A coupled plankton system with instantaneous and delayed predation

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We present two simple plankton population models: one has instantaneous predation, another has delayed predation. The models consist of two coupled differential equations representing the interaction between phytoplankton and herbivorous zooplankton with additional effect of zooplankton predation by a constant fish population. We study the dynamical behaviour and investigate the conditions to guarantee the coexistence of two species, and address the stability and bifurcation under different density of fish, with or without the maturation time delay. Analytical methods and numerical simulations are used to obtain information about the qualitative behaviour of the models.

Keywords: phytoplankton; herbivorous zooplankton; effect of fish; maturation time delay; stability; bifurcation

1. Introduction

Plankton play a key role in the aquatic community. Phytoplankton are the smallest creatures in the ocean and lakes which form the base of the food chain; herbivorous (plant-eating) zooplankton graze on phytoplankton and are eaten by zooplankton predators, such as fish. Understanding the dynamics of plankton populations and their interactions is of major importance.

There are extensive mathematical models dealing with plankton populations. Some of them (e.g. [4,9]) seek to contain a faithful representation of the physical and/or biological factors, based on the field data and experiment results. From a mathematical point of view, they are too complicated for the theoretical analyses and only amenable to numerical experimentation. Some others (e.g. [6, 7,28]) seek to explore simple models in order to recognize the possible qualitative behaviours of the system, although there are some obvious shortcomings and uncertainties. Besides abundant models represented by ordinary differential equations, the need for delays and consideration of spatial diffusion in population biology and spatial ecology have been emphasized from the 1920s onwards and received increasing attention recently. Beretta et al. [1] used a distributed delay to model nutrient recycling in a constructed chemostat-type model. Cushing [5] and Ruan [20] studied the effect of delays on stability and persistence in prey–predator plankton models. Nonlinear dynamics...
of predator–prey models with discrete delay was given by Ruan [21] in the survey paper. Gourley and Kuang [10] and Wang et al. [32] formulated some predator–prey models with stage structure and discussed the dynamical properties such as global attractivities, permanence and extinction of the population. The role of dispersal in the maintenance of patchiness, or spatial population variation, in planktonic systems has been studied by Steele [26,27]. In [31], Van Nes and Scheffer addressed the impact of the spatial pattern of heterogeneity and the occurrence of dispersion in the populations in space. In [14], we considered a single phytoplankton model describing the physical process by incorporating light, sinking and self-shading effect and showed that depending on the sinking rate of the phytoplankton, light intensity and water depth, the plankton can concentrate either near the surface, at the bottom of the water column or both. For more details about mathematical modelling in plankton ecosystem, we refer [16], the survey paper [18] and the references therein.

The interaction of phytoplankton and herbivorous zooplankton basically follows the prey– predator relation. Moreover, in water quality research, increased attention is being paid to the effect of fish on phytoplankton biomass [23]. Hrbáček’s [13] work showed the big differences between the plankton of different ponds depending on the presence of fish. Biologically, at low fish density, zooplankton is food-limited and phytoplankton density is controlled by zooplankton grazing. Whereas at high fish density, zooplankton is controlled by fish predation and phytoplankton is light or nutrient-limited.

When considering herbivorous zooplankton suffering losses from predation of fish, we propose two mathematical models to describe the interaction between phytoplankton and herbivorous zooplankton incorporating fish predation. First, we ignore the duration time of immature predator (herbivorous zooplankton), discuss a coupled ordinary differential system by regarding the herbivorous zooplankton as a predator of phytoplankton on the one hand and the prey of fish on the other. In the natural process, when the prey population falls below a certain level, the predator migrates to another region in search of food and return only when the prey population rises to the required level. Furthermore, adopting the idea used in [10], we assume that the herbivorous zooplankton are divided into immature and mature groups, and only mature predators are capable of preying on the phytoplankton; immature predators do not have the ability to reproduce. Taking the maturation time into account, we provide and discuss a system of coupled delay differential equations. The models given in this article belong to the classical predator–prey model with nonlinear harvesting.

The role of higher level predation in plankton population was discussed in [8]. Some types of predator–prey model with constant harvesting have been studied in [2,3,34]. We use the Holling [12] type III function as the harvesting function which was used in [16,17] where the authors have shown that very complicated dynamics and bifurcations can occur even in scalar equations.

The rest of the present paper is organized as follows. We introduce two mathematical models to describe the interaction between phytoplankton and herbivorous zooplankton with predator fish in Section 2 and discuss the dynamical properties of these two kinds of systems by using the analytical and numerical methods in Sections 3 and 4. For the instantaneous predation model, we derive the conditions for the existence and stability of the steady state, analyse the bifurcations when taking into account the impact of fish predation and give the respected biological interpretation. For the delayed model, we investigate the effect of maturation time delay with the interaction of fish in the qualitative behaviour of the system, such as stability of the steady state and oscillatory dynamics. Some comments are given in Section 5.

