Research article

Comparison of dynamic behavior between continuous- and discrete-time models of intraguild predation

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Abstract: Intraguild predation is a common ecological phenomenon that manifests itself by the aggression of one predator by another to obtain a shared prey species. In this paper, we develop a discrete analog of a stoichiometric continuous-time intraguild predation model. We analyze the dynamics of the discrete-time model, such as boundedness and invariance, stability of equilibria, and features of ecological matrices. The dynamic behavior of the two models is compared and analyzed through numerical analysis. We observe the same coexistence region of populations and stoichiometric effects of food quality of the shared prey in both models. Obvious differences between the discrete- and continuous-time models can be observed with intermediate and high levels of light intensity. The multistability characteristics and the existence interval of chaos differ among the different time scale models. This study provides evidence of the importance of time scales on intraguild predation.

1. Introduction

Ecological stoichiometry is an important part of ecology that links the metabolic demands of organisms with the relative supply of elements in the environment [1]. It examines the balance between energy and chemical elements and the extent to which this balance plays a part in determining the organisms' growth and reproduction and their ecological interactions. Recognizing the importance of stoichiometric limitations between predator requirements and the nutrient composition of prey has greatly enhanced our appreciation of trophic relationships. Many studies have demonstrated that ecological stoichiometry is a highly suitable framework for explaining predator responses to prey food quality [1–4].

Nature exhibits many interactions among individual organisms of different species (notably competition, predation/parasitism, mutualism, commensalism, or amensalism). Intraguild predation (IGP) within the cotope group contains two interaction types: competition and predation, and usually, there is not only a predatory relationship but also a potential competition relationship between two predatory species in order to compete for limited resources. IGP distinguishes itself from traditional predation by the fact that the behavior reduces potential competition for exploitation. The direct energy gain of predators makes IGP different from the traditional competition [5]. Thus, its effect on population dynamics is more complex and worth studying. IGP is a significant factor in predicting the stability of food webs and the maintenance of biodiversity, in addition to being a taxonomically widespread interaction within communities that can occur at different trophic levels [6]. The development of the IGP model can be traced back to Holt and Polis [7], who developed a three-species Lotka–Volterra food web model to study the species coexistence of IGP and found that achieving a stable three-species steady state is challenging. Following that, a series of studies examined IGP models with different structures and forms such as the Lotka–Volterra type [8–10], special forms of the functional and numerical response [11–13], prey switching or adaptive prey behavior [14, 15], generalist predators or time delays [16–18], stochastic approaches [19–21], and stoichiometry [22, 23].

Diehl [22] investigated a model of competition among predators to explore stoichiometry as an IGP-intraguild mechanism. Later, the dynamic resource model of Loladze et al. [24] assumed that omnivores were the inferior carbon competitors and showed that dynamic interaction between autotroph quality and quantity could facilitate coexistence when resource quality is low. The system investigated in [22] is based on a continuous time scale. However, many plants in the wild and agricultural contexts have non-overlapping generations, and many herbivores have distinct annual or seasonal dynamics. Therefore, the main purpose of this paper is to propose a discrete-time version of the stoichiometric IGP model based on the continuous stoichiometric IGP model [22] and compare the differences in the dynamic behavior of models under different time scales. In particular, we focus on the following four questions: 1) How do the stoichiometric effects of food quality affect IGP? 2) What is the coexistence interval of the population for both models when the environmental parameter changes? 3) Can chaotic dynamics emerge under a biologically plausible parameter set, and if so, do the parameter ranges of the discrete-time model admit chaos, as in the continuous-time model? 4) Does multistability exist in both models?

We construct the discrete-time IGP model with stoichiometry following the discretization approach in [25] and theoretically analyze the dynamical behavior of this model. The dynamical behavior is compared between the discrete- and continuous-time models, which leads to our conclusions.

2. Model construction

We consider the IGP system in [22] in the aquatic ecosystem. Zooplankton competes with fish for algae and is consumed by fish, which constitutes an IGP system. We use $A(t)$, $Z(t)$, and $F(t)$ to represent the population density of algae, zooplankton, and fish at time t, respectively. Then the continuous IGP model with stoichiometry takes the form [22]

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{\min\{K, (P_T - \theta_Z Z - \theta_F F)/q\}}\right) - a_{AZ}(A)Z - a_{AF}(A, Z)F,$$

$$\frac{dZ}{dt} = e_{AZ} \min\left\{1, \frac{(P_T - \theta_Z Z - \theta_F F)/A}{\theta_Z}\right\} a_{AZ}(A)Z - a_{ZF}(A,Z)F - d_Z Z, \tag{2.1}$$

$$\frac{dF}{dt} = e_{AF} \min\left\{1, \frac{(P_T - \theta_Z Z - \theta_F F)/A}{\theta_F}\right\} a_{AF}(A,Z)F + e_{ZF} \min\left\{1, \frac{\theta_Z}{\theta_F}\right\} a_{ZF}(A,Z)F - d_F F.$$

Here, r is the maximum growth rate of algae, K is the algae carrying capacity, and P_T is the total Phosphorus in the system. θ_Z and θ_F are the constant P (Phosphorus): C (Carbon) ratios of the zooplankton and fish, respectively. q is the minimal algae P:C ratio. d_Z and d_F are the specific loss rates of the zooplankton and fish, respectively. e_{AZ} denotes the conservation of algae into the zooplankton, e_{AF} represents the conservation of algae into the fish, and e_{ZF} denotes the conservation of zooplankton into the fish. The functions $a_{AZ}(A)$, $a_{AF}(A,Z)$, and $a_{ZF}(A,Z)$ are the functional responses of the zooplankton feeding on algae, the fish feeding on algae, and the fish feeding on zooplankton, respectively.

Similar to the functional response properties outlined in [26], it is assumed that $a_{AZ}(A)$, $a_{AF}(A,Z)$, and $a_{ZF}(A,Z)$ are bounded smooth functions satisfying the following conditions:

$$a_{AZ}(0) = 0, \ a'_{AZ}(A) > 0, \ \text{and} \ a''_{AZ}(A) < 0 \ \text{for} \ A > 0.$$

$$a_{AF}(0,Z) = 0, \ \frac{\partial a_{AF}(A,Z)}{\partial A} > 0, \ \frac{\partial^2 a_{AF}(A,Z)}{\partial^2 A} < 0, \ \text{and} \ \frac{\partial a_{AF}(A,Z)}{\partial Z} < 0 \ \text{for} \ A > 0, \ Z > 0.$$

$$a_{ZF}(A,0) = 0, \ \frac{\partial a_{ZF}(A,Z)}{\partial A} < 0, \ \frac{\partial a_{ZF}(A,Z)}{\partial Z} > 0, \ \text{and} \ \frac{\partial^2 a_{ZF}(A,Z)}{\partial^2 Z} < 0 \ \text{for} \ A > 0, \ Z > 0.$$

Based on the above model, the time is discretized, and a discrete stoichiometry model is established. There are several approaches to deriving discrete-time dynamical systems that correspond to continuous time [27, 28]. We discretize Eq (2.1) using the method developed by Fan [25]. This method employs differential equations with piecewise constant arguments by assuming that the per capita growth rate remains constant on a given time interval $[t, t+1]$. Then Eq (2.1) turns to the following system:

$$\frac{1}{A(t)}\frac{dA(t)}{dt} = r\left(1 - \frac{A[t]}{\min\{K, (P_T - \theta_Z Z[t] - \theta_F F[t])/q\}}\right) - \frac{a_{AZ}(A[t])Z[t]}{A[t]} - \frac{a_{AF}(A[t], Z[t])F[t]}{A[t]},$$

$$\frac{1}{Z(t)}\frac{dZ(t)}{dt} = e_{AZ} \min\left\{1, \frac{P_T - \theta_Z Z[t] - \theta_F F[t]}{\theta_Z A[t]}\right\} a_{AZ}(A[t]) - \frac{a_{ZF}(A[t], Z[t])F[t]}{Z[t]} - d_Z, \tag{2.2}$$

$$\frac{1}{F(t)}\frac{dF(t)}{dt} = e_{AF} \min\left\{1, \frac{P_T - \theta_Z Z[t] - \theta_F F[t]}{\theta_F A[t]}\right\} a_{AF}(A[t], Z[t]) + e_{ZF} \min\left\{1, \frac{\theta_Z}{\theta_F}\right\} a_{ZF}(A[t], Z[t]) - d_F,$$

$t \neq 0, 1, 2, \ldots$

where $[t]$ denotes the integer part of $t \in (0, +\infty)$. Then, we integrate both sides of Eq (2.2) on any interval $[n, n+1), n = 0, 1, 2, \ldots,$ and obtain, for $n \leq t < n+1, n = 0, 1, 2, \ldots,$

$$A(t) = A(n) \exp\left\{\left[r\left(1 - \frac{A(n)}{\min\{K, (P_T - \theta_Z Z(n) - \theta_F F(n))/q\}}\right) - \frac{a_{AZ}(A(n))Z(n)}{A(n)} - \frac{a_{AF}(A(n), Z(n))F(n)}{A(n)}\right](t-n)\right\},$$

$$Z(t) = Z(n) \exp\left\{\left[e_{AZ} \min\left\{1, \frac{P_T - \theta_Z Z(n) - \theta_F F(n)}{\theta_Z A(n)}\right\} a_{AZ}(A(n)) - \frac{a_{ZF}(A(n), Z(n))F(n)}{Z(n)} - d_Z\right](t-n)\right\},$$

$$F(t) = F(n) \exp\left\{\left[e_{AF} \min\left\{1, \frac{P_T - \theta_Z Z(n) - \theta_F F(n)}{\theta_F A(n)}\right\} a_{AF}(A(n), Z(n)) + e_{ZF} \min\left\{1, \frac{\theta_Z}{\theta_F}\right\} a_{ZF}(A(n), Z(n)) - d_F\right](t-n)\right\}.$$

