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Profitability of prey determines the response of population abundances to enrichment

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Theoretical and empirical evidence in a one-predator–two-prey system consistently indicates a regular trend that the less profitable (therefore, less vulnerable) prey increases in abundance with enrichment. The response in the abundance of the more profitable (more vulnerable) prey to enrichment has, however, remained unclear. Previous theoretical models have assumed the less profitable prey as inedible, though its actual profitability is unknown. Here, relaxing this assumption, we show that the response of the more profitable prey abundance to enrichment depends critically on the profitability of the less profitable prey. Specifically, the more profitable prey increases in abundance with enrichment if the profitability of the less profitable prey is lower than a critical value so that it cannot support the predator population by itself even at high densities (in this case, the prey is referred to as 'unpalatable') and decreases otherwise. This establishes a more general rule which unifies the previous works and resolves the indeterminacy on the response of the more profitable prey.

Keywords: enrichment; equilibrium abundance; less profitable prey; more profitable prey; predator–prey system; profitability

1. INTRODUCTION

Enrichment (or eutrophication as it is often referred to) is an increasingly widespread and serious trend in natural ecosystems and may become even more serious in the future due to an increased level of human activities. In such a trend, it is of importance to elucidate the response of ecosystems such as a predator–prey system to enrichment. The abundance of the less profitable prey in a one-predator–two-prey system has been shown to increase with enrichment theoretically (Phillips 1974; Vance 1978; Leibold 1989, 1996; Grover 1995) and empirically (Watson & McCauley 1988; Watson *et al.* 1992), whereas the response of the more profitable prey abundance has not been clear. This problem of response (i.e. the more profitable prey increases or decreases with enrichment) is critical because the prey is the main resource supporting the system.

Many theoretical models have predicted that the more profitable prey decreases with enrichment (Phillips 1974; Vance 1978; Leibold 1989, 1996), while another model predicts that it increases (Grover 1995). Although these models have assumed the less profitable prey as inedible, it is not always clear how profitable the less profitable prey actually is for the predator (Leibold 1989; Murdoch *et al.* 1998). In this article, by changing this unknown profitability of the less profitable prey, we investigate the response of population abundances to enrichment in a one-predator–two-prey system.

Here we focus on a system consisting of a predator species, such as a generalist filter feeder (*Daphnia*) and two prey species, such as two species of algae, with different profitability. The *Daphnia*–algal system is one of the most widespread and best studied systems in lakes. For *Daphnia*, unicellular algae (often called nanophytoplankton) are more profitable, while larger algae (net-phytoplankton) are less profitable (Sterner 1989; Kretzschmar *et al.* 1993). The ratio of the surface area to the volume of algal cells decreases with cell size, so smaller algae are generally superior in nutrient competition. The functional response of *Daphnia* can be well described by a type 2 equation (DeMott 1982; Paloheimo *et al.* 1982; Porter *et al.* 1982). There exists a difference in vulnerability between the two prey and the less profitable prey cannot be perfectly excluded from *Daphnia*'s diet because *Daphnia* mechanically selects its prey by a filtering comb. Using a theoretical model that incorporates these features, we investigate the response of the equilibrium abundances to enrichment which is defined as an increase in the total amount of nutrient in the system.

2. MODEL

We use the following set of differential equations:

$$\mathrm{d}X_1/\mathrm{d}t = \mu_1(N)X_1 - \varepsilon_1 X_1 - r_1(X_1, X_2)Y, \tag{1}$$

$$\mathrm{d}X_2/\mathrm{d}t = \mu_2(N)X_2 - \varepsilon_2 X_2 - r_2(X_1, X_2)Y, \tag{2}$$

$$\mathrm{d}Y/\mathrm{d}t = -\varepsilon_3 Y + k(g_1 r_1(X_1, X_2) + g_2 r_2(X_1, X_2))Y, \tag{3}$$

and

$$N + g_1X_1 + g_2X_2 + g_3Y = T, \tag{4}$$

where X_1, X_2 and Y are the abundances of the more profitable prey, the less profitable prey and the predator, respectively. The parameters are $\mu_i(N)$, the nutrient-dependent reproductive rate of prey i ($i = 1, 2$); ε_i (or ε_3), the density-independent loss rate of prey i (or predator); $r_i(X_1, X_2)$, the functional response of the predator modified to include two prey species; g_i (or g_3), the amount of nutrient bound in an individual of prey i (or predator); k, the conversion efficiency of the nutrient into the predator's reproduction rate; and T, the total amount of nutrient in the system. The equation for the nutrient dynamics (N) is not necessary in this closed system

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because of a simple algebraic mass-balance expression in equation (4). We define T, the total amount of nutrient, as the degree of enrichment in the system, as is commonly used in empirical studies (e.g. total phosphorus in lakes), rather than the carrying capacity or the intrinsic growth rate of prey, which is biologically obscure with relation to enrichment (Abrams & Roth 1994).