2. Mathematical model

We study a coupled model concerning the phytoplankton ($P$) and herbivorous zooplankton ($H$) interactions incorporating the zooplankton predation by a constant fish population, in a physically
homogeneous oceanic layer. We assume that the phytoplankton (the prey) grow in a logistic form when the consumer, herbivorous zooplankton (the predator), is absent; the dependence of the herbivorous zooplankton grazing rate on phytoplankton is of the form of Holling type II; and the zooplankton predation by fish follows a sigmoidal functional response of Holling type III, then we arrive at the following model:

$$\frac{dP(t)}{dt} = RP(t)\left(1 - \frac{P(t)}{K}\right) - \frac{AP(t)}{C_1 + P(t)}H(t),$$

$$\frac{dH(t)}{dt} = \alpha \frac{AP(t)}{C_1 + P(t)}H(t) - \beta H(t) - F \frac{H^2(t)}{C_2^2 + H^2(t)}, \quad (1)$$

where the parameters $R$ and $K$ denote the intrinsic growth rate and carry capacity of phytoplankton, respectively; $C_1$ represents the half-saturation abundance of phytoplankton; $A$ is the yield coefficient of phytoplankton to herbivorous zooplankton; parameter $\alpha$ is the rate of food utilization; $\beta$ is the mortality rate of the predator (herbivorous zooplankton); $F$ represents the plantivorous capacity of the fish community and $C_2$ parameterizes the saturating functional response of zooplankton. All the parameters in Equation (1) are positive. A similar model is studied numerically in [25].

When the influence of fish is ignored ($F = 0$), Equation (1) is a special case in [29] where the short-term oscillations can occur if the zooplankton mortality was modelled using a linear form. When $C_2 = 0$, Equation (1) becomes a predator–prey system with constant rate harvesting, and rich and complicated dynamical behaviour including Hopf, homoclinic and Bogdanov–Takens bifurcations have been discovered by Brauer and Soudack [2,3] and Xiao and Ruan [34].

Time delay plays an important role in many biological dynamical systems, being particularly relevant in ecology. Hence, a determination of the effect of delay on ecological models is of biological interest. Based on the model (1), we assume that there is a constant maturation time delay (through-stage time delay) in herbivorous zooplankton, and the immature herbivorous zooplankton suffer a mortality rate of $d$ and take $\tau$ units of time to mature, then Equation (1) becomes

$$\frac{dP(t)}{dt} = RP(t)\left(1 - \frac{P(t)}{K}\right) - \frac{AP(t)}{C_1 + P(t)}H(t),$$

$$\frac{dH(t)}{dt} = \alpha e^{-d\tau} \frac{AP(t-\tau)}{C_1 + P(t-\tau)}H(t-\tau) - \beta H(t) - F \frac{H^2(t)}{C_2^2 + H^2(t)}, \quad (2)$$

where the time delay $\tau \geq 0$ and $H(t)$ represents the matured herbivorous zooplankton. Here, we omit the equation related to the change of immatured herbivorous zooplankton since it is decoupled with Equation (2). For more details, we refer to [10].

Before analysing the model, it is essential, or rather obligatory, to express it in non-dimensional terms. We introduce non-dimensional quantities by

$$p = \frac{P}{K}, \quad h = \frac{H}{\alpha},$$

so Equation (1) can be rewritten as

$$\frac{dp(t)}{dt} = Rp(t)(1 - p(t)) - \frac{ap(t)}{1 + bp(t)}h(t),$$

$$\frac{dh(t)}{dt} = \frac{ap(t)}{1 + bp(t)}h(t) - \beta h(t) - F \frac{ch^2(t)}{1 + c^2h^2(t)}, \quad (3)$$

where $a = \alpha AK/C_1$, $b = K/C_1$ and $c = \alpha/C_2$ are all positive.
Parallely, Equation (2) becomes

\[
\frac{dp(t)}{dt} = Rp(t)(1 - p(t)) - \frac{ap(t)}{1 + bp} h(t)
\]

\[
\frac{dh(t)}{dt} = \frac{ae^{-d\tau} p(t - \tau)}{1 + bp(t - \tau)} h(t - \tau) - \beta h(t) - F \frac{ch^2(t)}{1 + c^2h^2(t)}.
\]

(4)

3. Instantaneous predation

First we neglect the time delays involved in the predation process of the herbivorous zooplankton by assuming the delay \(\tau = 0\) and investigate the general dynamical property of the solution in Equation (3) under the initial condition (IC) \(p(0) = p_0 \geq 0\) and \(h(0) = h_0 \geq 0\). Let \(D = \{(p, h) \in \mathbb{R}^2 : p \geq 0, h \geq 0\}\), we have the following.