Let t tends to $n + 1$, then we get the final discrete-time system

$$A(n+1) = A(n) \exp\left\{r\left(1 - \frac{A(n)}{\min\{K, (P_T - \theta_Z Z(n) - \theta_F F(n))/q\}}\right) - \frac{a_{AZ}(A(n))Z(n)}{A(n)} - \frac{a_{AF}(A(n), Z(n))F(n)}{A(n)}\right\},$$

$$Z(n+1) = Z(n) \exp\left\{e_{AZ} \min\left\{1, \frac{P_T - \theta_Z Z(n) - \theta_F F(n)}{\theta_Z A(n)}\right\} a_{AZ}(A(n)) - \frac{a_{ZF}(A(n), Z(n))F(n)}{Z(n)} - d_Z\right\},$$

$$F(n+1) = F(n) \exp\left\{e_{AF} \min\left\{1, \frac{P_T - \theta_Z Z(n) - \theta_F F(n)}{\theta_F A(n)}\right\} a_{AF}(A(n), Z(n)) + e_{ZF} \min\left\{1, \frac{\theta_Z}{\theta_F}\right\} a_{ZF}(A(n), Z(n)) - d_F\right\}$$

$$(2.3)$$

for $n \in \mathbb{N}$.

Table 1. Parameters of Models (2.1) and (2.3).

Parameter	Description	Values	Unit
P_T	Total phosphorus in system	0.33	mgPL^{-1}
e_{AZ}	Conservation of algae to zooplankton	0.8	–
e_{AF}	Conservation of algae to fish	0.6	–
e_{ZF}	Conservation of zooplankton to fish	0.6	–
r	Maximal growth rate of algae	0.58	day^{-1}
d_Z	Loss rate of zooplankton	0.25	day^{-1}
d_F	Loss rate of fish	0.15	day^{-1}
θ_Z	Constant P : C of zooplankton	0.03	mgP/mgC
θ_F	Constant P : C of fish	0.03	mgP/mgC
q	Minimal P : C of algae	0.003	mgP/mgC
s_{AZ}	Search and attack rate of zooplankton on algae	0.085	day^{-1}(mgC/m^3)$^{-1}$
h_{AZ}	Handing time of zooplankton feeding on algae	0.16	day/(mgC/m^3)
s_{AF}	Search and attack rate of fish on algae	0.08	day^{-1}(mgC/m^3)$^{-1}$
h_{AF}	Handing time of fish feeding on algae	0.4	day/(mgC/m^3)
s_{ZF}	Search and attack rate of fish on zooplankton	0.05	day^{-1}(mgC/m^3)$^{-1}$
h_{ZF}	Handing time of fish feeding on zooplankton	0.5	day/(mgC/m^3)
K	Carrying capacity of algae	0–120	mgCL^{-1}

Initial values should be considered in the biologically meaningful regions. Thus, we assume that $0 < A(0)$, $0 < Z(0) < P_T/\theta_Z$, and $0 < F(0) < P_T/\theta_F$. The meaning and values of most parameters are selected from [26] and [22], and are listed in Table 1.

3. Boundedness and invariance

In this section, boundedness and positive invariance results are fully analyzed for Eq (2.3) using arguments similar to those in Theorems 3.1 and 3.2 of [25]. It is easy to show that solutions of Eq (2.3) remain nonnegative when they exist.

For convenience, we assume that $a_{AZ}(A) = A f_{AZ}(A)$, $a_{AF}(A, Z) = A f_{AF}(A, Z)$, and $a_{ZF}(A, Z) = Z f_{ZF}(A, Z)$. From [29], we have

$$\lim_{A \to 0} f_{AZ}(A) = a'_{AZ}(0) < \infty, \text{ and } f'_{AZ}(A) < 0 \text{ for } A > 0.$$

$$\lim_{A \to 0} f_{AF}(A, Z) = \frac{\partial a_{AF}(0, Z)}{\partial A} < \infty, \quad \frac{\partial f_{AF}(A, Z)}{\partial A} < 0 \text{ and } \frac{\partial f_{AF}(A, Z)}{\partial Z} < 0 \text{ for } A > 0, \ Z > 0.$$

$$\lim_{Z \to 0} f_{ZF}(A, Z) = \frac{\partial a_{ZF}(A, 0)}{\partial Z} < \infty, \quad \frac{\partial f_{ZF}(A, Z)}{\partial A} < 0 \text{ and } \frac{\partial f_{ZF}(A, Z)}{\partial Z} < 0 \text{ for } A > 0, \ Z > 0.$$

Theorem 3.1. *For System* (2.3)*, the following statements hold for all $n > 0$;*

$$A(n) \le \max\{A(0), K/r \exp(r - 1)\} \equiv S,$$
$$Z(n) \le \max\{Z(0), g\} \exp(2e_{AZ}a_{AZ}(S) - 2d_Z) \equiv G,$$
$$F(n) \le \max\{F(0), h\} \exp(2e_{AF}a_{AF}(S, 0) + 2e_{ZF}a_{ZF}(0, G) - 2d_F) \equiv H,$$

where g and h satisfy

$$e_{AZ}a_{AZ}(\exp(r - f_{AZ}(S)g)) < d_Z \text{ and}$$
$$e_{AF}a_{AF}(S \exp(r - f_{AZ}(S)g - f_{AF}(S, G)h), 0) + e_{ZF}a_{ZF}(0, G \exp(e_{AZ}a_{AZ}(S) - f_{ZF}(S, G)h - d_Z)) < d_F.$$

Proof. Note that all components of the solution to Eq (2.3) are non-negative when they exist. It is easy to find that $R(A) = A \exp r(1 - A/K)$ attains its maximum value at $A = K/r$. We obtain

$$A(n + 1) < A(n) \exp\left\{r - \frac{rA(n)}{K}\right\} \le \frac{K}{r} \exp(r - 1) \equiv s.$$

Then

$$A(n) \le \max\{A(0), s\} \equiv S$$

for all non-negative integers n.

If $e_{AZ}a_{AZ}(S) \le d_Z$, it is easy to show that $Z(n) \le Z(0)$ for all $n > 0$. Thus, it is assumed that $e_{AZ}a_{AZ}(S) > d_Z$. Let g be sufficiently large such that

$$e_{AZ}a_{AZ}(\exp(r - f_{AZ}(S)g)) < d_Z.$$

We claim that

$$Z(n) \le \max\{Z(0), g\} \exp(2e_{AZ}a_{AZ}(S) - 2d_Z) \equiv G$$

for all non-negative integers n. This holds for $n = 1, 2$. Let us assume that this claim is false. We consider two cases.

(I) $Z(0) \leq g$. Then for some $n_1 > 2$, $g < Z(n_1 - 2) \leq G$, $g < Z(n_1 - 1) \leq G$, and $Z(n_1) > G$. In this case, we get

$$
\begin{aligned}
A(n_1 - 1) &\leq A(n_1 - 2) \exp\left(r - f_{AZ}(A(n_1 - 2))Z(n_1 - 2) - f_{AF}(A(n_1 - 2), Z(n_1 - 2))F(n_1 - 2)\right) \\
&\leq A(n_1 - 2) \exp\left(r - f_{AZ}(A(n_1 - 2))Z(n_1 - 2)\right) \\
&\leq S \exp\left(r - f_{AZ}(S)g\right).
\end{aligned}
$$

This implies that

$$
Z(n_1) < Z(n_1 - 1) \exp\left\{e_{AZ}a_{AZ}(S \exp(r - f_{AZ}(S)g)) - d_Z\right\} < Z(n_1 - 1) < G,
$$

which is a contradiction, implying that the claim is true for this case.

(II) $Z(0) > g$. In this case, we have

$$
A(1) < S \exp\left(r - f_{AZ}(S)g\right),
$$

which indicates that

$$
Z(2) < Z(1).
$$

That is, as long as $Z(n) > g$, then $Z(n + 2) < Z(n + 1)$. Then, there exists two cases: (i) $Z(n^*) \leq g$ for some $n^* > 0$ or (ii) $Z(n) > g$ for all $n > 0$. In case (ii), we have that $Z(n)$ is strictly decreasing for $n > 1$, and the claim is obviously true. In case (i), from the proof of case (I), we find that $Z(n) < G$ for $n > n^*$, and hence the claim is again true.

If $e_{AF}a_{AF}(S, 0) + e_{ZF}a_{ZF}(0, G) \leq d_F$, then it is clear that, for all $n > 0$, we have $F(n) \leq F(0)$. Thus, we assume that $e_{AF}a_{AF}(S, 0) + e_{ZF}a_{ZF}(0, G) > d_F$. Let g, h be sufficiently large such that

$$
e_{AF}a_{AF}(S \exp(r - f_{AZ}(S)g - f_{AF}(S, G)h), 0) + e_{ZF}a_{ZF}(0, G \exp(e_{AZ} - f_{ZF}(S, G)h - d_Z)) < d_F.
$$

We conclude that, for all non-negative integers n,

$$
F(n) \leq \max\{F(0), h\} \exp\left(2e_{AF}a_{AF}(S, 0) + 2e_{ZF}a_{ZF}(0, G) - 2d_F\right) \equiv H.
$$

This holds for $n = 1, 2$. Let us assume that this claim is not true. We consider two cases

(I′) $F(0) \leq h$. Then, for some $n_1 > 2$, $h < F(n_1 - 2) \leq H$, $h < F(n_1 - 1) \leq H$, and $F(n_1) > H$. In this case, we have

$$
\begin{aligned}
F(n_1) &< F(n_1 - 1) \exp\Big\{e_{AF}a_{AF}(S \exp(r - f_{AZ}(S)g - f_{AF}(S, G)h), 0) \\
&\quad + e_{ZF}a_{ZF}(0, G \exp(e_{AZ}a_{AZ}(S) - f_{ZF}(S, G)h - d_Z)) - d_F\Big\} \\
&< F(n_1 - 1) < H,
\end{aligned}
$$

which is a contradiction, implying that the claim is true for this case.

