the non-autonomous version of the proposed model by incorporating the seasonal variation of the rate parameters of the model. The sufficient conditions for the existence of positive periodic solutions are obtained. We also obtain the conditions for the global attractivity of positive periodic solutions. The numerical experiments are carried out to substantiate analytical findings.

1. Introduction

The diel vertical migration (DVM) of zooplankton in the water column is a well documented but poorly understood biological phenomenon. Diel vertical migration of zooplankton is a behavioral antipredator defense that is regulated by the trade-off between higher predation risk in surface water and reduced growth rate in deep water. It has been observed that zooplankton migrate vertically downward during day hours in the presence of predators (or predator kairomones), and it enters into the surface water again at night to graze phytoplankton [1–8]. Avoidance of visually orienting planktivorous fish and carnivorous invertebrate is the most important factor which regulates DVM in zooplankton [2,3,7,9–15]. The strength of downward migration of zooplankton increased with increases in concentration of fish or fish-exudates [5,16]. Usually, zooplankton take daytime refuge in the hypolimnion from the pelagic epilimnion to avoid light-dependent fish predation [3,17]. Zooplankton, those migrate downwards experience lower temperature and food deficiency, which force them to migrate vertically upward into the upper layer of the water column to predate phytoplankton. This upward migration of zooplankton from lower layer to upper layer is proportional to available phytoplankton density in the upper layer. Increase in

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phytoplankton density increases the strength of upward vertical migration of zooplankton by leaving the lower layer entering into the upper layer [18].

The light availability into the water column decisively determines the predation pressure on the zooplankton from visually orientated planktivorous fish. Concurrently, the abundance of phytoplankton, the main food source for zooplankton, is highest in the warm surface water, where the predation by visual planktivores is most intensive. Facing these two contradictory situations, most of the zooplankton species exhibit different strategies regarding their position in the water column. These strategies usually exhibit a trade-off between consumption of adequate food and decreasing the threat of predation. One possible strategy is "better hungry than dead" [3,19], seen in zooplankton that perform diel vertical migrations. They spend the daytime into the hypolimnion (safe but cold and food-poor lower layer), and migrate upward to the epilimnion (warm and food-rich surface water) at night. The contrasting "better dead than unfed" strategy is adopted by some zooplankton staying in the epilimnion until they feed sufficient amount of food to tolerate the metabolic cost and the cost of vertical migration, in spite of the greater danger of predation [20–22].

Experimental and field data revealed that besides biotic factors (predation pressure and food availability), abiotic factors such as light intensity [23], thermal stratification [24–26], dissolved oxygen [27,28] and salinity [29] stimulate the vertical distribution of zooplankton. Food availability, predation pressure and light are the major control variables of DVM [30–35]. Light, among the abiotic factors is the most important factor inducing diurnal vertical migrations of zooplankton in the upper water layer [36–38]. Light act as a visual cue which mediates strong effects on such avoidance behavior in the presence of predator population [2,39]. Changes in light intensity have been proposed as the main exogenous factor causing vertical migrations of zooplankton at dawn and dusk, in both marine and freshwater environments [39,40]. Although light induced swimming of Daphnia was found to be enhanced in the presence of a predator kairomone [41,42], food concentration also plays a vital role in the swimming velocity of zooplankton in response to light changes [43,44].

In this paper, we first formulate and analyze a simple tri-trophic food chain model regarding phytoplankton, zooplankton and fish populations, where the middle predator (zooplankton) can migrate. Predator avoidance and food dependent migrations make the zooplankton population switch between invulnerable and vulnerable state. In Section 2, detail assumptions and the model formulation are given, and the model analysis has been done in Section 3. In Section 4, we propose the non-autonomous version of the above model by incorporating the seasonality in rate parameters. The sufficient conditions for the existence of positive periodic solutions and the global attractiveness of these solutions are derived in Sections 5 and 6 respectively. In Section 7, numerical simulations are carried out, and finally the paper ends with a conclusion.

2. Mathematical model

Depending on the light availability into the water column, we split the whole pelagic water mass into two layers: surface water and deep water. The water column above the secchi depth is referred as surface water or upper layer, where light is available at daytime; whereas, below the secchi depth, the water column, where light is not available (or available light intensity is very low) during day hours, is refereed as the lower layer (deep water). We assume that phytoplankton (P) are present only in the upper layer, and its density is homogenous throughout the layer. Let, Z_1 and Z_2 be the abundance of zooplankton in the upper layer and lower layer respectively. We assume that zooplankton in the upper layer graze on phytoplankton and zooplankton in the lower layer cannot predate until they enter into surface water.

Most of the fishes show visually oriented predation (light-dependent predation) on zooplankton. Thus, we assume that fish predate zooplankton only in the upper layer. Zooplankton of upper layer migrates vertically downward to escape from the light-dependent mortality imposed by visually orienting predator (fish) during day hours. This down-ward migration of zooplankton from upper layer to lower layer is directly proportional to predation pressure (i.e., predator abundance). In the presence of kairomones (predator and/or predator exudates) a portion of zooplankton becomes invulnerable to predator through the prey refuge (via downward vertical migrations). On the other hand, zooplankton of lower layer experience lower temperature and food deficiency, which force them to migrate vertically upward into the upper layer of the water column to predate phytoplankton. This upward migration of zooplankton from lower layer to upper layer is also proportional to available phytoplankton density in the upper layer. Thus, zooplankton population makes the transition from vulnerable to invulnerable state through inducible defense mechanisms (vertical migration) in the presence of predators. We also assume that zooplankton living in the lower layer cannot reproduce.

Keeping the above facts in mind the dynamics of the system is governed by the following systems of nonlinear differential equations:

$$
\begin{aligned}
\frac{dP}{dt} &= rP\left(1-\frac{P}{K}\right)-\frac{a_1PZ_1}{b_1+P},\\
\frac{dZ_1}{dt} &= \frac{c_1a_1PZ_1}{b_1+P}-\frac{a_2Z_1^2F}{b_2^2+Z_1^2}-m_1Z_1F+m_2PZ_2-\mu Z_1,\\
\frac{dZ_2}{dt} &= m_1Z_1F-m_2PZ_2-\mu Z_2,\\
\frac{dF}{dt} &= \frac{c_2a_2Z_1^2F}{b_2^2+Z_1^2}-\phi F.
\end{aligned}
\tag{2.1}
$$