

Role of nutrient bound of prey on the dynamics of predator-mediated competitive-coexistence

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Abstract

The coexistence of competitive species with a shared predator is well established. The effect of ‘food-value’ on predator–prey dynamics has also received much attention. However, the study of a nutrient bound of prey, specifically on predator-mediated competitive-coexistence has not received much attention. Here we study the effects of the caloric content or a nutrient bound of prey on the dynamics of competitive-coexistence with the shared predator in a specific model. We propose and analyze a mathematical model for exploitative competition of two prey species with a shared predator. The change of dynamic stability due to the variation of a nutrient bound of each prey on predator-mediated dynamics is studied through extensive numerical experiments. Our analytical and numerical results demonstrate that variation in a nutrient bound promotes the switching of dynamics and may be treated as a driving force for the dynamics of competitive-coexistence with the shared predator.

Keywords: Food-value; Nutrient bound; Competitive-coexistence; Limit cycle; Extinction

1. Introduction

Generally, in predator–prey interactions, predation promotes the coexistence and biodiversity of the species (Darwin, 1859; Paine, 1966, 1980; Lubchenco, 1978). Theoretical works have proposed mainly two mechanisms whereby predation promotes coexistence: (i) a predator switches to prefer the most common prey (Murdoch and Oaten, 1975; Roughgarden and

Feldman, 1975) and (ii) a predator prefers the dominant competitor (Armstrong, 1979; Holt et al., 1994; Leibold, 1996). Although it is not discussed commonly, there is another (i.e., a third) potential mechanism: predation can cause changes in the resource used by prey, which reduces the amount of competition between them (Pianka, 1972). But this mechanism does not always work (Abrams, 1977). In particular, the coexistence of competitors for the same resource is impossible without a predator having a higher predation rate on the dominant competitor (Armstrong, 1979; Leibold, 1996). Analyses of competition (Armstrong and McGehee, 1976, 1980) have shown that the

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presence of limit cycles allows the coexistence of two or more consumer species in systems with a single resource. Analysis of two non-competitive prey species and a shared predator also showed that, when there are sustained cycles, the prey species exhibit apparent mutualism rather than competition (Abrams et al., 1998). However, further studies showed that sometimes cycles make predator-mediated coexistence less likely (Abrams, 1999).

The nutrient bound or caloric content of prey is an important factor on predator–prey dynamics. The effect of ‘food-value’ on the persistence and stability of predator–prey dynamics has been studied by many authors (e.g., van Baalen et al., 2001). Leibold (1996) showed that the predators can make a diamond food web persistent in a very restricted range of parameters. Krivan (2003) showed that adaptive switching increases the probability of species coexistence. The study of such predator switching is also extensive in the literature (e.g., Gleeson and Wilson, 1986; Fryxell and Lundberg, 1993, 1994; Krivan, 1996, 1997). Changes in the behaviour of prey due to the presence of a predator were also studied in the literature (e.g., Bolker et al., 2003; Krivan and Schmitz, 2004). Recently, Genkai-Kato (2004) has studied the nutritional value in a model of *Daphnia*–algal interaction. He found a critical nutritional value of secondary algae necessary for the persistence of the species. However, competition between the algae groups was not incorporated in the study.

The studies on predator-mediated dynamics of competitors have established that the rate of predation plays the most crucial role in the coexistence as well as other dynamics of the system. However, the caloric content or energy content of prey is a very important factor for the growth of the predator and has a significant contribution in predator-mediated dynamics of competitors. To the best of our knowledge, the variation in the caloric content of prey, specifically on the competitive-coexistence, has not been studied extensively.

In the present article, based on the analysis of a specific model, we study the effects of the variation in caloric content of prey on predator-mediated dynamics. A three-species model consisting of two competing-preys with a shared predator is proposed. We incorporate the interspecific competition in our model and study the contribution of the caloric content of prey on predator-mediated coexistence.

The organization of the paper is as follows: in Section 2 we have proposed and analyzed a mathematical model describing the competitive interactions between two prey with a shared predator. Section 3 deals with the analysis of local stability of the equilibria and bifurcation. Sufficient conditions for the local stability of the equilibria have been found. Parametric conditions for which the system around the positive equilibrium enter into Hopf-bifurcation have been derived. This result demonstrates the coexistence of the species through limit cycle oscillations. Then in Section 4, extensive numerical simulations have been performed to study the effect of the variation in the caloric content on the dynamics of competitive-coexistence with the shared predator. Finally in Section 5 we discuss the analytical and numerical results.

2. Mathematical model

In the formulation of the mathematical model we contemplate the following assumptions:

- (i) Prey 1 is much higher in abundance and more vulnerable compared with prey 2,
- (ii) Interspecific competition among the prey species is exploitative,
- (iii) Handling time for prey 1 is negligible, whereas the predator needs sufficient handling time for prey 2. We incorporate this assumption using two different functional responses of Holling types I and II.

A relevant biological situation for the last assumption may be the algal interactions in aquatic ecosystem. Marine algae are distinguishable on the basis of the size of body cell. Grazer zooplankton needs positive handling time for the large phytoplankton species. In addition, Chattopadhyay et al. (2004) considered two different functional forms to describe grazing by zooplankton on non-toxic and toxic phytoplankton.

Let $P_i(t)$ ($i = 1, 2$) and $Z(t)$ be the concentrations of prey i and the predator at time t , respectively. Let r and s be the per-capita growth rates of the two prey, respectively; K_i be the environmental carrying capacity for prey i . Let w_i be the maximum predator ingestion/predation rates for the prey i ; ξ_i , the amount of nutrient bound or caloric content of an individual prey

species; η , the conversion efficiency of the nutrient into the predator’s reproduction rate. Let c be the death rate of predator. Let a_1 and a_2 be the competition coefficients between the prey species.