(II′) $F(0) > h$. In this case, we have

$$A(1) < S \exp(r - f_{AZ}(S)g - f_{AF}(S, G)h),$$
$$Z(1) < G \exp(e_{AZ}a_{AZ}(S) - f_{ZF}(S, G)h - d_Z),$$

which implies that

$$F(2) < F(1).$$

In other words, as long as $F(n) > h$, then $F(n + 2) < F(n + 1)$. Hence, there are two possibilities: (i′) $F(n^*) \le h$ for some $n^* > 0$ or (ii′) $F(n) > h$ for all $n > 0$. In case (ii′), we have that $F(n)$ is strictly decreasing for $n > 1$, and the claim is obviously true. In case (i′), from the proof of case (I′), we see that $F(n) < H$ for $n > n^*$, and then the claim is again true.

From the above theorem, we obtain the conclusion that

$$\triangle = \left\{ (A, Z, F) : 0 < A < \frac{K}{r} \exp(r - 1), 0 < Z < g, 0 < F < h \right\}$$

is positively invariant. Indeed, we have the following theorem.

Theorem 3.2. $\triangle$ *is globally attractive for System* (2.3) *with initial values satisfying* $A(0) > 0$, $0 < Z(0) < P_T/\theta_Z$ *and* $0 < F(0) < P_T/\theta_F$.
Proof. From the above theorem, it is apparent that, for large values of n, $0 < A(n) < (K/r) \exp(r - 1)$. Note that if $Z(n) > g$ for $n \gg 0$, then $Z(n)$ tends to $Z^* \ge g$. Hence, for $n \gg 0$, we obtain

$$Z(n) < Z(n - 1) \exp \{ e_{AZ}a_{AZ}(S \exp(r - f_{AZ}(S)g)) - d_Z \}.$$

Letting $n \to \infty$ yields

$$Z^* \le Z^* \exp \{ e_{AZ}a_{AZ}(S \exp(r - f_{AZ}(S)g)) - d_Z \} < Z^*.$$

This contradicts $Z^* > g > 0$. Then, for $n \gg 0$, $0 < Z(n) < g$. Note that if $F(n) > h$ for any $n > 0$, then $F(n)$ tends to $F^* \ge h$. Hence, for $n \gg 0$, we obtain

$$F(n) < F(n - 1) \exp \{ e_{AF}a_{AF}(S \exp(r - f_{AZ}(S)g - f_{AF}(S, G)h), 0) + e_{ZF}a_{ZF}(0, G \exp(e_{AZ} - f_{ZF}(S, G)h - d_Z)) - d_F \}.$$

Letting $n \to \infty$ yields

$$F^* \le F^* \exp \{ e_{AF}a_{AF}(S \exp(r - f_{AZ}(S)g - f_{AF}(S, G)h), 0) + e_{ZF}a_{ZF}(0, G \exp(e_{AZ} - f_{ZF}(S, G)h - d_Z)) - d_F \} < F^*.$$

This contradicts $F^* > h > 0$, proving the theorem.

4. Equilibria

For convenience, we rewrite Eqs (2.1) and (2.3) as

$$\frac{dA}{dt} = AL(A, Z, F), \ \frac{dZ}{dt} = ZM(A, Z, F), \ \frac{dF}{dt} = FN(A, Z, F),$$

and

$$A(n + 1) = A(n) \exp \{L(A(n), Z(n), F(n))\},$$

$$Z(n + 1) = Z(n) \exp \{M(A(n), Z(n), F(n))\},$$

$$F(n + 1) = F(n) \exp \{N(A(n), Z(n), F(n))\},$$

respectively, where

$$L(A, Z, F) = r \left(1 - \frac{A}{\min\{K, (P_T - \theta_Z Z - \theta_F F)/q\}}\right) - f_{AZ}(A)Z - f_{AF}(A, Z)F,$$

$$M(A, Z, F) = e_{AZ} \min \left(1, \frac{P_T - \theta_Z Z - \theta_F F}{\theta_Z A}\right) a_{AZ}(A) - f_{ZF}(A, Z)F - d_Z,$$

$$N(A, Z, F) = e_{AF} \min \left\{1, \frac{P_T - \theta_Z Z - \theta_F F}{\theta_F A}\right\} a_{AF}(A, Z) + e_{ZF} \min \left\{1, \frac{\theta_Z}{\theta_F}\right\} a_{ZF}(A, Z) - d_F.$$

To find equilibria of Eqs (2.1) and (2.3), we solve the following equations

$$AL(A, Z, F) = 0, \ ZM(A, Z, F) = 0, \ FN(A, Z, F) = 0, \tag{4.1}$$

and

$$A[1 - \exp\{L(A, Z, F)\}] = 0, \ Z[1 - \exp\{M(A, Z, F)\}] = 0, \ F[1 - \exp\{N(A, Z, F)\}] = 0, \tag{4.2}$$

respectively. (4.1) and (4.2) both lead to

$$A = 0 \text{ or } L(A, Z, F) = 0,$$
$$Z = 0 \text{ or } M(A, Z, F) = 0,$$
$$F = 0 \text{ or } N(A, Z, F) = 0,$$

which shows that Systems (2.3) and (2.1) share exactly the same equilibria.

After some straightforward algebraic calculations, the variational matrix of Systems (2.1) and (2.3) lead

$$J(A, Z, F) = \begin{pmatrix} L + AL_A & AL_Z & AL_F \\ ZM_A & M + ZM_Z & ZM_F \\ FN_A & FN_Z & N + FN_F \end{pmatrix}$$

and

$$J(A, Z, F) = \begin{pmatrix} e^L + Ae^L L_A & Ae^L L_Z & Ae^L L_F \\ Ze^M M_A & e^M + Ze^M M_Z & Ze^M M_F \\ Fe^N N_A & Fe^N N_Z & e^N + Fe^N N_F \end{pmatrix},$$

respectively, where

$$L_A = \frac{\partial L}{\partial A} = -\frac{r}{\min\{K, (P_T - \theta_Z Z - \theta_F F)/q\}} - f'_{AZ}(A)Z - \frac{\partial f_{AF}(A,Z)}{\partial A}F.$$

$$L_Z = \frac{\partial L}{\partial Z} = \begin{cases} -f_{AZ}(A) - \frac{\partial f_{AF}(A,Z)}{\partial Z}F, & qK + \theta_Z Z + \theta_F F < P_T, \\[2mm] -\frac{rq\theta_Z A}{(P_T - \theta_Z Z - \theta_F F)^2} - f_{AZ}(A) - \frac{\partial f_{AF}(A,Z)}{\partial Z}F, & qK + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

$$L_F = \frac{\partial L}{\partial F} = \begin{cases} -f_{AF}(A,Z) < 0, & qK + \theta_Z Z + \theta_F F < P_T, \\[2mm] -\frac{rq\theta_F A}{(P_T - \theta_Z Z - \theta_F F)^2} - f_{AF}(A,Z) < 0, & qK + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

$$M_A = \frac{\partial M}{\partial A} = \begin{cases} e_{AZ}a'_{AZ}(A) - \frac{\partial f_{ZF}(A,Z)}{\partial A}F > 0, & \theta_Z A + \theta_Z Z + \theta_F F < P_T, \\[2mm] e_{AZ}\frac{P_T - \theta_Z Z - \theta_F F}{\theta_Z}f'_{AZ}(A) - \frac{\partial f_{ZF}(A,Z)}{\partial A}F, & \theta_Z A + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

$$M_Z = \frac{\partial M}{\partial Z} = \begin{cases} -\frac{\partial f_{ZF}(A,Z)}{\partial Z}F > 0, & \theta_Z A + \theta_Z Z + \theta_F F < P_T, \\[2mm] -e_{AZ}f_{AZ}(A) - \frac{\partial f_{ZF}(A,Z)}{\partial Z}F, & \theta_Z A + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

$$M_F = \frac{\partial M}{\partial F} = \begin{cases} -f_{ZF}(A,Z) < 0, & \theta_Z A + \theta_Z Z + \theta_F F < P_T, \\[2mm] -e_{AZ}\frac{\theta_F}{\theta_Z}f_{AZ}(A) - f_{ZF}(A,Z) < 0, & \theta_Z A + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

$$N_A = \frac{\partial N}{\partial A} = \begin{cases} e_{AF}\frac{\partial a_{AF}(A,Z)}{\partial A} + e_{ZF}\min\left\{1, \frac{\theta_Z}{\theta_F}\right\}\frac{\partial a_{ZF}(A,Z)}{\partial A}, & \theta_F A + \theta_Z Z + \theta_F F < P_T, \\[2mm] e_{AF}\frac{P_T - \theta_Z Z - \theta_F F}{\theta_F}\frac{\partial f_{AF}(A,Z)}{\partial A} + e_{ZF}\min\left\{1, \frac{\theta_Z}{\theta_F}\right\}\frac{\partial a_{ZF}(A,Z)}{\partial A} < 0, & \theta_F A + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

$$N_Z = \frac{\partial N}{\partial Z} = \begin{cases} e_{AF}\frac{\partial a_{AF}(A,Z)}{\partial Z} + e_{ZF}\min\left\{1, \frac{\theta_Z}{\theta_F}\right\}\frac{\partial a_{ZF}(A,Z)}{\partial Z}, & \theta_F A + \theta_Z Z + \theta_F F < P_T, \\[2mm] -e_{AF}f_{AF}(A,Z)\frac{\theta_Z}{\theta_F} + e_{AF}\frac{P_T - \theta_Z Z - \theta_F F}{\theta_F}\frac{\partial f_{AF}(A,Z)}{\partial Z} & \\ \quad + e_{ZF}\min\left\{1, \frac{\theta_Z}{\theta_F}\right\}\frac{\partial a_{ZF}(A,Z)}{\partial Z}, & \theta_F A + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

$$N_F = \frac{\partial N}{\partial F} = \begin{cases} 0, & \theta_F A + \theta_Z Z + \theta_F F < P_T, \\[2mm] -e_{AF}f_{AF}(A,Z) < 0, & \theta_F A + \theta_Z Z + \theta_F F > P_T. \end{cases}$$