According to Kretzschmar *et al.* (1993) and Grover (1995), the two-prey species version of the functional response of *Daphnia* is expressed by

$$r_i(X_1, X_2) = \frac{a_i X_i}{1 + h_1 a_1 X_1 + h_2 a_2 X_2}, \tag{5}$$

where a_i and h_i are, respectively, the consumption efficiency of and handling time for prey i. Since prey 1 is more profitable for and more vulnerable to the predator than prey 2, the following inequalities hold:

$$g_1/h_1 > g_2/h_2, \tag{6}$$

and

$$a_1 > a_2. \tag{7}$$

We assume that the more profitable prey X_1 is superior in nutrient competition to the less profitable prey X_2, because otherwise the two prey cannot coexist (Takeuchi 1996). We also assume that the more profitable prey yields enough nutrition to support a persisting predator population in the absence of the less profitable prey, which mathematically requires that there exists a range of X_1 such that $\mathrm{d}Y/\mathrm{d}t > 0$ when $X_2 = 0$ and $Y > 0$ in equation (3), i.e.

$$g_1/h_1 > \varepsilon_3/k. \tag{8}$$

3. RESULTS

In the X_1–X_2 space (figure 1), the equilibrium abundances of the two prey are given as the intersection point of the two lines, which is represented by the following equations:

$$(kg_1 - h_1\varepsilon_3)a_1X_1 + (kg_2 - h_2\varepsilon_3)a_2X_2 = \varepsilon_3, \tag{9}$$

and

$$(g_1 + g_3h_1a_1c)X_1 + (g_2 + g_3h_2a_2c)X_2 = T - N^* - g_3c, \tag{10}$$

where $c = (\mu_1(N^*) - \varepsilon_1)/a_1 = (\mu_2(N^*) - \varepsilon_2)/a_2$. Equation (9) is derived from equation (3) (the right-hand side equalling zero) and equation (10) from equations (1) and (4). Line (9), which is given by equation (9), has a negative slope if $g_2/h_2 > \varepsilon_3/k$ (figure 1*a*) and a positive slope if $g_2/h_2 < \varepsilon_3/k$ (figure 1*b*). Line (10), which has been referred to as a mass-balance constraint (Holt *et al.* 1994), always has a negative slope and moves away from the origin as T increases. The slope of line (9) when negative is always steeper than that of line (10) under the condition given in equations (6) and (7) (see Appendix A). Thus, the response of the prey abundances to enrichment at equilibrium (indicated as an increase in T from a lower level T_1 to a higher level T_2) exhibits two qualitatively different patterns depending on the profitability of the less profitable prey, g_2/h_2. The equilibrium abundance of the more profitable prey (X_1^*, the X_1 coordinate of the equilibrium point, indicated as the intersecting point of the two lines in figure 1) decreases while that of the less profitable prey (X_2^*) increases if the profitability of the less profitable prey (g_2/h_2) is higher than a critical value ε_3/k so that the slope of equation (9) is negative (figure 1*a*), whereas both increase otherwise (figure 1*b*). As seen from equation (8), because a less profitable prey with a profitability $g_2/h_2 > \varepsilon_3/k$ can yield sufficient nutrition to support the predator population in the absence of the more profitable prey, while a prey with a profitability $g_2/h_2 < \varepsilon_3/k$ cannot even at high densities, the less profitable prey can be called a 'palatable' prey for the former case and an 'unpalatable' prey for the latter case.