Based on the above assumptions, the mathematical model can be written as follows:

$$\begin{aligned} \frac{dP_1}{dt} &= rP_1 \left(1 - \frac{P_1}{K_1} \right) - a_1 P_1 P_2 - w_1 P_1 Z, \\ \frac{dP_2}{dt} &= sP_2 \left(1 - \frac{P_2}{K_2} \right) - a_2 P_1 P_2 - w_2 \frac{P_2 Z}{m + P_2}, \\ \frac{dZ}{dt} &= \eta \left\{ \xi_1 w_1 P_1 Z + \xi_2 w_2 \frac{P_2 Z}{m + P_2} \right\} - cZ \end{aligned} \quad (1)$$

System (1) has to be analyzed with the following initial conditions:

$$P_1(0) \geq 0, \quad P_2(0) \geq 0, \quad Z(0) \geq 0 \quad (2)$$

3. Some basic results

3.1. Boundedness of the system

All the solutions of (1) are ultimately bounded in R^3_+ (The proof is obvious).

3.2. Equilibria

The system (1) possesses the following equilibria: the prey–predator-free equilibrium $E_0(0, 0, 0)$; prey 2 and the predator-free equilibrium $E_1(K_1, 0, 0)$; prey 1 and the predator-free equilibrium $E_2(0, K_2, 0)$.

A feasible predator-free equilibrium $E_3(\hat{P}_1, \hat{P}_2, 0)$, where $\hat{P}_1 = \frac{K_1 s(a_1 K_2 - r)}{a_1 a_2 K_1 K_2 - rs}$, $\hat{P}_2 = \frac{K_2 r(a_2 K_1 - s)}{a_1 a_2 K_1 K_2 - rs}$, which exists if $r > a_1 K_2$ and $s > a_2 K_1$.

A feasible prey 2-free equilibrium $E_4(P_1', 0, Z')$ where $P_1' = \frac{c}{\eta \xi_1 w_1}$ and $Z' = \frac{r(\eta \xi_1 w_1 K_1 - c)}{w_1 \eta \xi_1 w_1 K_1}$ which exists for $\xi_1 > c/\eta w_1 K_1$.

Prey 1 free equilibrium $E_5(0, P_2'', Z'')$ where $P_2'' = \frac{cm}{\eta \xi_2 w_2 - c}$ and $Z'' = \frac{sm\eta \xi_2 w_2 (K_2 \eta \xi_2 w_2 - K_2 c - cm)}{w_2 K_2 (\eta \xi_2 w_2^2 - 2\eta \xi_2 w_2 c + c^2)}$.

The positive interior equilibrium is $E^* = (P_1^*, P_2^*, Z^*)$ where, $P_2^* = \frac{m(c - \eta \xi_1 w_1 P_1^*)}{\eta \xi_1 w_1 P_1^* + \eta \xi_2 w_2 - c}$, $Z^* = \frac{r}{w_1} \left[1 - \frac{rP_1^*}{w_1 K_1} \right] - \frac{a_1 m(\eta \xi_1 w_1 P_1^* - c)}{w_1 (\eta \xi_1 w_1 P_1^* + \eta \xi_2 w_2 - c)}$ and P_1^* satisfies

the relation:

$$\theta_1 P_1^{*3} + \theta_2 P_1^{*2} + \theta_3 P_1^* + \theta_4 = 0$$

where $\theta_1 = w_2 \eta \xi_1 w_1^2 r K_2$,

$$\begin{aligned} \theta_2 &= -\eta \xi_1 w_1 K_2 [(w_2 K_1 r + w_2 a_1 m K_1) \eta \xi_1 w_1 \\ &\quad + (w_1 K_1 m a_2 - 2w_2 r) \eta \xi_2 w_2 + 2w_2 r c] \end{aligned}$$

$$\begin{aligned} \theta_3 &= (w_2 r - w_1 m a_2 K_1) K_2 \eta \xi_2 w_2^2 \\ &\quad + \{-2w_2 K_2 c + w_1 K_1 m^2 s \eta \xi_1 w_1 \\ &\quad + K_1 K_2 (-2\eta \xi_1 w_1 w_2 - \eta \xi_1 w_1 \eta \xi_2 w_2 a_1 \\ &\quad + w_1 m a_2 c + w_1 m s \eta \xi_1 w_1)\} \eta \xi_2 w_2 + w_2 K_2 r c^2 \\ &\quad + 2w_2 K_2 a_1 m K_1 \eta \xi_1 w_1 c + 2w_2 \eta \xi_1 w_1 K_2 K_1 r c \end{aligned}$$

$$\begin{aligned} \theta_4 &= -w_1 \eta \xi_2 w_2 c s m^2 - K_1 K_2 (w_2 \eta \xi_2 w_2^2 r + w_2 r c^2 \\ &\quad - w_2 a_1 m \eta \xi_2 w_2 c - 2w_2 r \eta \xi_2 w_2 c + w_1 \eta \xi_2 w_2 m s c \\ &\quad + w_2 a_1 m c^2 - w_1 m s \eta \xi_2 w_2^2) \end{aligned}$$

Some algebraic manipulations show that the above cubic equation in P_1^* possesses at least one positive root, and in turn, the system (1) has at least one positive interior equilibrium if the following conditions hold:

- (i) $c > 2\eta \xi_2 w_2$
- (ii) $\frac{ms}{r} < \frac{w_2}{w_1} < \frac{s}{a_1}$
- (iii) $a_2 K_1 \left(1 + \frac{a_1 m}{2r} \right) > 1$

Lemma 3.1. The steady state E_0 of the system (1) is a saddle point. (The proof is obvious).

Lemma 3.2. The existence of E^* implies that the prey 2 and the predator-free steady state E_1 of the system (1) is an unstable saddle if $s > a_2 K_1$. (The proof is obvious.)