4.1. Boundary equilibria

System (2.3) has four possible boundary equilibria: $E_0(0,0,0)$, $E_1(k,0,0)$, $E_2(\bar{A}, \bar{Z}, 0)$, and $E_3(\tilde{A}, 0, \tilde{F})$, where $k = \min(K, P_T/q)$. The equilibrium $E_0(0,0,0)$ represents the extinction of all species; The equilibrium $E_1(k,0,0)$ denotes the extinction of zooplankton and fish and the persistence of algae; The equilibrium $E_2(\bar{A}, \bar{Z}, 0)$ represents the extinction of fish and persistence of algae and zooplankton; The equilibrium $E_3(\tilde{A}, 0, \tilde{F})$ denotes the extinction of zooplankton and persistence of algae and fish.

Theorem 4.1. *For System* (2.3), *E_0 is always unstable. E_1 is locally asymptotically stable if*

$$0 < r < 2, e_{AZ}\min\left\{1, \frac{P_T}{k\theta_Z}\right\}a_{AZ}(k) < d_Z \text{ and } , e_{AF}\min\left\{1, \frac{P_T}{k\theta_F}\right\}a_{AF}(k,0) < d_F;$$

E_1 is unstable if

$$r > 2 \text{ or } e_{AZ} \min\left\{1, \frac{P_T}{k\theta_Z}\right\} a_{AZ}(k) > d_Z \text{ or } e_{AF} \min\left\{1, \frac{P_T}{k\theta_F}\right\} a_{AF}(k,0) > d_F.$$

Proof. At the extinction equilibrium $E_0(0,0,0)$, the form of Jacobian matrix is as follows

$$J(E_0) = \begin{pmatrix} e^r & 0 & 0 \\ 0 & e^{-d_Z} & 0 \\ 0 & 0 & e^{-d_F} \end{pmatrix}.$$

Obviously, the characteristic roots e^{-d_Z} and e^{-d_F} are less than 1, while the other characteristic root e^r is greater than 1. Therefore, the extinction equilibrium E_0 is always unstable.

At $E_1(k,0,0)$ the Jacobian is

$$J(E_1) = \begin{pmatrix} 1-r & kL_Z(k,0,0) & kL_F(k,0,0) \\ 0 & \exp\{M(k,0,0)\} & 0 \\ 0 & 0 & \exp\{N(k,0,0)\} \end{pmatrix},$$

where

$$M(k,0,0) = e_{AZ} \min\left\{1, \frac{P_T}{k\theta_Z} a_{AZ}(k)\right\} - d_Z,$$

$$N(k,0,0) = e_{AF} \min\left\{1, \frac{P_T}{k\theta_F} a_{AF}(k,0)\right\} - d_F.$$

Let λ_1, λ_2 and λ_3 denote the characteristic roots of $J(E_1)$, then the following inequalities

$$0 < r < 2, e_{AZ} \min\left\{1, \frac{P_T}{k\theta_Z}\right\} a_{AZ}(k) < d_Z \text{ and }, e_{AF} \min\left\{1, \frac{P_T}{k\theta_F}\right\} a_{AF}(k,0) < d_F$$

ensure that $|\lambda_i| < 1$, $i = 1, 2, 3$. While the following inequalities

$$r > 2 \text{ or } e_{AZ} \min\left\{1, \frac{P_T}{k\theta_Z}\right\} a_{AZ}(k) > d_Z \text{ or } e_{AF} \min\left\{1, \frac{P_T}{k\theta_F}\right\} a_{AF}(k,0) > d_F$$

imply $\lambda_i > 1$ for some i.

The equilibrium $E_2(\bar{A}, \bar{Z}, 0)$ represents the extinction of fish. So, E_2 is the internal equilibrium of a two-dimensional system in which only algae and zooplankton exist. $E_2(\bar{A}, \bar{Z}, 0)$ can be explored in the $A - Z$ phase plane. Since both Eqs (2.1) and (2.3) share the same equilibria, from [29], we can conclude that E_2 in Eq (2.3) possibly contains multiple equilibria.

Theorem 4.2. *If $N(\bar{A}, \bar{Z}, 0) < 0$, then the following hold.*

• *In region i (i.e., $\bar{Z} < P_T/\theta_Z - \bar{A}$), if the algae's nullcline is decreasing at E_2(i.e., $L_A < 0$), and*

$$\frac{1}{2}\bar{A}\bar{Z}L_Z M_A - 2 < \bar{A}L_A < \bar{A}\bar{Z}L_Z M_A, \tag{4.3}$$

then E_2 is locally asymptotically stable.

- *In region ii (i.e., $\bar{Z} > P_T/\theta_Z - \bar{A}$), if the slope of the zooplankton's nullcline at E_2 is greater than the algae's (i.e., $-M_A/M_Z > -L_A/L_Z$), and*

$$\frac{1}{2}\bar{A}\bar{Z}[L_Z M_A - L_A M_Z] - 2 < \bar{A}L_A + \bar{Z}M_Z < \bar{A}\bar{Z}[L_Z M_A - L_A M_Z], \tag{4.4}$$

then E_2 is locally asymptotically stable.

Proof. In order to study local stability of E_2, the Jacobian at $E_2(\bar{A}, \bar{Z}, 0)$ can be described as

$$J(E_2) = \begin{pmatrix} J_{sub}(E_2) & J_1 \\ \mathbf{0} & \exp\left\{N(\bar{A}, \bar{Z}, 0)\right\} \end{pmatrix}$$

where

$$J_{sub}(E_2) = \begin{pmatrix} 1 + \bar{A}L_A & \bar{A}L_Z \\ \bar{Z}M_A & 1 + \bar{Z}M_Z \end{pmatrix} \text{ and } J_1 = \begin{pmatrix} \bar{A}L_F \\ \bar{Z}M_F \end{pmatrix}.$$

$N(\bar{A}, \bar{Z}, 0) < 0$ ensures that one characteristic root has a magnitude less than 1. Then we focus on the characteristic roots of $J_{sub}(E_2)$. The trace and determinant of $J_{sub}(E_2)$ are

$$\text{Tr}(J_{sub}(E_2)) = 2 + \bar{A}L_A + \bar{Z}M_Z$$

and

$$\text{Det}(J_{sub}(E_2)) = \text{Tr}(J_{sub}(E_2)) - 1 + \bar{A}\bar{Z}[L_A M_Z - L_Z M_A].$$

We discuss the stability of E_2 in region i and region ii, respectively.

Suppose E_2 lies in region i. Then $L_Z < 0$, $M_A > 0$, $M_Z = 0$. Note that,

$$\text{Tr}(J_{sub}(E_2)) = 2 + \bar{A}L_A = 2 + A\left(-\frac{L_A}{L_Z}\right)(-L_Z),$$

where $-(L_A/L_Z)$ is the slope of the algae's nullcline. Assume that the algae's nullcline is increasing at E_2, i.e., $L_A > 0$. Then $\text{Tr}(J_{sub}(E_2)) > 2$ and E_2 is unstable. If the algae's nullcline is decreasing at E_2, i.e., $L_A < 0$, and Eq (4.3) holds, then one can prove that $2 > 1 + \text{Det}(J_{sub}(E_2)) > |\text{Tr}(J_{sub}(E_2))|$. From Jury Test in [25], E_2 is stable. On the contrary, if Eq (4.3) does not hold, then E_2 is unstable.

Suppose E_2 is in region ii. Then at E_2, $L_Z < 0$, $M_A < 0$, $M_Z < 0$. Note that

$$\text{Det}(J_{sub}(E_2)) = 1 + \bar{A}L_A + \bar{Z}M_Z + \bar{A}\bar{Z}L_Z M_Z \left[\left(-\frac{M_A}{M_Z}\right) - \left(-\frac{L_A}{L_Z}\right)\right].$$

If the slope of the algae's nullcline at E_2 is greater than the zooplankton's, i.e., $-M_A/M_Z < -L_A/L_Z$, then $1 + \text{Det}(J_{sub}(E_2)) < |\text{Tr}(J_{sub}(E_2))|$, which means that E_2 is unstable. If the slope of the zooplankton's nullcline at E_2 is greater than the algae's, then $-L_A/L_Z < -M_A/M_Z < 0$. If Eq (4.4) holds, then $2 > 1 + \text{Det}(J_{sub}(E_2)) > |\text{Tr}(J_{sub}(E_2))|$ holds and E_2 is stable. On the contrary, if Eq (4.4) does not hold, then E_2 is unstable.