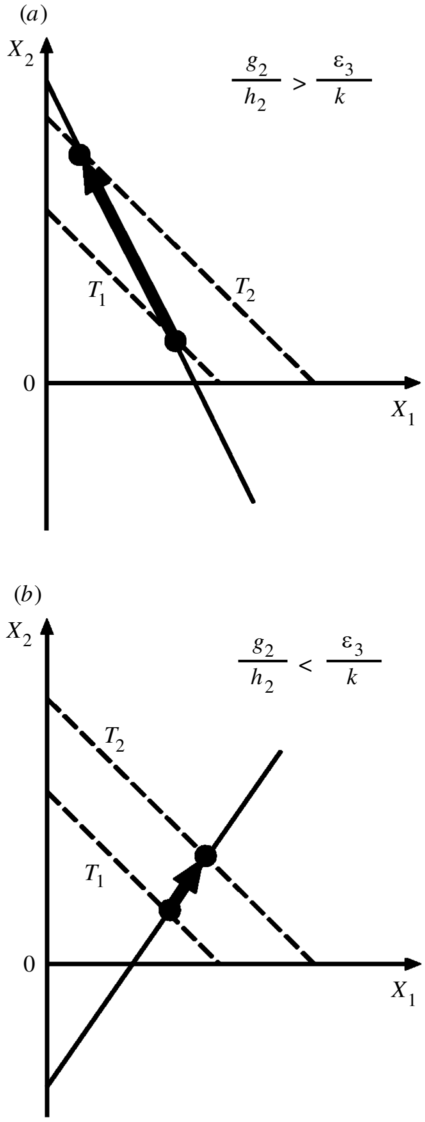

Figure 1. Graphical representation of the effects of enrichment on the abundances of two competing prey, the more profitable prey (X_1) and the less profitable prey (X_2), in the X_1–X_2 space (*a*) when the less profitable prey is palatable, i.e. $g_2/h_2 > \varepsilon_3/k$ and (*b*) when the prey is unpalatable, i.e. $g_2/h_2 < \varepsilon_3/k$. Their equilibrium abundances are expressed by the intersection point of the solid (corresponding to equation (9)) and dashed lines (corresponding to equation (10)). The dashed line moves away from the origin as the system is enriched, which is defined as an increase in the total amount of nutrient (T) in the system ($T_1 < T_2$).