Lemma 3.3. The existence of E^* implies that the prey 1 and the predator-free steady state E_2 of the system (1) is an unstable saddle if $r > a_1 K_2$. (The proof is obvious.)

Lemma 3.4. If the inequality $\eta \xi_1 w_1 \hat{P}_1 \hat{P}_2 + m \eta \xi_1 w_1 \hat{P}_1 + (\eta \xi_2 w_2 - c) \hat{P}_2 > mc$ holds then

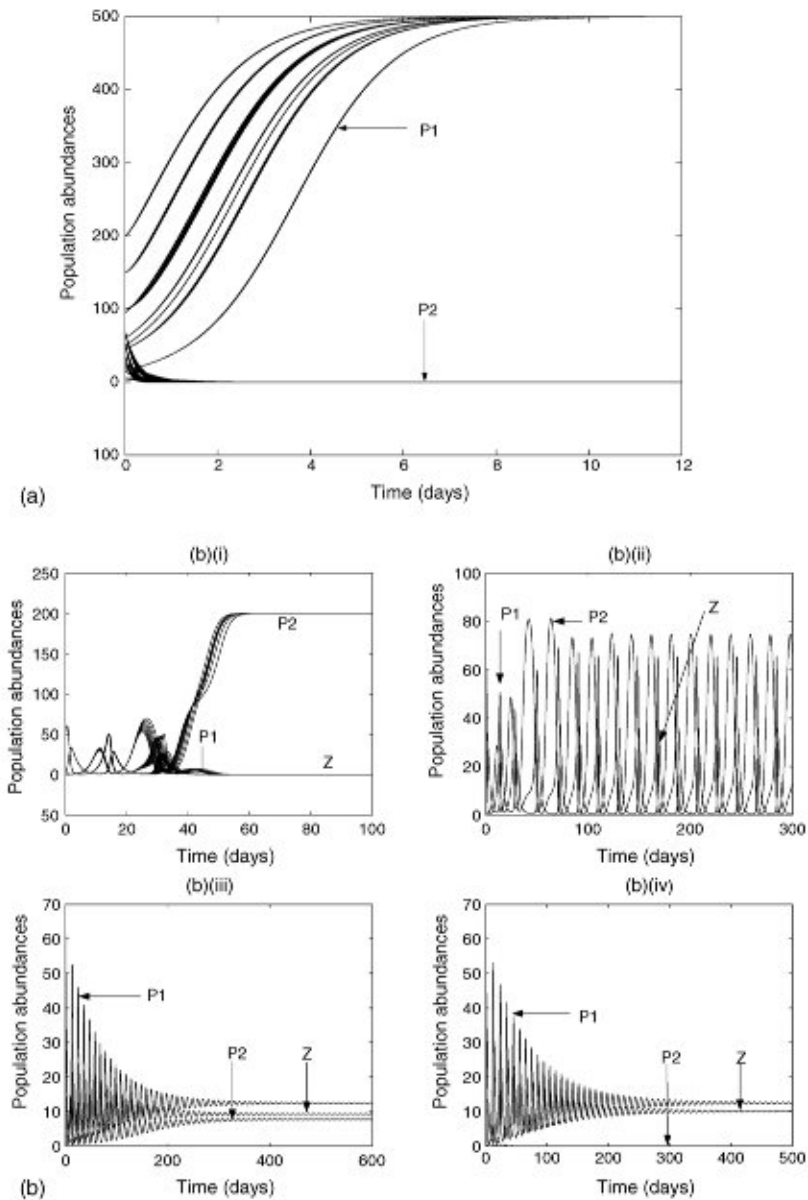


Fig. 1. (a) Competitive exclusion in the absence of the predator: extinction of the weak competitor P_2 for $0.039 \leq a_2 \leq 0.055$ i.e., for $3.9 \leq a_2/a_1 \leq 5.5$ where other parameters are fixed ($r = 0.943 \text{ day}^{-1}$, $s = 0.6 \text{ day}^{-1}$, $w_1 = 0.091 \text{ biomass}^{-1} \text{ day}^{-1}$, $w_2 = 0.04 \text{ day}^{-1}$, $\eta = 0.75 \text{ calorie biomass}^{-1}$, $\xi_1 = 0.59 \text{ calorie biomass}^{-1}$, $\xi_2 = 0.4 \text{ calorie biomass}^{-1}$, $c = 0.5 \text{ day}^{-1}$, $K_1 = 500 \text{ biomass}$, $K_2 = 200 \text{ biomass}$, $m = 40 \text{ biomass}$). (b) Effect of different competition coefficients in the presence of predator; 1(b)(i) for $3.9 \leq a_2/a_1 \leq 3.97$: extinction of P_1 and Z whereas persistence of P_2 at the same carrying capacity; 1(b)(ii) for $(a_2/a_1) = 4$: predator-mediated competitive-coexistence with large-amplitude fluctuation; 1(b)(iii) for $(a_2/a_1) = 4.57$: predator-mediated stable coexistence; 1(b)(iv) for $(a_2/a_1) = 5.4$: extinction of P_2 but stable coexistence of P_1 and Z .

the predator-free equilibria E_3 is an unstable saddle. (For the proof, see Appendix A.)

Lemma 3.5. If the inequality $s - a_2 P_1' - \frac{w_2 Z'}{m} > 0$ holds true then prey 2-free equilibria E_4 is an unstable saddle. (For the proof, see Appendix A.)

Lemma 3.6. Prey 1 free equilibrium $E_5(0, P_2'', Z'')$ is unstable if $r - a_1 P_2'' - w_1 Z'' > 0$. (For the proof, see Appendix A.)