**Theorem 3.1** The solution of Equation (3) is positively invariant and bounded in \(D\).

**Proof** Since

\[
\frac{dp}{dt} = pf_1(p, h), \quad \frac{dh}{dt} = hf_2(p, h),
\]

with

\[
f_1(p, h) = R(1 - p) - \frac{ah}{1 + bp}, \quad f_2(p, h) = \frac{ap}{1 + bp} - \beta - F \frac{ch}{1 + c^2h^2},
\]

it is obvious that \(\frac{dp}{dt}\big|_{p=0} = \frac{dh}{dt}\big|_{h=0} = 0\), hence all the solutions of Equation (3) are positive for \(t \geq 0\).

From \(\frac{dp}{dt} < Rp(1 - p)\), we have \(\lim_{t \to \infty} \sup p(t) \leq 1\). Furthermore, since \(\frac{dp}{dt}\big|_{p=1} < 0\), we can see that \(p(t) \leq 1\) for large \(t\); hence, \(p(t)\) is bounded in \(D\).

Let \(V(p, h) = p(t) + h(t)\), then

\[
\dot{V} = p' + h' = Rp(1 - p) - \beta h - F \frac{ch^2}{1 + c^2h^2} = R - R \left(p - \frac{1}{2}\right)^2 - \beta h - F \frac{ch^2}{1 + c^2h^2},
\]

therefore \(p' + h' < R/4 - \beta h\). Because of the boundedness of \(p(t)\), we have \(h(t) \to 0\) when \(t\) approaches \(\infty\), implying that \(h(t)\) is bounded in \(D\) as well. \(\blacksquare\)

3.1. Existence and stability of the steady state

It is easy to observe that the system (3) always has a plankton-free steady state \(E_0 = (0, 0)\) and a feasible zooplankton-free steady state \(E_1 = (1, 0)\); however, there is no phytoplankton-free steady state. By computing the Jacobian matrix of the system,

\[
J(0, 0) = \begin{bmatrix} R & 0 \\ 0 & -\beta \end{bmatrix}, \quad J(1, 0) = \begin{bmatrix} -R & -\frac{a}{1 + b} \\ 0 & \frac{a - \beta(1 + b)}{1 + b} \end{bmatrix},
\]

we know that the steady state \(E_0\) is a saddle point while the feasible zooplankton-free steady state \(E_1 = (1, 0)\) is stable if the parameters satisfy \(a < \beta(1 + b)\). Moreover, we have the following global stability result for \(E_1\).
THEOREM 3.2 When $a \leq \beta(1 + b)$, then all the solutions of Equation (3) admit that $\lim_{t \to \infty} p(t) = 1$ and $\lim_{t \to \infty} h(t) = 0$.

Proof From the positivity of the solutions in Theorem 3.1 and $p'(t) \leq Rp(t)(1 - p(t))$, we have $\lim_{t \to \infty} \sup p(t) \leq 1$. Let $\epsilon > 0$ be arbitrary. Then, there exists $t_0 > 0$ such that $p(t) < 1 + \epsilon$ for all $t > t_0$.

Since $u(p) = a p/(1 + bp)$ is increasing with respect to $p$, i.e. $u(p) \leq u(1 + \epsilon), h'(t) \leq u(1 + \epsilon)$, we have

$$h(t) - \beta h(t) = (u(1 + \epsilon) - \beta)h(t).$$

Under the condition $a \leq \beta(1 + b)$, there are two cases:

(i) If $a < \beta(1 + b)$, then, by continuity, $u(1 + \epsilon) < \beta$ for a suitably chosen small $\epsilon > 0$ and so, by comparison, $\lim_{t \to \infty} h(t) = 0$.

From $(ap(t)/(1 + bp(t)))h(t) = (a/(1 + bp(t)))p(t)h(t)$, since $a/(1 + bp(t)) \leq a$ is bounded and we have shown that $\lim_{t \to \infty} h(t) = 0$, there must exist $0 < \eta < 1, t_1 > 0$ such that, for all $t > t_1$, $(ap(t)/(1 + bp(t)))h(t) \leq \eta p(t)$ and

$$p'(t) = Rp(t)(1 - p(t)) - \frac{ap(t)}{1 + bp(t)}h(t) \geq p(t)(R - \eta - Rp(t)).$$

Using the comparison argument again, we know $\lim_{t \to \infty} \inf p(t) \geq 1 - \eta/R$ implying that $\lim_{t \to \infty} \inf p(t) \geq 1$. Combining with $\lim_{t \to \infty} \sup p(t) \leq 1, \lim_{t \to \infty} p(t) = 1$ must hold.

(ii) When $a = \beta(1 + b)$, from $p'(t) \leq Rp(t)(1 - p(t))$, there are two subcases: (a) $p(t) > 1$ and $\lim_{t \to \infty} p(t) = 1$, or (b) there exist $t_2 > 0$ such that $p(t) < 1$ when $t > t_2$. Using similar methods to that in [10], we can obtain that $\lim_{t \to \infty} p(t) = 1, \lim_{t \to \infty} h(t) = 0$.