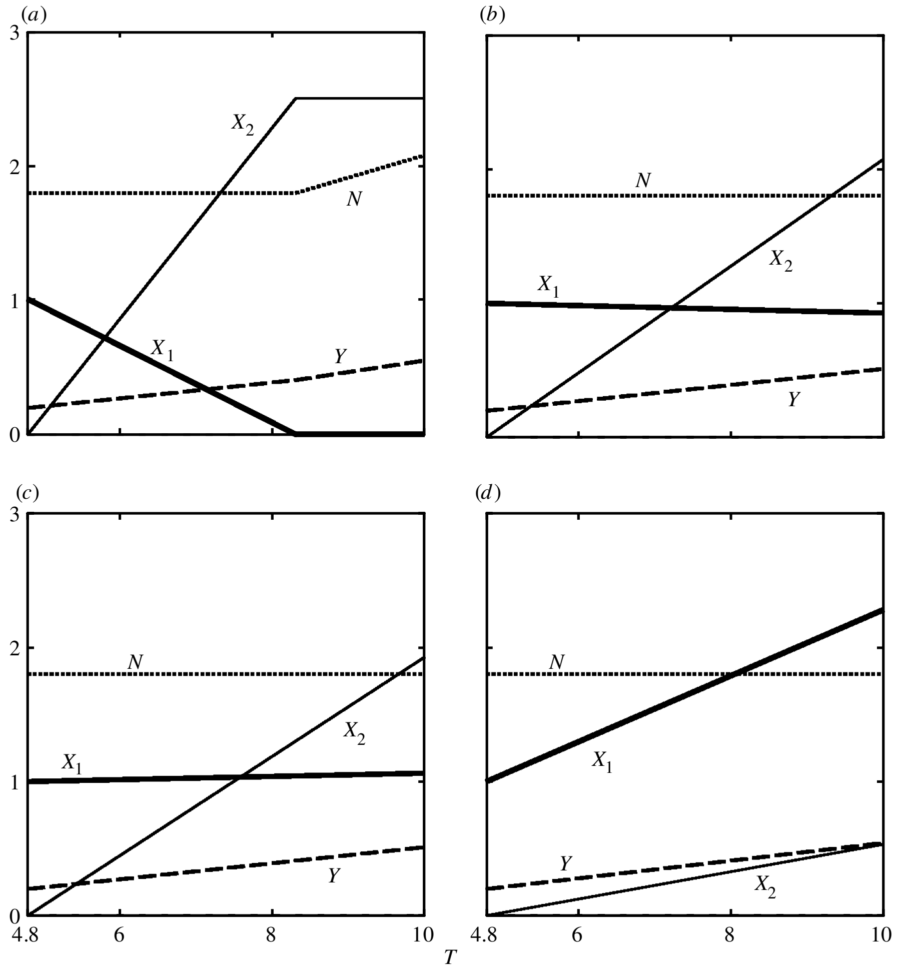

Figure 2. Examples of the response of the nutrient (dotted line), the more profitable prey (thick line), the less profitable prey (thin line) and the predator (dashed line) at equilibrium to enrichment (*a*,*b*), when the less profitable prey is palatable (*a*, $g_2/h_2 = 6.7$; *b*, 5.1) i.e. $g_2/h_2 > \varepsilon_3/k$ and (*c*,*d*) when the prey is unpalatable (*c*, 4.9; *d*, 2) i.e. $g_2/h_2 < \varepsilon_3/k$. The critical profitability (ε_3/k) is 5 and the profitability of the less profitable prey g_2/h_2 was changed by changing the h_2-value. The profitability of the more profitable prey (g_1/h_1) is 10. The degree of enrichment is defined as the total amount of nutrient (T) in the system. We assumed that $\mu_i(N) = b_i N (i = 1,2)$. The following parameter values were used: $b_1 = b_2 = 1$, $\varepsilon_1 = 0.8$, $\varepsilon_2 = 1$, $a_1 = 10$, $a_2 = 8$, $g_1 = g_2 = 1$, $h_1 = 0.1$, $\varepsilon_3 = 0.5$, $k = 0.1$ and $g_3 = 10$.

The equilibrium concentration of the nutrient (N^*), which is obtained from equations (1) and (2), is independent of the degree of enrichment (T) as long as the two prey coexist (figure 2). The equilibrium abundance of the predator (Y^*) always increases with enrichment (see Appendix A). When the less profitable prey (X_2) is palatable, the decline of the more profitable prey with enrichment finally leads to its extinction, resulting in a one-predator–one-prey system, as shown in figure 2*a*. In this reduced system, both the nutrient concentration and the predator abundance increase, whereas the less profitable prey abundance remains unchanged, with further enrichment, as shown by previous works (Grover 1995; Leibold 1996). As the profitability of the less profitable prey (g_2/h_2) decreases (the transition $a \rightarrow b \rightarrow c \rightarrow d$ in figure 2), the rate of increase in the equilibrium abundance of the more profitable prey (the slope of the line representing X_1^* in figure 2) increases so that it turns from negative (figure 2*a*,*b*, corresponding to figure 1*a*) into positive (figure 2*c*,*d*, corresponding to figure 1*b*). When the less profitable prey has a profitability close to the critical value ε_3/k, X_1^* scarcely changes with enrichment (figure 2*b*,*c*).

4. DISCUSSION

In this paper, we concentrated our focus on the equilibrium abundances because a population abundance at equilibrium can be regarded as a representative value of the population even if the system displays a cyclic dynamics (but see Grover & Holt (1998) for a stability analysis of this system). In their analysis, Grover & Holt (1998) confirmed that stability depends on the balance between the stabilizing factor of intraspecific competition among prey for nutrients and the destabilizing factor of satiation in predation. A follow-up paper (Genkai-Kato 2001) deals with the stability of the system in relation to the profitability of the less profitable prey by following the relationship between the equilibrium abundances and the profitability analysed here. At the least, we have preliminarily confirmed by numerical simulation that the equilibria of the systems with the parameter values used in figure 2 were all stable.

The equilibrium abundance of the less profitable prey increased with enrichment, independent of its profitability, as shown in previous models (Phillips 1974; Vance 1978; Leibold 1989, 1996; Grover 1995). The outcome of our model with respect to the predator abundance conforms to some of these models in which the predator increases in abundance with enrichment (Leibold 1989; Grover 1995), but differs from other models in which the predator does not change in abundance (Phillips 1974; Leibold 1996). As for the more profitable prey, the response was dependent upon the profitability of the less profitable prey. The two qualitatively different predictions made by previous models can be interpreted in the context of our model, although some of these models defined enrichment in slightly different ways. In one prediction where the more profitable prey decreases in abundance with enrichment (Phillips 1974; Vance 1978; Leibold 1989, 1996), a linear functional response was assumed (the case $h_i = 0$ in our model and, hence, the profitability is infinity), implying that the less profitable prey was able to support the predator population by itself unless it is completely valueless (i.e. $g_2 \neq 0$), which corresponds to a palatable prey in our model. On the other hand, in the other prediction where the more profitable prey increases in abundance with enrichment (Grover 1995), the less profitable prey was assumed not to yield any nutrition to the predator ($g_2 = 0$), corresponding to an unpalatable prey in our model. These qualitatively different responses of the more profitable prey abundance may be explained by the fact that, although enrichment in general leads to increases in both prey abundances, the presence of a less profitable but palatable prey strongly suppresses the more profitable prey by raising the abundance of the common predator, namely the effect of apparent competition (Holt 1977).