Lemma 3.7. (Local stability of interior equilibrium): If $Z^* < \frac{sm^2}{w_2 K_2}$, $a_1 a_2 < \frac{rs}{K_1 K_2}$ and $P_2^* > \frac{rc - w_1 \eta \xi_2 w_2}{r(\eta \xi_2 w_2 - c)}$ then the interior equilibrium is locally asymptotically stable.

This gives a sufficient condition for the stable coexistence of the competitive prey species

and the herbivore predator. (For the proof, see Appendix A.)

Theorem 3.1 (Hopf-bifurcation). The system (1) enters into Hopf-bifurcation if the following conditions hold true:

$$(i) \quad a_1 a_2 > \frac{sr}{K_1 K_2}$$

and

$$(ii) \quad P_1^* > \frac{\eta \xi_2 w_2 K_1}{r}$$

(For the proof, see Appendix B.)

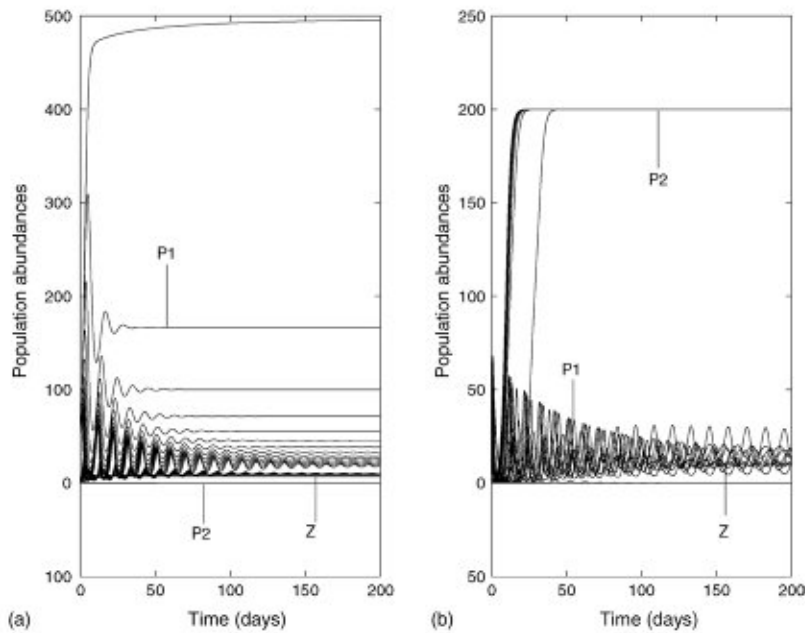


Fig. 2. Effect of variation in the nutrient bound of prey 1 on predator-mediated stable coexistence (fixed parameters $r = 0.943 \text{ day}^{-1}$, $s = 0.6 \text{ day}^{-1}$, $w_1 = 0.091 \text{ biomass}^{-1} \text{ day}^{-1}$, $w_2 = 0.04 \text{ day}^{-1}$, $\eta = 0.75 \text{ caloric biomass}^{-1}$, $c = 0.5 \text{ day}^{-1}$, $K_1 = 500 \text{ biomass}$, $K_2 = 200 \text{ biomass}$, $m = 40 \text{ biomass}$). (a) Simulation results on the assumption that the nutrient bound of prey 1 is less than or equal to that of prey 2 (i.e., $\xi_1 \leq \xi_2$): for fixed $\xi_2 = 0.40$, variation of ξ_1 in the range (0.014, 0.40) shows the extinction of prey 2 and stable coexistence of prey 1 along with the predator (Z). (b) Simulation results on the assumption that the nutrient bound of prey 1 is greater than that of prey 2 (i.e., $\xi_1 > \xi_2$): for fixed $\xi_2 = 0.40$, variation of ξ_1 in the range (0.401, 1.33) shows different dynamics (extinction, oscillation and stability). Close inside of (b): shifting of predator-mediated dynamics due to variation of the nutrient bound of prey 1; (b)(i) extinction of prey 2 but coexistence of prey 1 and Z for $0.401 \leq \xi_1 \leq 0.57$; (b)(ii) stable or very small-amplitude oscillating-coexistence of all the species for $0.5714 \leq \xi_1 \leq 0.6154$; (b)(iii) coexistence of all the species with large-amplitude oscillation for $0.62 \leq \xi_1 \leq 0.6664$; (b)(iv) extinction of P_1 and Z but persistence of P_2 for $0.67 \leq \xi_1 \leq 1.33$.

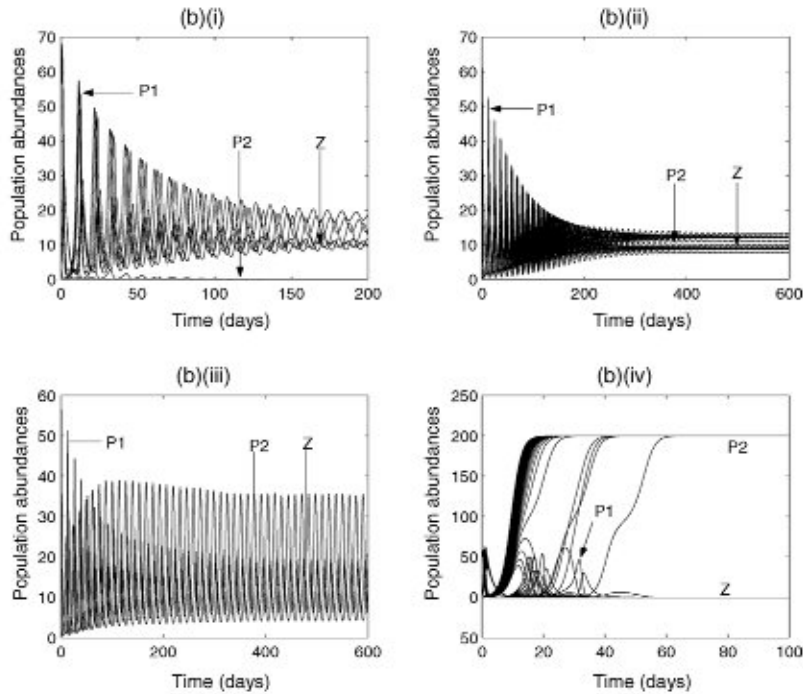


Fig. 2. (Continued).