Similarly, the boundary equilibrium $E_3(\tilde{A}, 0, \tilde{F})$ indicates the extinction of zooplankton. $E_3(\tilde{A}, 0, \tilde{F})$ can be considered the internal equilibrium of a simple two-dimensional system with only fish and algae. $E_3(\tilde{A}, 0, \tilde{F})$ can be explored in the $A - F$ phase plane. The Jacobian at $E_3(\tilde{A}, 0, \tilde{F})$ can be described as

$$J(E_3) = \begin{pmatrix} J_{sub}(E_3) & J_2 \\ \mathbf{0} & \exp\left\{M(\tilde{A}, 0, \tilde{F})\right\} \end{pmatrix}$$

where

$$J_{sub}(E_3) = \begin{pmatrix} 1 + \tilde{A}L_A & \tilde{A}L_F \\ \tilde{F}N_A & 1 + \tilde{F}N_F \end{pmatrix} \text{ and } J_2 = \begin{pmatrix} \tilde{A}L_Z \\ \tilde{F}N_Z \end{pmatrix}$$

The trace and determinant of $J_{sub}(E_3)$ are

$$\text{Tr}(J_{sub}(E_3)) = 2 + \tilde{A}L_A + \tilde{F}N_F$$

and

$$\text{Det}(J_{sub}(E_3)) = \text{Tr}(J_{sub}(E_3)) - 1 + \tilde{A}\tilde{F}[L_A N_F - L_F N_A].$$

We find that the Jacobian matrixes of $E_2(\bar{A}, \bar{Z}, 0)$ and $E_3(\tilde{A}, 0, \tilde{F})$ take similar forms. The locally asymptotic stabilities of E_2 and E_3 can both be studied with the help of the stability of internal equilibria of a stoichiometric predator-prey system in discrete time scale [25]. Due to the similarity between the stability conditions of E_2 and E_3 and the similar argument in [25], we only provide the conclusion on the stability of E_3. Therefore, details of proofs will be skipped here.

Theorem 4.3. *If $M(\tilde{A}, 0, \tilde{F}) < 0$, then the following are true.*

• *In region i(i.e., $\tilde{F} < P_T/\theta_F - \tilde{A}$), if algae's nullcline is decreasing at E_3 (i.e., $L_A > 0$), and*

$$\frac{1}{2}\tilde{A}\tilde{F}L_F N_A - 2 < \tilde{A}L_A < \tilde{A}\tilde{F}L_F N_A, \tag{4.5}$$

then E_3 is locally asymptotically stable.

• *In region ii (i.e., $\tilde{F} > P_T/\theta_F - \tilde{A}$), if the slope of the fish's nullcline at E_3 is greater than algae's (i.e., $-N_A/N_F > -L_A/L_F$), and*

$$\frac{1}{2}\tilde{A}\tilde{F}[L_F N_A - L_A N_F] - 2 < \tilde{A}L_A + \tilde{F}N_F < \tilde{A}\tilde{F}[L_F N_A - L_A N_F], \tag{4.6}$$

then E_3 is locally asymptotically stable.

Through theoretical analysis, we present Table 2 to better summarize stability conditions of boundary equilibria between continuous model and discrete model.

4.2. Internal equilibria

The coexistence equilibrium $E^*(A^*, Z^*, F^*)$ can be solved by

$$L(A^*, Z^*, F^*) = 0, \ M(A^*, Z^*, F^*) = 0 \text{ and } N(A^*, Z^*, F^*) = 0.$$

To determine the species interactions of intraguild predation, it is necessary to explore the Jacobian matrix of continuous model (System (2.1)) and discrete model (System (2.3)) at E^*, which present as follows,

$$J(A^*, Z^*, F^*)|_{(2.1)} = \begin{pmatrix} A^*L_A & A^*L_Z & A^*L_F \\ Z^*M_A & Z^*M_Z & Z^*M_F \\ F^*N_A & F^*N_Z & F^*N_F \end{pmatrix} = \begin{pmatrix} A^* & 0 & 0 \\ 0 & Z^* & 0 \\ 0 & 0 & F^* \end{pmatrix} \begin{pmatrix} \frac{\partial L}{\partial A} & \frac{\partial L}{\partial Z} & \frac{\partial L}{\partial F} \\ \frac{\partial M}{\partial A} & \frac{\partial M}{\partial Z} & \frac{\partial M}{\partial F} \\ \frac{\partial N}{\partial A} & \frac{\partial N}{\partial Z} & \frac{\partial N}{\partial F} \end{pmatrix}$$

Table 2. Comparison of stability conditions of boundary equilibria.

Equilibria	Discrete model System (2.3)	Continuous model System (2.1)	Results
$E_0(0,0,0)$	Always unstable.	Always unstable.	Same
$E_1(k,0,0)$	$M(k,0,0) < 0, N(k,0,0) < 0,$ $0 < r < 2.$	$M(k,0,0) < 0, N(k,0,0) < 0.$	Eq (2.3) Stronger
$E_2(\bar{A}, \bar{Z}, 0)$	$N(\bar{A}, \bar{Z}, 0) < 0.$ Region i: $L_A < 0$ and Eq (4.3); Region ii: $-M_A/M_Z > -L_A/L_Z$ and Eq (4.4).	$N(\bar{A}, \bar{Z}, 0) < 0.$ Region i: $L_A < 0$; Region ii: $-M_A/M_Z > -L_A/L_Z.$	Eq (2.3) Stronger
$E_3(\tilde{A}, 0, \tilde{F})$	$M(\tilde{A}, 0, \tilde{F}) < 0.$ Region i: $L_A < 0$ and Eq (4.5); Region ii: $-N_A/N_F > -L_A/L_F$ and Eq (4.6).	$M(\tilde{A}, 0, \tilde{F}) < 0.$ Region i: $L_A < 0$; Region ii: $-N_A/N_F > -L_A/L_F.$	Eq (2.3) Stronger

and

$$
\begin{aligned}
J(A^*, Z^*, F^*)|_{(2.3)} &=
\begin{pmatrix}
1 + A^* L_A & A^* L_Z & A^* L_F \\
Z^* M_A & 1 + Z^* M_Z & Z^* M_F \\
F^* N_A & F^* N_Z & 1 + F^* N_F
\end{pmatrix} \\
&=
\begin{pmatrix}
1 & 0 & 0 \\
0 & 1 & 0 \\
0 & 0 & 1
\end{pmatrix}
+
\begin{pmatrix}
A^* & 0 & 0 \\
0 & Z^* & 0 \\
0 & 0 & F^*
\end{pmatrix}
\begin{pmatrix}
\frac{\partial L}{\partial A} & \frac{\partial L}{\partial Z} & \frac{\partial L}{\partial F} \\
\frac{\partial M}{\partial A} & \frac{\partial M}{\partial Z} & \frac{\partial M}{\partial F} \\
\frac{\partial N}{\partial A} & \frac{\partial N}{\partial Z} & \frac{\partial N}{\partial F}
\end{pmatrix}.
\end{aligned}
$$

Define

$$
M(A^*, Z^*, F^*) =
\begin{pmatrix}
\frac{\partial L}{\partial A} & \frac{\partial L}{\partial Z} & \frac{\partial L}{\partial F} \\
\frac{\partial M}{\partial A} & \frac{\partial M}{\partial Z} & \frac{\partial M}{\partial F} \\
\frac{\partial N}{\partial A} & \frac{\partial N}{\partial Z} & \frac{\partial N}{\partial F}
\end{pmatrix}
$$

as the ecosystem matrix of Systems (2.1) and (2.3) at E^*.

The ecological matrix of the continuous model and discrete model take the same form. We can use the ecosystem matrix to study the interactions between species in intraguild predations. In this matrix, the ij-th term measures the effect of the j-th species on the i-th species' per capita growth rate [30]. That is, the positive sign in the ecological matrix means that the j-th species is favorable to the growth of the i-th species, and the negative sign means that the j-th species is adverse to the growth of the i-th species. According to the relationship between the P:C ratio in the three species, the symbol of the ecological matrix is determined. The differences in P:C ratio of the three species affect the system. We study the matrix in two cases: $\theta_Z > \theta_F$ and $\theta_Z < \theta_F$. The different cases on the ecological matrix can be shown in Table 3.

When the P:C ratio in algae is bigger than those in zooplankton and fish, the algae quality is good for both zooplankton and fish. The ecological matrices for both cases take the same form. The relationship between algae and zooplankton is $(+, +/-)$. The increase in algae is certainly positive for zooplankton. Due to the existence of fish, the effect of zooplankton on algae is unconcern. The interactions of

algae–fish and zooplankton–fish take the form $(+/-, -)$. The effect of algae and zooplankton on fish is unconcern. When the P:C ratio in algae changes between the P:C ratio of zooplankton (θ_Z) and the P:C ratio of fish (θ_F), something shows different. 1) When $\theta_Z > \theta_F$, the quality of the algae is good for the fish but bad for the zooplankton. The interaction between algae and zooplankton has changed from $(+, +/-)$ to $(+/-, +/-)$. The increase of algae is uncertain for zooplankton due to the decline in food quality. 2) When $\theta_Z < \theta_F$, the quality of the algae is good for the zooplankton but bad for the fish. The increase of algae is positive for zooplankton. The relationship between algae and fish has changed from traditional $(+/-, -)$ to $(-, -)$. The increase in algae is certainly negative for fish due to poor food quality. When the P:C ratio in algae is smaller than those in zooplankton and fish, the algae quality is bad for both zooplankton and fish. The ecological matrices for both cases take the same form. The algae-zooplankton relationship is $(+/-, +/-)$. And algae-fish interactions take the form $(-, -)$. The symbols of ecological matrixes reveal that the increase in algae has an uncertain effect on zooplankton, but can have a certain negative impact on fish.