The proof is complete. $\blacksquare$

The above result indicates that $E_1$ attracts all feasible solutions under the condition $a \leq \beta(1 + b)$. Biologically, it means that when the herbivorous zooplankton’s grazing rate at the peak of phytoplankton abundance is less than their death rate, then the herbivorous zooplankton cannot survive.

Is it possible for phytoplankton and herbivorous zooplankton to coexist? From the dynamical point of view, we seek the conditions for the existence of the positive steady state $(p^*, h^*)$. From the first equation in Equation (3), we have $h^* = (R(1 - p^*)/(1 + bp^*)/a) > 0$, then $0 < p^* < 1$. Substituting this expression of $h^*$ into the second equation in Equation (3), after a tedious computation, we know $p^*$ must be a real positive root of a fifth-order polynomial

$$P_5(p) = a_0 p^5 + a_1 p^4 + a_2 p^3 + a_3 p^2 + a_4 p + a_5 = 0$$  \hspace{1cm} (5)

with

$$a_0 = b^2 c^2 R^2(\beta b - a), \quad a_1 = bc^2 R^2(-2\beta b^2 + 2ab + 3\beta b - 2a),$$
$$a_2 = -c R(ac R + ab^2 c R + 6\beta b^2 c R - 3\beta bc R - \beta b^3 c R - 4abc R + ab^2 F),$$
$$a_3 = c R(2ac R + 3\beta b^2 c R - 6\beta bc R + \beta c R - 2abc R + ab^2 F - 2ab F),$$
$$a_4 = -ac^2 R^2 - 2\beta c^2 R^2 + \beta ba^2 - a^3 + 3\beta bc^2 R^2 + 2abc FR - ac FR,$$
$$a_5 = \beta c^2 R^2 + \beta a^2 + ac FR.$$

Unfortunately, we cannot solve this quintic equation by the extraction of roots and the elementary operations generally. However, we notice that $a_5$ is always positive and $a_0 < 0$ if $a > \beta b$.

Therefore, we can obtain a sufficient condition for the existence of both plankton.
**Lemma 3.3** When $a > \beta (1 + b)$, there exists at least one positive equilibrium point $E_* = (p^*, h^*)$ with $0 < p^* < 1$ and $h^* > 0$.

**Proof** When $a > \beta (1 + b)$, $a > \beta b$ is obvious from $\beta > 0$, then we have $a_0 < 0$ and $a_0 a_5 < 0$. The condition $a_0 a_5 < 0$ guarantees one positive real root in Equation (5), although it is possible to have more than one root. In addition,

$$P_5(0) = a_5 > 0, \quad P_5(1) = \sum_{i=0}^{5} a_i = a^2(1 + b) - a < 0,$$

$P_5(p)$ is continuous with respect to $p$, therefore there exists $0 < p^* < 1$ such that $P_5(p^*) = 0$.

The proof is complete. \[\blacksquare\]

**Remark 3.4** If and only if $P'_5(p) = 5a_0 p^4 + 4a_1 p^3 + 3a_2 p^2 + a_3 p + a_4 < 0$ for $0 \leq p \leq 1$, the positive equilibrium point $E_*$ is unique.

From now on, in this section, we always assume $(C_1) : a > \beta (1 + b)$.

More specifically, the positive equilibrium point(s) of Equation (3) is (are) determined by

$$h = \frac{R(1 - p)(1 + bp)}{a},$$

$$\frac{1}{F} \left( \frac{ap}{1 + bp} - \beta \right) = \frac{ch}{1 + c^2 h^2}. \quad (6)$$

Let $G_1(p, F) = (1/F)(ap/(1 + bp) - \beta)$ and $G_2(p) = ch(p)/(1 + c^2 h(p)^2)$ with $h(p) = (R(1 - p)(1 + bp))/a$. We notice that $G_2(p)$ is independent of the parameter $F$. Thus, with the variation of $F$, we can observe that there may be one, two or three positive equilibrium points (Figure 1) by fixing the parameters

$$a = 6, \quad b = 5, \quad c = 4, \quad R = 2, \quad \beta = 0.4 \quad (7)$$

satisfying the assumption $(C_1)$. Obviously, we can see that the system undergoes some critical movement with the variation of the coefficient $F$ which corresponds to the effect of fish. This demonstrates that the model can exhibit rich dynamics, agreeing with the study in [16,17].