4. Numerical experiments

In this section, through extensive numerical simulations, we study the effect of variation in the caloric content or a nutrient bound of prey on predator-mediated competitive-coexistence. In the first step, we find a hypothetical parameter set for competitive exclusion in the absence of the predator. Next we find a suitable parameter set that overcomes competitive exclusion and promotes stable coexistence of the species in the presence of the predator. Finally, we allow variation of the nutrient bound of the prey and study the effect on predator-mediated stable-dynamics.

We assume that prey 1 is a stronger competitor than prey 2. Hence for numerical experiments, we take the competition coefficient a_2 to be greater than a_1 . For a hypothetical set of parameters ($r = 0.943 \text{ day}^{-1}$, $s = 0.6 \text{ day}^{-1}$, $a_1 = 0.01 \text{ biomass}^{-1} \text{ day}^{-1}$, $a_2 = 0.039 \text{ biomass}^{-1} \text{ day}^{-1}$, $K_1 = 500 \text{ biomass}$, $K_2 = 200 \text{ biomass}$), we find the competitive exclusion of the weak competitor (i.e., P_2) in the absence of the predator. Now, keeping all

other parameters fixed, we determine a range of competition coefficients (rather the range of their ratio ($3.9 \leq a_2/a_1 \leq 5.5$)) showing competitive exclusion of prey 1 (Fig. 1(a)).

Next, in the presence of the predator, for a_2 in the range $0.039 \leq a_2 \leq 0.0397$ with fixed $a_1 = 0.01$ we see the extinction of prey 1 and the predator but prey 2 persists (Fig. 1(b)(i)). On the other hand, extinction of prey 2 occurs for $4.8 \leq a_2/a_1 \leq 5.5$ (Fig. 1(b)(iv)). However, predator-mediated coexistence occurs for $4.0 < a_2/a_1 < 4.8$ (Fig. 1(b)(ii) and (iii)).

Now, we fix the competition coefficient at ($a_1 = 0.01$, $a_2 = 0.0457$) so that predator-mediated stable coexistence occurs (Fig. 1(b)(iii)). Next we study the effect of variation in the caloric content or nutrient bound of each prey on this stable-dynamics in the following cases.

4.1. Results of variation of the nutrient bound of prey 1

Case-A: When the nutrient bound of prey 1 is less than or equal to the nutrient bound of prey 2, the

variation of ξ_1 in the range $0.014 \leq \xi_1 \leq 0.40$ leads to the extinction of prey 2, but stable coexistence of prey 1 and predator. This result implies that the variation (rather increment) in the nutrient bound of prey 1 when that of prey 2 is fixed, leads to the disappearance of the positive interior equilibrium (Fig. 2(a)).

Case-B: When the nutrient bound of prey 1 is greater than that of prey 2, variation of ξ_1 leads to different dynamics (Fig. 2(b)). Shifting of dynamics occurs for the variation of the nutrient bound of prey 1. For $0.401 \leq \xi_1 \leq 0.57$, prey 2 goes to the extinction, however, prey 1 and the predator coexist (Fig. 2(b)(i)). For some other ranges of ξ_1 , we observe the coexistence of all the species (stable coexistence or large-amplitude oscillations). For $0.5714 \leq \xi_1 \leq 0.6154$, the stable coexistence occurs (see Fig. 2(b)(ii)), whereas for $0.62 \leq \xi_1 \leq 0.6664$, the coexistence occurs with large-amplitude oscillation (see Fig. 2(b)(iii)). This result indicates that there is a tolerance level of enrichment in the nutrient bound or caloric content of prey.

Further increment in the caloric content of prey 1 ($0.67 \leq \xi_1 \leq 1.33$) leads to extinction of prey 1 and the predator (see Fig. 2(b)(iv)).

4.2. Results of variation in the nutrient bound of prey 2

Variation of the nutrient bound of prey 2 alone does not show any change in the predator-mediated stable-dynamics (Fig. 3(a) and (b)). If other parameters are fixed, the stability of the model remains in spite of variation in the nutrient bound of prey 2. However, when we consider joint variation in the caloric content of both preys, this variation is significant.

4.3. Results of joint variation in the nutrient bound of prey 1 and 2

When we consider the variation in the nutrient bound of prey 1 and 2 (i.e., ξ_1 and ξ_2) simultaneously,