In summary, with the decline of algae food quality, the relationship between algae and fish changes from positive correlation $(+, +/-)$ to uncertainty $(+/-, +/-)$. The relationship between algae and fish changes from uncertainty $(+/-, -)$ to negative correlation $(-, -)$. The interaction of zooplankton – fish takes $(+/-, -)$ form. The impact of the increase of zooplankton on fish is uncertain. The interaction between fish and zooplankton is not only predation but also competition. Predation in accompanies by competition jointly affects the interaction between fish and zooplankton. In general, the decline in food quality has a negative impact on the flow of energy.

Table 3. The ecosystem matrix of model (2.3).

Conditions	$\theta_Z > \theta_F$	$\theta_Z < \theta_F$
$Q^* = (P_T - \theta_Z Z^* - \theta_F F^*)/A^* > \max\{\theta_Z, \theta_F\}$	$\begin{pmatrix} +/- & +/- & - \\ + & + & - \\ +/- & +/- & 0 \end{pmatrix}$	$\begin{pmatrix} +/- & +/- & - \\ + & + & - \\ +/- & +/- & 0 \end{pmatrix}$
$\min\{\theta_Z, \theta_F\} < Q^* < \max\{\theta_Z, \theta_F\}$	$\begin{pmatrix} +/- & +/- & - \\ +/- & +/- & - \\ +/- & +/- & 0 \end{pmatrix}$	$\begin{pmatrix} +/- & +/- & - \\ + & + & - \\ - & +/- & - \end{pmatrix}$
$Q^* < \min\{\theta_Z, \theta_F\}$	$\begin{pmatrix} +/- & +/- & - \\ +/- & +/- & - \\ - & +/- & - \end{pmatrix}$	$\begin{pmatrix} +/- & +/- & - \\ +/- & +/- & - \\ - & +/- & - \end{pmatrix}$

5. Numerical simulations

Numerical simulations on the continuous model and discrete model can be conducted to verify and deepen the results of our analysis. We will compare the two models with intraguild structure by choosing Holling type II functional response, which has been used in [22]. Let

$$a_{AZ}(A) = \frac{s_{AZ}A}{1 + s_{AZ}h_{AZ}A}, \ a_{AF}(A, Z) = \frac{s_{AF}A}{1 + s_{AF}h_{AF}A + s_{ZF}h_{ZF}Z}, \ a_{ZF}(A, Z) = \frac{s_{ZF}Z}{1 + s_{AF}h_{AF}A + s_{ZF}h_{ZF}Z},$$

where the meanings of the related parameters have been listed in Table 1. The three functional response functions mean that the predations in the intraguild structure are saturated. We numerically study the following models:

$$A(n+1) = A(n)\exp\left\{r\left(1 - \frac{A(n)}{\min\{K, (P_T - \theta_Z Z(n) - \theta_F F(n))/q\}}\right) - \frac{s_{AZ}Z(n)}{1 + s_{AZ}h_{AZ}A(n)} - \frac{s_{AF}F(n)}{1 + s_{AF}h_{AF}A(n) + s_{ZF}h_{ZF}Z(n)}\right\},$$

$$Z(n+1) = Z(n)\exp\left\{e_{AZ}\min\left\{1, \frac{P_T - \theta_Z Z(n) - \theta_F F(n)}{\theta_Z A(n)}\right\}\frac{s_{AZ}A(n)}{1 + s_{AZ}h_{AZ}A(n)} - \frac{s_{ZF}F(n)}{1 + s_{AF}h_{AF}A(n) + s_{ZF}h_{ZF}Z(n)} - d_Z\right\}, \quad (5.1)$$

$$\begin{aligned}F(n+1) = F(n)\exp\Big\{&e_{AF}\min\left\{1, \frac{P_T - \theta_Z Z(n) - \theta_F F(n)}{\theta_F A(n)}\right\}\frac{s_{AF}A(n)}{1 + s_{AF}h_{AF}A(n) + s_{ZF}h_{ZF}Z(n)}\\&+ e_{ZF}\min\left(1, \frac{\theta_Z}{\theta_F}\right)\frac{s_{ZF}Z(n)}{1 + s_{AF}h_{AF}A(n) + s_{ZF}h_{ZF}Z(n)} - d_F\Big\},\end{aligned}$$

and

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{\min\{K, (P_T - \theta_Z Z - \theta_F F)/q\}}\right) - \frac{s_{AZ}AZ}{1 + s_{AZ}h_{AZ}A} - \frac{s_{AF}AF}{1 + s_{AF}h_{AF}A + s_{ZF}h_{ZF}Z},$$

$$\frac{dZ}{dt} = e_{AZ}\min\left(1, \frac{P_T - \theta_Z Z - \theta_F F}{\theta_Z A}\right)\frac{s_{AZ}AZ}{1 + s_{AZ}h_{AZ}A} - \frac{s_{ZF}ZF}{1 + s_{AF}h_{AF}A + s_{ZF}h_{ZF}Z} - d_Z Z, \quad (5.2)$$

$$\frac{dF}{dt} = e_{AF}\min\left\{1, \frac{P_T - \theta_Z Z - \theta_F F}{\theta_F A}\right\}\frac{s_{AF}AF}{1 + s_{AF}h_{AF}A + s_{ZF}h_{ZF}Z} + e_{ZF}\min\left\{1, \frac{\theta_Z}{\theta_F}\right\}\frac{s_{ZF}ZF}{1 + s_{AF}h_{AF}A + s_{ZF}h_{ZF}Z} - d_F F.$$

The main parameters are selected from [26] and [22] for numerical simulation of the two models at different initial conditions, as shown in Table 1. For convenience, we record four typical initial conditions. 1st initial conditions is $(A(0), Z(0), F(0)) = (58.5, 1.07, 1.6)$; 2nd initial conditions is $(A(0), Z(0), F(0)) = (0.5, 0.5, 0.5)$; 3rd initial conditions is $(A(0), Z(0), F(0)) = (5, 5, 5)$; and 4th initial conditions is $(A(0), Z(0), F(0)) = (0.1, 0.05, 0.01)$. The carrying capacity of the primary producer, K, is an indirect index to evaluate the light intensity or energy input of the system. Bifurcation diagrams can intuitively show the equilibrium of a dynamical model changing with a parameter. The bifurcation diagrams in Figure 1 reveal how the dynamics of the populations in Systems (5.1) and (5.2) change with K. To facilitate intuitive analysis, Figure 2 fully reflects the dynamic behavior differences between the discrete model and the continuous model along the gradient of light levels K from 0 to 120 mg CL^{-1} with different initial values.

5.1. Low carrying capacity

When the carrying capacity varies at the low level (e.g., $0 < K < 18.2$ in Figure 1), both discrete model and continuous model show similar dynamic behaviors. When the carrying capacity is extremely low (e.g., $0 < K < 3.4$ in Figure 1 and $K = 3$ in Figure 2a_1,b_1), the zooplankton and the fish of discrete model and continuous model cannot be sustained due to starvation and the equilibrium $E_1(k, 0, 0)$ is stable. When carrying capacity further increases (e.g., $3.4 < K < 18.2$ in Figure 1), the algae and fish persist but the lack of food and the pressure of predator still can't maintain the survival of fish, which
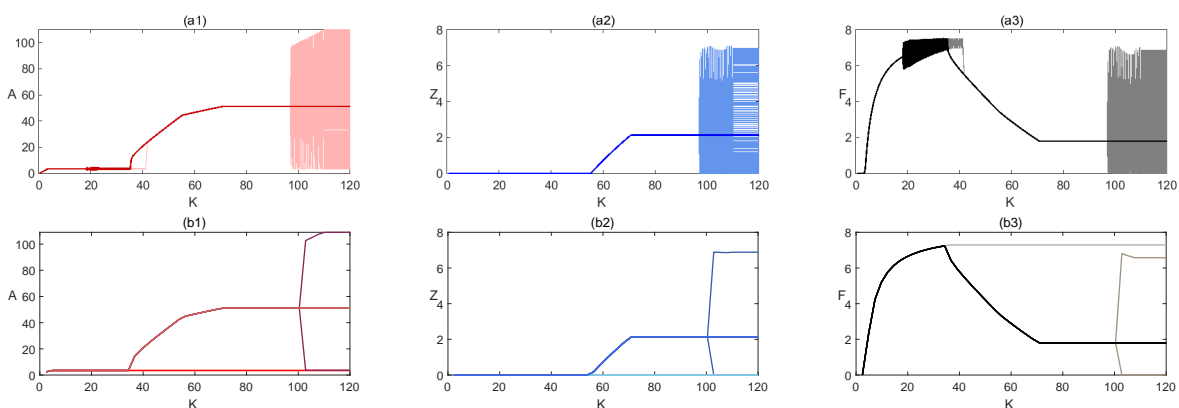
Figure 1. The bifurcation curves versus carrying capacity for the discrete model (a_i, $i = 1, 2, 3$) and continuous model (b_i, $i = 1, 2, 3$). The red, blue, and black lines represent the bifurcation diagrams of algae, zooplankton, and fish, respectively.