Generally speaking, to check the stability at the positive equilibrium point $E_*$ in Equation (3), we need to find some information from the linearized system. Let $x = p - p^*$ and $y = h - h^*$, then the linearization of Equation (3) at $(x, y) = (0, 0)$ is

$$\dot{x} = [R(1 - 2p^*) - h^* u'_s] x(t) - u_s y(t),$$

$$\dot{y} = h^* u'_s x(t) - F h^* v'_s y(t), \quad (8)$$

where $u_s, u'_s$ is the value of $u(p), u'(p)$ at $p = p^*$ and $v_s, v'_s$ is the value of $v(h), v'(h)$ at $h = h^*$, respectively,

$$u(p) = \frac{ap}{1 + bp}, \quad v(h) = \frac{ch}{1 + c^2 h^2}. \quad (9)$$

The characteristic equation of Equation (8) is $\lambda^2 + (B_2 - A_1) \lambda - A_1 B_2 + A_2 B_1 = 0$, where

$$A_1 = R(1 - 2p^*) - h^* u'_s, \quad A_2 = u_s > 0, \quad B_1 = h^* u'_s > 0, \quad B_2 = F h^* v'_s. \quad (10)$$

Since we do not have the exact expressions of $p^*$ and $h^*$ with respect to the original system parameters, the determination of the stability of $E_*$ is far more than trivial. However, by analysing
the distribution of the roots in the characteristic equation, we can summarize some sufficient conditions with respect to the coefficients $A_i$ and $B_i$ ($i = 1, 2$), as the following.

**Theorem 3.5**

(i) When $A_1 < B_2$. If $A_1B_2 < A_2B_1$, $E_*$ is locally asymptotically stable; if $A_1B_2 = A_2B_1$, $E_*$ is stable but not locally asymptotically stable since $\lambda = 0$ is an eigenvalue. The fold bifurcation appears at $A_1B_2 = A_2B_1$.

(ii) Under either of the three cases, $E_*$ is unstable.

(a) $A_1B_2 > A_2B_1$;  
(b) $A_1B_2 < A_2B_1$, $A_1 \geq B_2$;  
(c) $A_1B_2 = A_2B_1$, $A_1 > B_2$.

Moreover, there is a pair of purely imaginary eigenvalues when $A_1 = B_2$ in the case (b). If the transversality condition is satisfied, then periodic solutions bifurcate from $E_*$ via Hopf bifurcation (HB).

(iii) When $A_1B_2 = A_2B_1$ and $A_1 = B_2$, $E_*$ may be stable or unstable, and second-order effects need to be examined in order to determine the stability. The system may undergo Bogdanov–Takens bifurcation when $\lambda = 0$ is a repeated eigenvalue or Hopf-zero bifurcation if $\lambda = 0$ and $\lambda = i\omega$ are all eigenvalues.

### 3.2. Bifurcation analysis

From Figure 1 and Theorem 3.4, we understand that the system may undergo some bifurcations as the variation of parameters. For fold bifurcation, it is easy to see that when $A_1B_2 = A_2B_1$, the bifurcated non-zero solution is stable if $A_1 < B_2$ and unstable if $A_1 > B_2$. Due to the complicity of the system, the analysis of Hopf, Bogdanov–Takens and other high-codimensional bifurcation is very complicated and tedious, although the centre manifold theory and normal form methods [11] can be used.

With the help of XPPAUTO, we shall do some numerical analysis to illustrate some of the rich dynamics exhibited in the system. Let $F$ be a bifurcation parameter and using the parameter values given in Equation (7), the bifurcation diagram depicted in Figure 2 shows some interesting
Figure 2. Variations in the steady-state values of (a) phytoplankton and (b) herbivorous zooplankton vs. the predator fish $F$.

features:

(i) when the value of $F$ is small, there is only one unstable steady-state positive equilibrium with a small value of $p$ and a large value of $h$. By analysing the nullclines and directions in each regions of $(p, h)$ (Figure 3(a)), we can claim the existence of the stable limit cycle from Poincaré–Bendixson’s theorem. So the steady state is surrounded by a stable limit cycle and the kinetics of the system is oscillatory. Figure 3(b) shows that trajectories are attracted to a stable limit cycle.

(ii) when $F$ is sufficiently large, there exists a stable equilibrium state with high value of $p$ and low value of $h$ (see Figure 4 with different IC).

(iii) The most interesting part is that for the intermediate values of $F$, the system exhibits very rich dynamics. First, note that as $F$ is increased from zero to the first critical value, the system undergoes an abrupt jump, a stable steady state with a high value of $p$ and a low value of $h$ emanates from the cusp catastrophe bifurcation; as $F$ is increased a little further, the branch of periodic orbits that comes out of the Hopf point is subcritical (open circle), which means the branch of the limit cycle which emanates from the HB appears as $F$ is decreased, rather than increased. So in a small range of $F$, as $F$ decreases, there is bistability that includes the

Figure 3. (a) Nullclines and directions and (b) the stable oscillatory orbits.
stable fixed point and the stable limit cycle (Figure 5). The stable limit cycle terminates on
the fold and gives rise to a Bogdanov–Takens bifurcation (double zero eigenvalues). In fact,
the frequency of the limit cycle goes to zero as the saddle node (SN) is approached (Figure 6).
With $F$ crossing the critical value of the Hopf point, the model exhibits a hysteresis effect.
There is a jump for $p$ from a low to a high value and the opposite for $h$. We can observe two
stable steady states (Figure 7).

