Nutritional value of algae: a critical control on the stability of *Daphnia*–algal systems

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In Daphnia–algal systems, the effect of nutrient enrichment on stability is an important ecological issue. Here I consider a system of Daphnia and two potential prey; one prey termed primary algae, which are preferentially consumed, and the other secondary algae, which yield less nutrition and are more resistant to the grazer. The presence of secondary algae is a key to the stability, but their nutritional value has not been clearly defined in the previous theory and the actual value varies. Here I use a simple mathematical model defining explicitly the nutritional values of algae and examine the stability of the systems as a function of phosphorus enrichment. Whether or not all three species can stably coexist depended on the combination of the algal species used for simulation. In systems where all the species coexist in a stable manner, in which enrichment does not necessarily lead to destabilization, there is always a critical nutritional value of the secondary algae. Empirical work supports the possibility that the unknown nutritional value of secondary algae takes a value close to the critical one. Furthermore, at the critical nutritional value, the population response in the systems to enrichment is consistent with the observed trend in natural systems. This suggests that Daphnia–algal systems in nature can maintain stability in the face of enrichment, without requiring specific assumptions such as spatial heterogeneity.

INTRODUCTION

Enrichment in a predator–prey system leads, in theory, to the destruction of a stable equilibrium (Rosenzweig, 1971). Instability of a system may result in extinction of species. *Daphnia*–algal interaction is one of the best-studied systems with which to test this theoretical prediction. McCauley and Murdoch (McCauley and Murdoch, 1990), using a *Daphnia*–algal system, showed that the system did not always become unstable with the addition of nutrients, raising questions as to the effect of enrichment on the stability of predator–prey interaction.

In *Daphnia*–algal systems, the presence of secondary algae is proposed as a likely mechanism for the resolution of the issue on stability (Murdoch *et al.*, 1998; McCauley *et al.*, 1999). The secondary algae have been assumed to be completely inedible prey [e.g. (Kretzschmar *et al.*, 1993; Grover, 1995)] or prey with one certain fixed value or several different values of nutrition lower than that of the primary algae [e.g. (Holt *et al.*, 1994; Leibold, 1996; Grover and Holt, 1998; Gragnani *et al.*, 1999)]. However, it is not always clear how nutritionally valuable the

secondary algae are for *Daphnia* (Leibold, 1989; Murdoch *et al.*, 1998). Cyanobacteria are in general known to have low nutritional values for zooplankton [e.g. (Arnold, 1971)], whereas there is evidence that they are readily consumed by *Daphnia* (Matveev *et al.*, 1994).

The nutritional value of secondary algae may influence stability through changes in *Daphnia* density and in grazing pressure on the primary algae. These imply that the nutritional value of these algae should be carefully considered when we deal with systems involving two algal species. Here I study explicitly the effect of the nutritional value of the secondary algae on the stability as a function of enrichment using realistic *Daphnia*–algal interaction. This paper is constructed with the aim that the prediction here can be easily understandable, especially for empirical readers, so the arguments are developed in simple terms and mathematics, rather than as more general and complete analyses with complicated mathematical expressions (Gragnani *et al.*, 1999).

The primary algae correspond in practice to relatively small forms (nano-phytoplankton); the secondary algae

to larger forms (micro-phytoplankton). The secondary algae are regarded here as those that can yield some nutrition (within the range between zero and the value equivalent to the primary algae) to *Daphnia*. It is assumed here that the *Daphnia* simply filter-feed these algae, rather than selectively picking them out. Consumption of algae by *Daphnia* is often well described by a type 2 functional response (Porter *et al.*, 1982). My model includes the dynamics of nutrients, because many empirical works use the total amount of nutrient (e.g. total phosphorus in lakes) as an indicator of enrichment.

Although parameter values are basically chosen from the estimation (Grover, 1995) as representatives, the parameter values with regard to the nutrient-dependent growth rate of algae are chosen from several other sources in the literature because the values did not correspond to one identical species in the estimation. I chose a green alga, *Scenedesmus quadricauda*, and a diatom, *Cyclotella meneghiniana*, as representatives of the primary algae, and cyanobacteria, *Anabaena flos-aquae* and *Oscillatoria agardhii*, as the representatives of the secondary algae, because these are widespread species in freshwater systems and I am able to refer to each set of the parameter values for each species with regard to the nutrient-dependent growth rate from one original literature source.