implies that $E_3(\tilde{A}, 0, \tilde{F})$ is stable. Figure $2a_2, b_2$ show the typical case with $K = 10$. Space trajectories with different initial values tend to steady state.
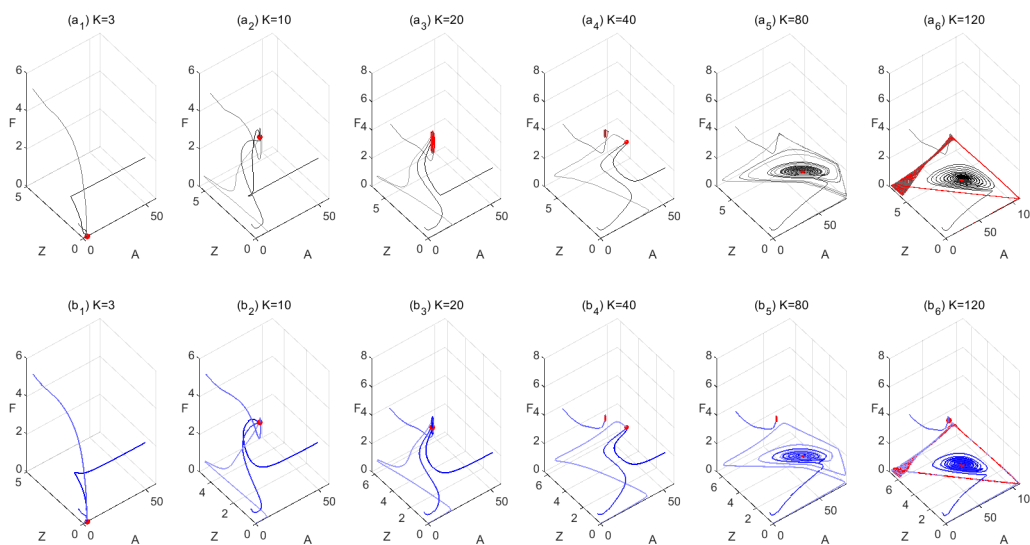

Figure 2. Phase plot for discrete model (a_i, $i = 1, 2, ..., 6$) and continuous model (b_i, $i = 1, 2, ..., 6$). The red points and cycles denote the stable equilibria and limit cycle, respectively.

5.2. Intermediate carrying capacity

When K varies in the intermediate level, a clear difference between the continuous and discrete models appears for the first time, as shown in $18.2 < K < 55.6$ in Figure 1. When $K = 18.2$, Hopf bifurcation appears in the discrete model, and a limit cycle is generated. But the continuous model is always in a stable state (e.g., $K = 20$ in Figure $2a_3, b_3$). This region shows that, compared

with the continuous model, the discrete model is more prone to oscillations. We notice that when $37.2 < K < 42.2$, different types of bistability appeared in the discrete model and continuous model. For the discrete model, one stable state maintains the previous periodic oscillation. Another stable state ends the oscillation, and the system is in a stable equilibrium state (e.g., $K = 40$ in Figure $2a_4$); For the continuous model, two local stable steady states coexist (e.g., $K = 40$ in Figure $2b_4$). With the further increase of K ($42.2 < K < 55.6$), the continuous model still admits two local stable steady states. While the discrete model shows one global stable state. As K increases in this region, the density of algae increases while the density of fish decreases due to poor food quality. The stoichiometric effect can be found in this region.

5.3. High carrying capacity

When carrying capacity varies at the high level (e.g., $55.6 < K < 120$ in Figure 1), models with different initial values show different dynamic behaviors. Some differences in dynamical behaviors between the continuous model and discrete model can also be observed in this region. During this interval, different from the previous, due to the abundance of food and the reduction of predation pressure, the zooplankton can persist. Three species can coexist in this interval. That is the equilibrium $E^*(A^*, Z^*, F^*)$ is stable. Especially, for the discrete model, $E^*(A^*, Z^*, F^*)$ is globally asymptotically stable (e.g., $55.6 < K < 97.5$ in Figure 1); for the continuous model, the model exhibits bistable states (e.g., $55.6 < K < 101.5$ in Figure 1). $E^*(A^*, Z^*, F^*)$ together with $E_3(\tilde{A}, 0, \tilde{F})$ are both locally asymptotically stable. The survival of the zooplankton in the continuous model will be affected by different initial values, while the survival of the zooplankton in the discrete model will not be affected by the initial values. Figure $2a_5, b_5$ show the typical cases with $K = 80$.

When carrying capacity varies at an extremely high level, rich dynamic behaviors show in this region. The discrete model exhibits bistable states (e.g., $97.5 < K < 120$ in Figure 1), while the continuous model shows tristable states (e.g., $101.5 < K < 120$ in Figure 1). For the discrete model, the limit set can be a stable equilibrium and a strange attractor (e.g., $K = 120$ in Figure $2a_6$); For the continuous model, the limit set can be two local stable equilibria and a strange attractor (e.g., $K = 120$ in Figure $2b_6$).
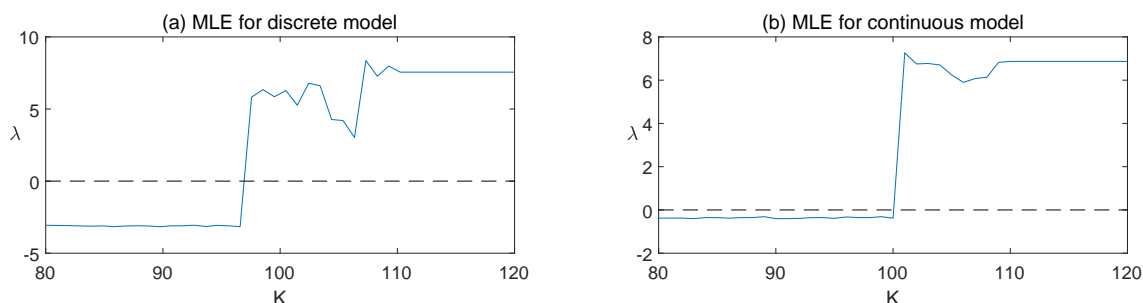

Figure 3. Spectrum of the maximum Lyapunov exponent (λ) with respect to carrying capacity (K) for the discrete-time model (a) and continuous-time model (b).

6. Discussion

The continuous stoichiometric model with intraguild structure can be used to explore interactions of the species with overlapping generations. However, when facing the situation of non-overlapping generations of herbivores, annuals, and regularly collected experimental data, we need to consider the impact of time discretization on the model. In this paper, discrete intraguild predation models with biological stoichiometry are developed and analyzed. The continuous model and discrete model share the same ecological matrix, which helps us study the interspecific relationship under different food qualities. In comparing the dynamic behaviors of the continuous model and discrete model, we conduct numerical simulations and mainly focus on the following aspects: the stoichiometric effects of food quality, multistability, coexistence, and chaos.
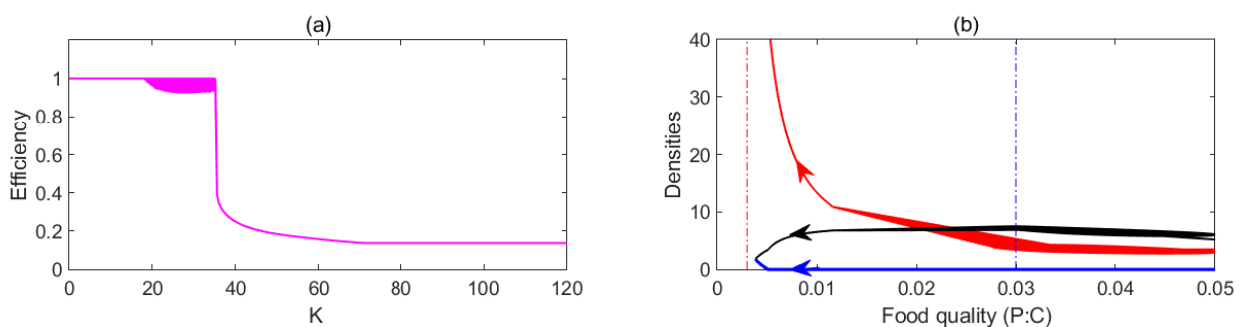

Figure 4. Bifurcation diagram of the densities of algae, zooplankton, and fish plotted against food quality for Model (2.3). The red curve, the blue curve, and the black curve represent the density of algae, zooplankton, and fish with respect to food quality, respectively. The red vertical dashed lines represent the algae minimal P:C (q). The blue vertical dashed line represents the zooplankton constant P:C (θ_Z) and fish constant P:C (θ_F), here $\theta_Z = \theta_F = 0.03$.

Nutrient recycling rates have a significant impact on ecosystem-level nutrient availability. Figure 4 shows the density of algae, zooplankton, and fish with respect to food quality ($P : C$). When the carrying capacity is low, the transfer efficiency of zooplankton and fish can reach their maximum value. As K increases, the food quality of algae shows a decreasing trend (Figure 4a). When the food quality varies in (q, θ_F), the density of algae increases, but the density of fish decreases (Figure 4b). Poor food quality causes negative effects on fish. Due to the combined effects of food quality and high trophic level predation, the impact of increased algae on zooplankton is uncertain. Due to the combined effects of interspecific competition and high trophic level predation, the impact of increased zooplankton on fish is also uncertain. This phenomenon is consistent with the results of the ecological matrix.

In some parameter intervals, the attractors of continuous and discrete models differ. When the carrying capacity varies at an intermediate level, the steady state of the continuous model is a stable equilibrium, and the steady state of the discrete model is a stable limit cycle. When the carrying capacity is at a high level, there exist three and two stable states in the continuous model and discrete model, respectively. The reason why the steady state of the continuous model is more than that of the discrete model is that the stability condition of the equilibrium point of the discrete model is stronger than that of the continuous model [31].

The coexistence regions of three species in continuous and discrete models are the same, which

both persist when the carrying capacity is high. When the carrying capacity is high, both types of models exhibit chaos. Figure 3 shows the spectrum of the maximum Lyapunov exponent (MLE) for K, revealing the presence of chaotic behavior for both discrete and continuous models. The difference point is that the interval of existence of chaotic behavior of the continuous model is smaller than that of the discrete model.

In comparison, the continuous model has a high level of robustness to time discretization. The population changes of continuous and discrete models show similar trends as parameters are changed. Some interesting dynamical features can be simulated in both continuous and discrete models, according to the numerical simulations. There are also distinctions to be made between continuous and discrete models. The results show that we should pay close attention to the selection of time scale in the research of intraguild system model prediction.