Biologically, if the food utilization rate is very low, that is, the yield coefficient of phytoplank-
ton to zooplankton is relatively small, the condition $(C_1)$ does not hold, then the zooplankton is
gradually going to die out, the phytoplankton is growing and reaching a very high level which
is called ‘phytoplankton bloom’. This is the situation we should avoid and control in the real
ecosystem. If both phytoplankton and zooplankton can coexist in an appropriate environment,
due to the consumption of phytoplankton by zooplankton, and zooplankton by fish, starting from
a fishless situation, addition of fish results in an increase in phytoplankton density and a relatively
small increase in zooplankton, keeping the system undergoing a sustained large oscillation, until
at a certain fish density, the ‘regime shift’ [24] takes place. Gradual increasing of fish starting at
this stage will cause the appearance of a phytoplankton-dominated stable stationary state, together
Figure 6. Frequency of the periodic orbits.

Figure 7. (a) Phase portrait and (b) time series when $F = 1.01$.

With the stable limit cycle making the system bistable. As fish density is increased further, the stable oscillation state disappears and a stable steady state appears, keeping the system’s bistability with two stable steady states. The steady state with intermediate density of both plankton is usually called the refuge equilibrium while the steady state with high density of phytoplankton and low density of zooplankton is called the outbreak equilibrium. Phytoplankton-dominated stationary states are typical for high predation rates. From the view point of controlling ‘phytoplankton bloom’, to keep the populations at a refuge state rather than allow them to reach an outbreak situation, one may keep the fish density below the critical level. Then the phytoplankton productivity will be reduced to a certain extent.

Since the earliest days of phytoplankton ecology, nutrients have been invoked as one of the variables controlling phytoplankton community structure and biomass [30]. In our model (3), the nutrient uptake by phytoplankton is reflected by the parameter $R$. Fish density and nutrient concentration are environmental factors that can be manipulated. We can track the dynamics of Equation (3) by varying the two parameters $F$ and $R$. 
Figure 8. Variations of the bifurcation diagram with different values of $R = 1, 2, 3$.

Definitely, the effect of fish on the steady states of the system depends on the nutrient concentration. First, we can observe from the bifurcation diagram with bifurcation variable $F$ (Figure 8) that, at the low level of nutrient, the response of fish density is simple. With the low density of fish, the system exhibits a relative large oscillation until the store of fish reaches a critical level, then the system will remain in a phytoplankton-dominated steady state (Figure 8(a), $R = 1$). If the nutrient supply is sufficient, when the predation rate by fish crosses the critical value, the catastrophic regime shift occurs (Figure 8(b), $R = 2$). As the nutrient level increases, the region of fish with bistability (one stable steady state and one stable limit cycle or two stable steady states) will increase and the system can tolerate more fish before switching to the phytoplankton-dominated state than at intermediate nutrient concentrations (Figure 8(c), $R = 3$).

In fact, in [22,33], the authors explained the patterns in the abundance of phytoplankton among lakes using some real data by focusing on the supply of limiting nutrients and on grazing pressure by zooplankton; in [19], three different situations, (i) stable coexistence of species, (ii) alternative stable states or (iii) competitive exclusion, were investigated by experiments. If we take both $F$ and $R$ as the bifurcation parameters, we can obtain the two-parameter bifurcation diagram which is given in Figure 9. The three bifurcation curves (two SN and one HB) divide the whole plane into four parts. In part I (left of the first SN bifurcation curve and above the HB curve), there is only one unstable equilibrium point, and all the orbits will be attracted to a stable limit cycle (Figure 3) since all the states are bounded. In this region with a relatively small amount of fish, the system always keeps oscillation even when the nutrient uptake rate is large. Whereas in part II (below the right SN and HB curves), there is only one stable equilibrium point with a large value of $R$ and adequate value of $F$. This is a phytoplankton-dominated region. If the parameters ($F, R$) moves from Part I to Part III, (above the HB and between two SN curves), there is an abrupt jump of the plankton concentration. When ($F, R$) closes to the HB curve, a stable branch of limit cycles
emanates from the HB. Corresponding to the intermediate range in Figure 2, the hysteresis effect occurs in part IV, that is, the stable limit cycle disappears, and two stable steady states coexist with an unstable steady state in this region. More complicated and high-codimensional bifurcation can occur at the intersection points of each of the three basic bifurcation curves.