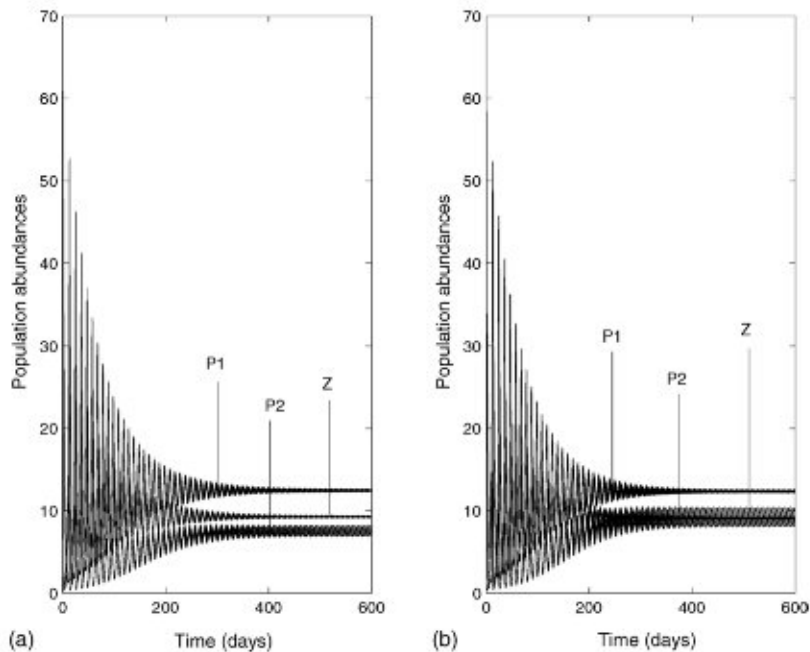


Fig. 3. Effect of variation in the nutrient bound of prey 2 on predator-mediated stable coexistence (fixed parameter set of values $r = 0.943 \text{ day}^{-1}$, $s = 0.6 \text{ day}^{-1}$, $w_1 = 0.091 \text{ biomass}^{-1} \text{ day}^{-1}$, $w_2 = 0.04 \text{ day}^{-1}$, $\eta = 0.75 \text{ biomass caloric}^{-1}$, $c = 0.5 \text{ day}^{-1}$, $K_1 = 500 \text{ biomass}$, $K_2 = 200 \text{ biomass}$, $m = 40 \text{ biomass}$). (a) Simulation results on the assumption that the nutrient bound of prey 1 is less than or equal to that of prey 2 (i.e., $\xi_1 \leq \xi_2$): for fixed $\xi_1 = 0.59$ variation of ξ_2 in the range (0.595, 1.33) shows the stable coexistence of all the three species. (b) Simulation results on the assumption that nutrient bound of prey 1 is greater than that of prey 2 (i.e., $\xi_1 > \xi_2$): for fixed $\xi_1 = 0.59$, variation of ξ_2 in the range (0.033, 0.59) also shows the stable coexistence of all the three species.

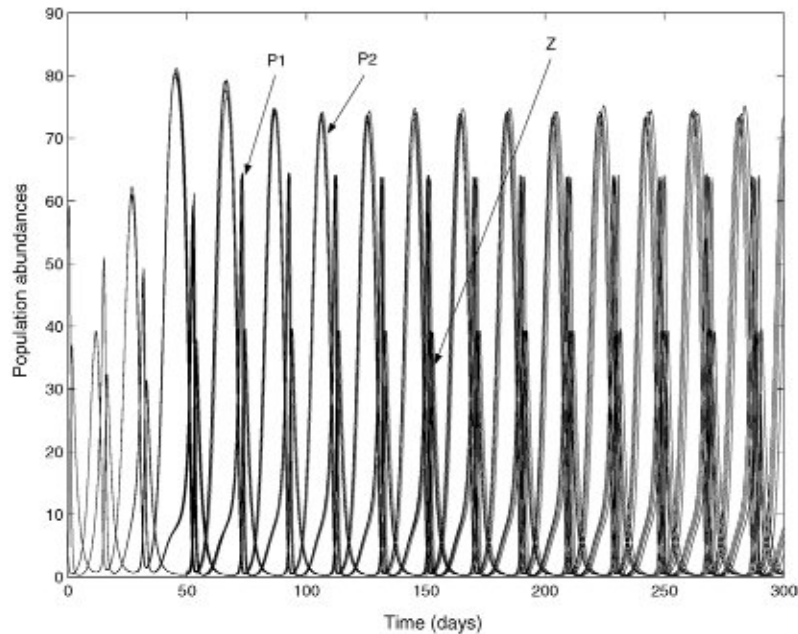


Fig. 4. Effect of the nutrient bound of P_2 on the extinction due to nutrient bound of P_1 : for a particular value of $\xi_1 = 0.6667$ (other parameters fixed), where P_1 and Z go to extinction, a range of ξ_2 (range $0.0013 \leq \xi_2 \leq 0.0116$), is obtained for which all the three species coexist (with large-amplitude oscillation).

we see that the behaviour of the dynamics determined by ξ_1 is changed by ξ_2 . Variation of the nutrient bound of prey 2 overcomes the extinction caused by the enrichment in the nutrient bound of prey 1; thus, all the species coexist through large-amplitude oscillations (Fig. 4).

5. Discussion

Studies on the competitive interaction of species with a shared predator have shown that 'prey species apparently coexist by virtue of negatively correlated competitive and antipredator abilities' (see reviews in Mills et al., 1993; Menge et al., 1994; Leibold, 1996; Bohannan and Lenski, 1997; Abrams et al., 1998). Coexistence in exploitative competition seeks a large difference in vulnerabilities of the prey species (Abrams, 1999). In our study, we have assumed each of these criteria. Competition has been taken to be exploitative with prey 1 as the stronger competitor than prey 2. Also, prey 1 is assumed to be more vulnerable to the predator than that of prey 2. A set

of sufficient conditions has been worked out for the stability of the interior equilibrium point. Moreover, the conditions for which the system enters Hopf-bifurcation have been obtained. From the numerical experiments, we have found a hypothetical parameter set for predator-mediated coexistence. Starting from a parameter set for competitive exclusion, we have arrived at the predator-mediated competitive-coexistence (Fig. 1(b)(ii)) through predator-prey cycle (limit cycle oscillation) and stability (Fig. 1(b)(iii)). Then by subsequent numerical analyses, step-by-step we have established that beyond each of those criterion for predator-mediated coexistence, the nutrient bound or caloric content of each prey plays a vital role in determining the stability and oscillatory dynamics.