In summary, our analytical and numerical analysis suggest the following similarities and differences between continuous model and discrete model, which have been listed in Table 4.

Table 4. Comparisons between continuous model (2.1) and discrete model (2.3).

Similarities	Differences
1) The equilibria and the ecological matrix take the same forms. A negative effect of poor food quality on top predator can be observed.	1) The stability conditions of equilibria in the discrete model are stronger than those in the continuous model.
2) The coexistence regions of populations in continuous and discrete models are the same and occur under high carrying capacity conditions.	2) The coexistence of populations in continuous models depends on initial values, while in discrete models, the coexistence of populations does not depend on initial values.
3) Chaos phenomena can be observed in both types of model dynamics.	3) The chaos interval of the discrete model is larger than that of the continuous model.
4) Multistability can be observed in both types of model dynamics.	4) There are more types of multistabilities in the continuous model than in the discrete model.

Models on algae-zooplankton-fish have been widely studied from many perspectives, like bifurcation [32, 33], chaos [34], toxicity [35], and fear effect [33, 34]. The effect of discretization on the dynamic behavior of these models is worth studying. Because of the difference in dynamic behavior between continuous and discrete models, we can try to fit the predictions of the two types of models with the collected experimental data. The comparisons can be used to test which model is more suitable for prediction. This question can be used as a subject for future research.

Acknowledgments

Conflict of interest

The authors declare there is no conflict of interest.

References

1. R. W. Sterner, J. J. Elser, *Ecological Stoichiometry: the Biology of Elements from Molecules to the Biosphere*, 1st edition, Princeton University Press, 2002. https://doi.org/10.1515/9781400885695

2. R. W. Sterner, The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena, *Am. Nat.*, **136** (1990), 209–229. https://doi.org/10.1086/285092

3. R. W. Sterner, D. O. Hessen, Algal nutrient limitation and the nutrition of aquatic herbivores, *Ann. Rev. Ecol. Evol. Syst.*, **5** (1994), 1–29.

4. D. Waal, J. Elser, A. Martiny, R. Sterner, J. Cotner, Progress in ecological stoichiometry, *Front. Microbiol.*, **9** (2018), 1957. https://doi.org/10.3389/fmicb.2018.01957

5. G. Polis, C. Myers, R. Holt, The ecology and evolution of intraguild predation: potential competitors that eat each other, *Annu. Rev. Ecol. Syst.*, **20** (1989), 297–330.

6. Y. Kuang, M. Fan, S. Liu, W. Ma, *Dynamical Models of Biology and Medicine*, 1st edition, MDPI, 2019. https://doi.org/10.3390/books978-3-03921-218-7

7. R. Holt, G. Polis, A theoretical framework for intraguild predation, *Am. Nat.*, **149** (1997), 745–764. https://doi.org/10.1086/286018

8. S. Hsu, S. Ruan, T. Yang, Analysis of three species Lotka-Volterra food web models with omnivory, *J. Math. Anal. Appl.*, **426** (2015), 659–687. https://doi.org/10.1016/j.jmaa.2015.01.035

9. E. Shchekinova, M. Loder, M. Boersma, K. Wiltshire, Facilitation of intraguild prey by its intraguild predator in a three-species Lotka-Volterra model, *Theor. Popul. Biol.*, **92** (2014), 55–61. https://doi.org/10.1016/j.tpb.2013.11.005

10. I. Velazquez, D. Kaplan, J. Velasco-Hernandez, S. Navarrete, Multistability in an open recruitment food web model, *Appl. Math. Comput.*, **163** (2005), 275–294. https://doi.org/10.1016/j.amc.2004.02.005

11. P. Abrams, S. Fung, Prey persistence and abundance in systems with intraguild predation and type-2 functional responses, *J. Theor. Biol.*, **264** (2010), 1033–1042. https://doi.org/10.1016/j.jtbi.2010.02.045

12. M. Freeze, Y. Chang, W. Feng, Analysis of dynamics in a complex food chain with ratio-dependent functional response, *J. Appl. Anal.*, **4** (2014), 69–87. https://doi.org/10.11948/2014002

13. A. Verdy, P. Amarasekare, Alternative stable states in communities with intraguild predation, *J. Theor. Biol.*, **262** (2010), 116–128. https://doi.org/10.1016/j.jtbi.2009.09.011

14. P. Urbani, R. Ramos-Jiliberto, Adaptive prey behavior and the dynamics of intraguild predation systems, *Ecol. Model.*, **221** (2010), 2628–2633. https://doi.org/10.1016/j.ecolmodel.2010.08.009

15. J. Zabalo, Permanence in an intraguild predation model with prey switching, *Bull. Math. Biol.*, **74** (2012), 1957–1984. https://doi.org/10.1007/s11538-012-9740-2

16. M. Fan, Y. Kuang, Z. Feng, Cats protecting birds revisited, *Bull. Math. Biol.*, **67** (2005), 1081–1106. https://doi.org/10.1016/j.bulm.2004.12.002

17. Y. Kang, L. Wedekin, Dynamics of a intraguild predation model with generalist or specialist predator, *J. Math. Biol.*, **67** (2013), 1227–1259. https://doi.org/10.1007/s00285-012-0584-z

18. H. Shu, X. Hu, L. Wang, J. Watmough, Delay induced stability switch, multitype bistability and chaos in an intraguild predation model, *J. Math. Biol.*, **71** (2015), 1269–1298. https://doi.org/10.1007/s00285-015-0857-4

19. R. Liu, G. Liu, Dynamics of a stochastic three species prey-predator model with intraguild predation, *J. Appl. Anal. Comput.*, **10** (2020), 81–103. https://doi.org/10.11948/jaac20190002

20. Z. Xing, H. Cui, J. Zhang, Dynamics of a stochastic intraguild predation model, *Appl. Sci.*, **6** (2016), 118. https://doi.org/10.3390/app6040118

21. J. Yang, W. Wang, Persistence in a stochastic intraguild predation model, *Appl. Math. Lett.*, **63** (2017), 59–64. https://doi.org/10.1016/j.aml.2016.07.022

22. S. Diehl, The evolution and maintenance of omnivory: dynamic constraints and the role of food quality, *Ecology*, **84** (2003), 2557–2567. https://doi.org/10.1890/02-0399

23. G. Takimoto, T. Miki, M. Kagami, Intraguild predation promotes complex alternative states along a productivity gradient, *Theor. Popul. Biol.*, **72** (2007), 264–273. https://doi.org/10.1016/j.tpb.2007.04.005

24. I. Loladze, Y. Kuang, J. J. Elser, W. F. Fagan, Competition and stoichiometry: coexistence of two predators on one prey, *Theor. Popul. Biol.*, **65** (2004), 1–15. https://doi.org/10.1016/S0040-5809(03)00105-9

25. M. Fan, I. Loladze, Y. Kuang, J. J. Elser, Dynamics of a stoichiometric discrete prey-grazer model, *J. Differ. Equations*, **11** (2005), 347–364. https://doi.org/10.1080/10236190412331335427

26. M. Chen, M. Fan, Y. Kuang, Global dynamics in a stoichiometric food chain model with two limiting nutrients, *Math. Biosci.*, **298** (2017), 9–19. https://doi.org/10.1016/j.mbs.2017.04.004

27. S. Kartal, Flip and Neimark–Sacker bifurcation in a differential equation with piecewise constant arguments model, *J. Differ. Equations Appl.*, **23** (2017), 763–778. https://doi.org/10.1080/10236198.2016.1277214

28. S. Kartal, Multiple bifurcations in an early brain tumor model with piecewise constant arguments, *Int. J. Biomath.*, **11** (2018), 1850055. https://doi.org/10.1142/S1793524518500559

29. I. Loladze, Y. Kuang, J. J. Elser, Stoichiometry in prey-grazer systems: linking energy flow with element cycling, *Bull. Math. Biol.*, **62** (2000), 1137–1162. https://doi.org/10.1006/bulm.2000.0201

30. M. Chen, M. Fan, C. B. Xie, A. Peace, H. Wang, Stoichiometric food chain model on discrete time scale, *Math. Biosci. Eng.*, **16** (2018), 101–118. https://doi.org/10.3934/mbe.2019005

31. M. Chen, H. Wang, M. L. Gong, Discrete-time versus continuous-time toxic predation models, *J. Differ. Equations*, **28** (2022), 244–258. https://doi.org/10.1080/10236198.2022.2038586

32. T. Gao, X. Y. Meng, Stability and Hopf bifurcation of a delayed diffusive phytoplankton-zooplankton-fish model with refuge and two functional responses, *AIMS Math.*, **8** (2023), 8867–8901. https://doi.org/10.3934/math.2023445

33. P. Panja, T. Kar, D. K. Jana, Stability and bifurcation analysis of a phytoplankton-zooplankton-fish model involving fear in zooplankton species and fish harvesting, *Int. J. Model. Simul.*, **2022** (2022), 1–16. http://doi.org/10.1080/02286203.2022.2118020

34. Sajan, S. K. Sasmal, B. Dubey, A phytoplankton-zooplankton-fish model with chaos control: In the presence of fear effect and an additional food, *Chaos*, **32** (2022), 103114. http://doi.org/10.1063/5.0069474

35. M. Babaei, M. B. Tayemeh, M. S. Jo, I. J. Yu, S. A. Johari, Trophic transfer and toxicity of silver nanoparticles along a phytoplankton-zooplankton-fish food chain, *Sci. Total. Environ.,* **842** (2022), 156807. https://doi.org/10.1016/j.scitotenv.2022.156807