Figure 10 shows some trajectories with different values of $R$ and fixed $F$. We can observe, in Figure 10(a), that when $F$ is small ($F = 0.5$), with the same initial condition, for small value of $R$ ($R = 0.5$), the solution approaches a stable equilibrium point; for a slightly large $R$ ($R = 0.6$), the solution becomes oscillatory, and the amplitude gets larger with the increase of the value of $R$ ($R = 0.7$); when $F$ is sufficiently large, with the appropriate value of $R$, there exists multistability implying different stable equilibrium points or a stable equilibrium point and stable periodic solutions can coexist, depending on the initial conditions. Figure 10(b) shows the orbits with two different stable equilibrium points when $R = 2.5$ and one stable equilibrium and one stable periodic wave when $R = 2.8$. 
4. Delayed predation

In this section, we discuss the model with delayed predation and focus on the effect of delay in the system (4) which is rewritten as
\[
\begin{align*}
\frac{dp(t)}{dt} &= Rp(t)(1 - p(t)) - u(p(t))h(t), \\
\frac{dh(t)}{dt} &= e^{-d\tau}u(p(t - \tau))h(t - \tau) - \beta h(t) - Fv(h(t))h(t),
\end{align*}
\] (11)

where the functions $u, v$ are given in Equation (9).

Following the argument in the proof of Theorem (3.1) in Section 3, one can derive the boundedness of the solutions of Equation (11).

**Theorem 4.1** The solution of Equation (11) is positively invariant and bounded under the IC
\[
p(t) = \phi_1(t), \quad h(t) = \phi_2(t), \quad \text{for } -\tau < t \leq 0,
\] where $\phi_i (i = 1, 2)$ are positive continuous functions.

Parallel to the discussion in Section 3, it is obvious that the trivial equilibrium point $E_0 = (0, 0)$ is always a saddle point and the feasible zooplankton-free equilibrium point $E_1 = (1, 0)$ always exists. About the global stability of $E_1$, we have the following.

**Theorem 4.2** When $ae^{-d\tau} \leq \beta(1 + b)$, then all the solutions of Equation (11) admit that $\lim_{t \to \infty} p(t) = 1$ and $\lim_{t \to \infty} h(t) = 0$.

Similarly, we can obtain that when the condition $(C_2)$: $ae^{-d\tau} > \beta(1 + b)$ holds, there exists at least one positive steady state $E_*(p^*, h^*)$ in Equation (11), and with the increasing of delay $\tau$, the number of the positive steady state decreases, and the equilibrium loses feasibility at a finite value of $\tau^* = -(1/d) \ln(\beta(1 + b)/a)$. To investigate the stability of the positive equilibria $E_*$ with the possible impact of the time delay, we linearize the system (11) as
\[
\begin{align*}
\dot{x} &= [R(1 - 2p^*) - h^*u'_x]x(t) - u_s y(t), \\
\dot{y} &= e^{-d\tau}[h^*u'_s x(t - \tau) + u_s y(t - \tau)] - (e^{-d\tau}u_s + Fh^*v'_s)y(t).
\end{align*}
\] (12)

The characteristic equation is
\[
\lambda^2 + (B_3 - A_1)\lambda - B_2\lambda e^{-\lambda\tau} + (A_1B_2 + B_1A_2)e^{-\lambda\tau} - A_1B_3 = 0
\] (13)

with
\[
A_1 = R(1 - 2p^*) - h^*u'_s, \quad B_1 = u_s, \quad A_2 = e^{-d\tau}h^*u'_s, \\
B_2 = e^{-d\tau}u_s, \quad B_3 = e^{-d\tau}u_s + Fh^*v'_s.
\]

We notice that since the values of the positive equilibrium point are dependent on the delay $\tau$, so for all the coefficients in Equation (12), the well-developed theory and methods (e.g. in [15,21]) cannot be used. The most serious complication is that we cannot even obtain the explicit relation of the equilibrium with respect to the time delay $\tau$. Thus, the theoretical analysis of the stability at $E_*$ becomes impossible.
By using numerical computation and simulation, we can observe some interesting dynamical behaviour. In the following, we still fix the parameters given in Equation (7) and choose appropriate $d$ and $\tau$ to satisfy the condition $(C_2)$, (note that when $d$ or $\tau$ is zero, $(C_2)$ becomes $(C_1)$) and if both $d$ and $\tau$ are zero, then the delayed model (11) is coincidental with the instantaneous model (3)).

![Graphs showing oscillatory behavior](image1)

Figure 11. $d = 0.5, \tau = 0$: The system is oscillatory with relative small value of $F$ and becomes stable with the increasing of $F$ to a certain level: (a) $F = 0.5$ and (b) $F = 1.2$.