In the first step, keeping all the parameters fixed at the initial level, we have allowed the variation of nutrient bound of the abundant prey (i.e., prey 1). Results demonstrate that variation of the nutrient bound of prey 1 leads to the extinction of less abundant prey 2 but stable coexistence of prey 1 with the predator (Fig. 2(b)(i)) (which resembles the result drawn by Holt (1977)). However, further increment

of the nutrient bound of prey 1 causes change in the dynamics (Fig. 2(b)). Gradual increment even leads to the extinction of prey 1 itself along with the predator (Fig. 2(b)(iv)). Thus, variation in the nutrient bound of the stronger competitor acts as a driving force for predator-mediated stable coexistence by causing the dynamic shift from the extinction of the weak competitor to the extinction of the predator and the vulnerable prey through large-amplitude oscillation and stability (see Fig. 2(b)(i)–(iv)).

Next, keeping all other parameters fixed, we have studied the variation of the nutrient bound of prey 2. This variation does not affect the stable coexistence with the shared predator (Fig. 3). However, when we consider the joint variation of the nutrient bound of both prey, it shows a significant effect on the dynamics. Simulation results demonstrate that variation in the caloric content of a weak competitor drives the system from the extinction

predator and in that case the optimal foraging behaviour can be studied based on the nutrient bound.

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Appendix A

Proofs of the lemmas of local stability.

Let $E = (\bar{P}_1, \bar{P}_2, \bar{Z})$ be any arbitrary equilibrium. Then the variational matrix about \bar{E} is given by:

$$\bar{V} = \begin{bmatrix} r - \frac{2\bar{P}_1}{K_1} - a_1\bar{P}_2 - w_1\bar{Z} & -a_1\bar{P}_1 & -w_2\bar{P}_1 \\ -a_2\bar{P}_2 & s - \frac{2s\bar{P}_2}{K_2} - a_2\bar{P}_1 - \frac{w_2m\bar{z}}{(m + \bar{P}_2)^2} & \frac{-w_2\bar{P}_2}{m + \bar{P}_2} \\ \eta\xi_1w_1\bar{Z} & \frac{\eta\xi_2w_2m\bar{Z}}{(m + \bar{P}_2)^2} & \eta\xi_1w_1\bar{P}_1 + \frac{\eta\xi_2w_2\bar{P}_2}{m + \bar{P}_2} - c \end{bmatrix}$$

(caused by the enrichment due to the nutrient bound of strong competitor) to the coexistence with large-amplitude oscillations (Fig. 4). Thus, while addressing the issue of predator-mediated coexistence, consideration of the level of the nutrient bound or caloric content of prey might be highlighted.

Another interesting result is noteworthy. We see that increased caloric content of a vulnerable prey leads to dynamical instability (Fig. 2(b)(iv)). This result may be supported as a consequence of the principle of the ‘paradox of enrichment’ provided we broaden the concept of enrichment by incorporating the nutrient bound or caloric content of prey (see, Roy et al., submitted). Does this result enlighten us with some ‘generalized principle of the paradox of enrichment’ that should be of interest for further investigations before defining precisely?

Further study of the nutrient bound on the predator-mediated coexistence can be done with two prey species not behaving similarly in vulnerability to the

By computing the variational matrix for the equilibrium E_0 of the system (2.1) we find that the eigenvalues of the variational matrix V_0 are $\lambda_1 = r > 0$, $\lambda_2 = s > 0$, $\lambda_3 = -c < 0$.

Clearly the plankton-free steady state is unstable (saddle).

Further the eigenvalues of the variational matrix V_1 of the equilibrium E_1 of the system (2.1) are $\lambda_1 = -r < 0$, $\lambda_2 = s - a_2K_1$ and $\lambda_3 = \eta\xi_1w_1K_1 - c$. This steady state is unstable if either $s > a_2K_1$ or $\eta\xi_1w_1K_1 > c$ (for existence of E^*).

The eigenvalues of the variational matrix V_2 are $\lambda_1 = -s < 0$, $\lambda_2 = r - a_1K_2$ and $\lambda_3 = \frac{\eta\xi_2w_2K_2}{m + K_2} - c$.

Thus the steady state E_2 is unstable if either $r > a_1K_2$ or $\eta\xi_2w_2 > \frac{c(m + K_2)}{K_2}$ (for existence of E^*).

Further the eigenvalues of the variational matrix V_3 around the equilibrium E_3 of the system (2.1) are λ_1' , λ_2' which are the roots of the equation:

$$\lambda^2 + \lambda \left(\frac{r\hat{P}_1}{K_1} + \frac{s\hat{P}_2}{K_2} \right) + \hat{P}_1\hat{P}_2 \frac{(rs - a_1a_2K_1K_2)}{K_1K_2} = 0$$

and $\lambda_3' = \eta\xi_1 w_1 \hat{P}_1 + \frac{\eta\xi_2 w_2 \hat{P}_2}{m + P_2} - c$. Clearly λ_1' and λ_2' have negative real parts. Now if $\lambda_3' > 0$ i.e. $\eta\xi_1 w_1 \hat{P}_1 + \frac{\eta\xi_2 w_2 \hat{P}_2}{m + P_2} > c$ or, $\eta\xi_1 w_1 \hat{P}_1 \hat{P}_2 + m\eta\xi_1 w_1 \hat{P}_1 + (\eta\xi_2 w_2 - c)\hat{P}_2 > mc$ then E_3 is an unstable saddle.

In similar manner, the equilibrium $E_4(P_1', 0, Z')$ of the system (2.1) is unstable saddle if $s - a_2 P_1' - \frac{w_2 Z'}{m} > 0$.

The equilibrium $E_5(0, P_2'', Z'')$ of the system (2.1) is unstable if $r - a_1 P_2'' - w_1 Z'' > 0$.