Leibold (1989) summarized results from numerous experiments involving nutrient enrichment in which the most general outcome was an increase in all abundances of more profitable (edible) prey, less profitable (inedible) prey and predators (herbivores). According to our model, this outcome suggests that the less profitable prey was nutritionally inadequate in supporting the predator populations in the absence of the more profitable prey. In this sense, the prey could be called unpalatable prey. Moreover, other empirical data which have been compiled (Watson & McCauley 1988; Watson *et al.* 1992) have shown that the less profitable prey increased greatly whereas the more profitable prey scarcely changed with increasing total phosphorus, suggesting that the profitability of the less profitable prey in these cases was close to the critical value ε_3/k.

Besides our finding in the present model, another one-predator–two-prey system in which the predator displayed optimally selective feeding, like calanoid copepods, showed that a less profitable prey with a profitability lower than the critical value (thus, unpalatable prey) increases the robustness of the system against enrichment (Genkai-Kato & Yamamura 1999). Thus, the profitability of less profitable prey has the potential to become a key predictor for the behaviour of predator–prey systems in nature.

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APPENDIX A. THE EQUILIBRIUM ABUNDANCE OF THE PREDATOR AND THE STEEPNESS OF LINES GIVEN BY EQUATIONS (9) AND (10)

The equilibrium abundance of the predator ($\mathcal{Y}^*$) is given from equations (2)–(4) by

$$\begin{aligned}\mathcal{Y}^* = {} & \{kh_1h_2a_1a_2c(g_1/h_1 - g_2/h_2)\}\mathcal{T}/\{a_1(kg_1 - h_1\varepsilon_3) \\ & \times (g_2 + g_3h_2a_2c) - a_2(kg_2 - h_2\varepsilon_3) \\ & \times (g_1 + g_3h_1a_1c)\} + \text{constant}, \end{aligned} \tag{A1}$$

where $c = (\mu_1(\mathcal{N}^*) - \varepsilon_1)/a_1 = (\mu_2(\mathcal{N}^*) - \varepsilon_2)/a_2$ and the 'constant' term is independent of $\mathcal{T}$. The numerator is positive under the condition given in equations (6) and (7) (hereafter called condition (6–7)). The denominator is also positive if

$$\{(p_1 + sa_1)a_2 - (p_1 - q)a_1\}p_2 < (q + sa_1)p_1a_2,$$

where $p_i = g_i/h_i$, $q = \varepsilon_3/k$, $s = g_3c$. This is equivalent to

$$p_2 < f(a_2) \qquad \text{when} \quad a_2 > \hat{a}_2, \tag{A2}$$

and

$$p_2 > f(a_2) \qquad \text{when} \quad a_2 < \hat{a}_2, \tag{A3}$$

where $f(a_2) = (q + sa_1)p_1a_2/\{(p_1 + sa_1)a_2 - (p_1 - q)a_1\}$ and $0 < \hat{a}_2 = (p_1 - q)a_1/(p_1 + sa_1) < a_1$. It is obvious that equation (A3) always holds because $f(a_2) < 0$. Since $f(a_2)$ is a decreasing function of a_2, it takes its minimum p_1 at $a_2 = a_1$ in the interval, $\hat{a}_2 \leqslant a_2 \leqslant a_1$. Thus, equation (A2) is also satisfied as long as $p_2 < p_1$ and $a_2 < a_1$. Therefore, $\mathrm{d}\mathcal{Y}^*/\mathrm{d}\mathcal{T} > 0$ under condition (6–7).

'The slope of line (9) when negative is steeper than that of line (10)' is mathematically equivalent to 'the denominator of the coefficient of $\mathcal{T}$ in equation (A1) is positive', which has already been proved above under condition (6–7).

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