![Graphs showing oscillatory behavior](image2)

Figure 12. $d = 0.5, \tau = 0.5$: (a) $F = 0$; (b) $F = 0.3$ and (c) $F = 1.2$. 
Case 1: If $d > 0$, $\tau = 0$.
At this case, the positive equilibrium $E_*$ and all the coefficients in Equation (13) are independent of time delay. For the stability of $E_*$, since Equation (13) becomes $\lambda^2 + C_1 \lambda + C_0 = 0$ with

$$C_1 = R(2p^* - 1) + h^*(u_1' + Fv_1'), \quad C_0 = FRh^*(2p^* - 1) + h^*u_1'(u_1 + Fh^*v_1'),$$

we need both $C_1$ and $C_0$ positive which is assured if we choose parameters so that $p^* > \frac{1}{2}$ and $h^* < 1/c$ due to that $v_1' = c(1 - c^2 h^2)/(1 + c^2 h^2)^2$. With these in mind, we can check that, when $F = 0.5$, there is a unique positive equilibrium $E_* \approx (0.195, 0.530)$ which is an unstable spiral source; when $F = 1.2$, there are three positive equilibrium points, but only one of them ($E_* \approx (0.894, 0.193)$) is stable. Figure 11 gives an good agreement.

Case 2: If $d > 0$, $\tau > 0$.
With the increasing of $\tau$ from zero, the equilibrium point and all the coefficients in Equation (13) are related to the choice of $d$ and $\tau$. In addition, we know that when $\tau < \tau^*$, there exists positive equilibrium point(s). Let $d = 0.5$, then $\tau^* \approx 1.83$ under Equation (7). When $\tau = 0.5$, as the variation of parameter $F$, we can observe different dynamical properties. For instance, there is a unique positive stationary point $E_* \approx (0.150, 0.496)$ if $F = 0$. The number of positive steady state is changeable as $F$ increases. Geometrically, we can check that there is unique $E_* \approx (0.242, 0.558)$ if $F = 0.3$ and $E_* \approx (0.955, 0.087)$ if $F = 1.2$. The trajectories are given in Figure 12.

![Figure 13](image1.png)

Figure 13. $d = 0.5$, $\tau = 1$: (a) $F = 0$; (b) $F = 0.3$ and (c) $F = 1.2$. 
Similarly, when $\tau = 1$, there exists a unique positive steady state $E_* \approx (0.244, 0.559)$ when $F = 0$, and $E_* \approx (0.460, 0.594)$ when $F = 0.3$, $E_* \approx (0.978, 0.044)$ when $F = 1.2$. The corresponding solution curves are shown in Figure 13.

From Figures 12 and 13, it is interesting to see that increasing of $\tau$ can ‘stabilize’ the system. When $F = 0$, it is oscillatory with either $\tau = 0.5$ or 1. However, the amplitude and frequency are decreasing with the increasing of delay $\tau$; while when $F = 0.3$, the oscillation remains at $\tau = 0.5$ but disappears at $\tau = 1$; in addition, the system is oscillatory with small $F$, and becomes stable when $F$ is relatively large.

Case 3: If $d = 0$, $\tau > 0$.

Since $d = 0$, the value of $\tau$ does not affect the equilibrium point(s). With fixed $F = 0.5$, we can observe that the oscillation is persistent. With the increasing of $\tau$ to a certain level, the frequency of oscillation is slowed down (Figure 14).

From the biological point of view, $d = 0$ represents the absence of mortality in the immature group while $d > 0$ corresponds to the presence of the immature mortality. If the immature population does not suffer any mortality ($d = 0$ or $d > 0$, $\tau = 0$ which has the same influence), the dynamical behaviour gains complexity as the maturation time delay increases. With the impact of fish, the system may keep in a steady state, phytoplankton and herbivorous zooplankton can coexist or remain in oscillation (Figures 11–13). With a high density of fish, phytoplankton and herbivorous zooplankton exist with sustainable oscillatory dynamics when the maturation time delay is relatively long and there is no immature mortality (Figure 14). Combination of the long mature
time and the high density of fish can stabilize the interaction of phytoplankton and herbivorous zooplankton. This provides other evidence of the importance of incorporating the through-stage death rate in stage-structured population models shown in \[10\].

5. Comments

We have constructed two simple plankton models which are slight extensions of classical prey–predation models by incorporating nonlinear harvesting from fish, in the hope of providing insight into the possible factors which may cause the critical trends in the phytoplankton and zooplankton system. Some techniques including the stability and bifurcation analysis are used to show how several important features of plankton dynamics can be understood. The theoretical analysis and numerical computation and simulations provide evidences of the sensitivity of the model dynamics on the effects of fish predation and maturation (through-stage) time delay. The results obtained in this research inform us that, under certain conditions, with the variation of fish density and maturation delay, both phytoplankton and herbivorous zooplankton can coexist, or oscillate each other. Due to the complexity of the models and the dependence on the steady states on the system parameters, even of the ODE model (1), it is almost impossible to do the theoretical and deep analysis of the stability and bifurcation for the model. On the other hand, although we suggest that predation by fish, the nutrient limitation and time delay in the maturation processes are the major factors in controlling the composition of phytoplankton communities, we believe that such emphases will require a series of tests or experiments from a broadening group of aquatic ecologists. Furthermore, the approaches used in this article are not really suitable for addressing dynamics either in a seasonally changing environment or in the situation when the spatial diffusion cannot be overlooked, which require much more complex techniques. We are continuing work on these areas.

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