The variational matrix of system (2.1) around the positive equilibrium $E^* = (P_1^*, P_2^*, Z^*)$ is:

$$V^* = \begin{bmatrix} \frac{-rP_1^*}{K_1} & -a_1 P_1^* & -w_1 P_1^* \\ -a_2 P_2^* & \frac{-sP_2^*}{K_2} + \frac{w_2 Z^* P_2^*}{(m + P_2^*)^2} & -\frac{w_2 P_2^*}{m + P_2^*} \\ \eta\xi_1 w_1 Z^* & \frac{\eta\xi_2 w_2 m Z^*}{(m + P_2^*)^2} & 0 \end{bmatrix}$$

The characteristic equation is:

$$\lambda^3 + Q_1 \lambda^2 + Q_2 \lambda + Q_3 = 0$$

where the coefficients $Q_I, I = 1, 2, 3$ are:

$$Q_1 = \frac{rP_1^*}{K_1} + \frac{sP_2^*}{K_2} - \frac{w_2 Z^* P_2^*}{(m + P_2^*)^2},$$

$$Q_2 = -a_1 a_2 P_1^* P_2^* - \frac{rP_1^*}{K_1} \frac{w_2 Z^* P_2^*}{(m + P_2^*)^2} - \frac{sP_2^*}{K_2} + w_2 \eta\xi_1 w_1 P_1^* Z^* + \frac{w_2 P_2^* \eta\xi_2 w_2 m Z^*}{(m + P_2^*)^2},$$

$$Q_3 = P_1^* P_2^* P_3^* \left[-\frac{w_1 a_1 \eta\xi_2 w_2 m}{(m + P_2^*)^2} - w_1 \eta\xi_1 w_1 \left(\frac{w_2 Z^*}{(m + P_2^*)^2} - \frac{sP_2^*}{K_2} \right) - \frac{a_1 w_2 \eta\xi_1 w_1}{m + P_2^*} + \frac{r w_2 \eta\xi_2 w_2 m}{K_1 (m + P_2^*)^3} \right]$$

Since $P_1^*, P_2^* > 0$ (from (3.5)) then $Q_1 > 0$ always if $Z^* < \frac{sm^2}{w_2 K_2}$. Now let us define:

$$\delta^{(2)} = Q_1 Q_2 - Q_3 = \left[\frac{sP_2^*}{K_2} + \frac{rP_1^*}{K_1} - \frac{w_2 Z^* P_2^*}{(m + P_2^*)^2} \right] \left[-a_1 a_2 P_1^* P_2^* - \frac{rP_1^*}{K_1} \frac{w_2 Z^* P_2^*}{(m + P_2^*)^2} - \frac{sP_2^*}{K_2} + w_2 \eta\xi_1 w_1 P_1^* Z^* + \frac{w_2 P_2^* \eta\xi_2 w_2 m Z^*}{(m + P_2^*)^2} \right] + P_1^* P_2^* P_3^* \left[\frac{w_1 a_1 \eta\xi_2 w_2 m}{(m + P_2^*)^2} + w_1 \eta\xi_1 w_1 \times \left(\frac{w_2 Z^*}{(m + P_2^*)^2} - \frac{sP_2^*}{K_2} \right) + \frac{a_1 w_2 \eta\xi_1 w_1}{m + P_2^*} - \frac{r w_2 \eta\xi_2 w_2 m}{K_1 (m + P_2^*)^3} \right]$$

After manipulation of the expression and simplification one can find out that $Q_3 > 0$ and $\delta^{(2)} > 0$ if the inequalities, $a_1 a_2 < \frac{rs}{K_1 K_2}$ and $P_2^* > \frac{rc - w_1 \eta\xi_2 w_2}{r(\eta\xi_2 w_2 - c)}$ are satisfied.

Therefore, according to Routh-Hurwitz criterion, E^* is locally asymptotically stable under the above conditions.

Appendix B

The expression $\delta^{(2)} = Q_1 Q_2 - Q_3$ may be written as a quadratic of the parameter w_2 as:

$$\delta^{(2)}(w_2) = d_1 w_2^2 + d_2 \eta\xi_1 w_1 + d_3$$

where

$$d_1 = \frac{Z^{*2} P_2^{*2} (m r P_1^* + r P_1^* P_2^* - \eta\xi_2 w_2 m K_1)}{K_1 (m + P_2^*)^5}$$

$$d_2 = \frac{s \eta\xi_2 w_2 m Z^{*2} P_2^{*2}}{K_2 (m + P_2^*)^3} - \frac{Z^* P_1^* P_2^* (r^2 K_2 P_1^{*2} + 2 P_2^* r s K_1 - P_2^* a_1 a_2 K_1^2 K_2)}{K_2 K_1^2 (m + P_2^*)^2} + \frac{a_1 \eta\xi_1 w_1 P_1^* P_2^* Z^*}{m + P_2^*}$$

and

$$d_3 = \frac{P_1^* P_2^{*2}}{K_2} \left(\frac{rs^2}{K_1 K_2} - sa_1 a_2 \right) + \frac{P_1^{*2} P_2^*}{K_1} \left(\frac{r^2 s}{K_1 K_2} - ra_1 a_2 \right) + \frac{Z^* P_1^* (rw_1 \eta \xi_1 w_1)}{K_1}$$

We observe that, $d_1 > 0$ if $P_1^* > \frac{\eta \xi_2 w_2 K_1}{r}$ and $d_3 < 0$ if $a_1 a_2 > \frac{sr}{K_1 K_2}$. Hence from the elementary theory of equations it follows that the equation:

$$\delta^{(2)}(w_2) = d_1 w_2^2 + d_2 w_2 + d_3 = 0$$

has only one positive real root, say, w_2^* .

Now, a necessary and sufficient condition for Hopf-bifurcation (Hassard and Kazarinoff, 1981) is:

$$\delta^{(2)}(w_2^*) = 0 \quad \text{and} \quad \left[\frac{d\delta^{(2)}(w_2)}{dw_2} \right]_{w_2=w_2^*} \neq 0$$

The second condition can easily be verified. Hence the theorem.

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