MODEL

Model formation

The following model was used to incorporate values of parameters based on laboratory studies of *Daphnia* and algae:

$$\dot{X}_1 = \mu_1(\mathcal{N})X_1 - \varepsilon_1 X_1 - r_1(X_1, X_2)Y \qquad (1)$$

$$\dot{X}_2 = \mu_2(\mathcal{N})X_2 - \varepsilon_2 X_2 - r_2(X_1, X_2)Y \qquad (2)$$

$$\dot{Y} = -\varepsilon_3 Y + s_1 r_1(X_1, X_2)Y + s_2 r_2(X_1, X_2)Y \qquad (3)$$

$$\mathcal{N} + q_1 X_1 + q_2 X_2 + q_3 Y = T. \qquad (4)$$

The state variables are the densities of the primary algae [X_1 (cells L^{-1})], the secondary algae [X_2 (cells L^{-1})], and *Daphnia* [Y (animals L^{-1})], and the concentration of nutrient (phosphorus) available for the algae [$\mathcal{N}$ (µmol L^{-1})]. The degree of enrichment is expressed by the total amount of nutrient in the system [T (µmol L^{-1})]. A saturating function of nutrient was adopted for the nutrient-dependent growth rate of algal species i (Monod equation):

$$\mu_i(\mathcal{N}) = \frac{b_i \mathcal{N}}{K_i + \mathcal{N}} \quad i = 1, 2.$$

For the functional response of *Daphnia*, a type 2 equation was used including two algal species:

$$r_i(X_1, X_2) = \frac{a_i X_i}{1 + h_1 a_1 X_1 + h_2 a_2 X_2} \quad i = 1, 2.$$

Notation of parameters is listed in Table I. The nutritional value of algal species i is defined as the ratio of assimilation index to handling time, s_i/h_i. This assimilation index, s, is the ratio of *Daphnia* to algal carbon content (animals $cell^{-1}$) multiplied by assimilation efficiency (dimensionless). It was assumed that the nutritional value and *Daphnia* filtering rate of the primary algae were higher than those of the secondary algae:

$$s_1/h_1 > s_2/h_2 \text{ and } a_1 > a_2 \qquad (5)$$

Units per cell are used for parameters regarding consumption of the secondary algae (which are often colonial), since among freshwater zooplankton *Daphnia* is

Table I: Notation of parameters and their estimated values

Symbol	Meaning	Units	Values used
b_1, b_2	Maximum growth rate of algae	day^{-1}	see Table II
K_1, K_2	Half-saturation constant for growth rate of algae	µmol P L^{-1}	see Table II
ε_1, ε_2	Density-independent death rate of algae	day^{-1}	0.02, 0.1*
a_1, a_2	*Daphnia* filtering rate	L $animal^{-1}$ day^{-1}	0.04, 0.032*
h_1, h_2	Handling time for algae	animal day $cell^{-1}$	2.2×10^{-6}, 2.8×10^{-6}*
ε_3	Per capita death rate of *Daphnia*	day^{-1}	0.1
s_1, s_2	Assimilation index of algae	animal $cell^{-1}$	5.7×10^{-7}, various*
q_1, q_2	Cellular nutrient content of algae	µmol P $cell^{-1}$	9.1×10^{-9}, 1.8×10^{-8}*
q_3	Per capita nutrient content of *Daphnia*	µmol P $animal^{-1}$	1.6×10^{-2}

Values are derived from Grover (1995).
*indicates parameter values for the secondary algae X_2.

Table II: Algal species for the calculation of stability and their estimated values for the maximum growth rate (b) and half-saturation constant (K)

Species	b (day^{-1})	K (µmol P L^{-1})	Reference
Primary algae (X_1)			
Scenedesmus quadricauda	0.6	0.034	(Sommer, 1989)
Cyclotella meneghiniana	0.78	0.25	(Tilman and Kilham, 1976)[a]
Secondary algae (X_2)			
Anabaena flos-aquae	1	0.06	(Morel, 1987)
Oscillatoria agardhii	0.5	0.032	(Ahlgren, 1977)

[a] Based on data (Gotham and Rhee, 1981).

particularly good at consuming cyanobacteria [e.g. (Arnold, 1971)].

Parameterization

The estimations of Grover (Grover, 1995) were adopted as values for most parameters (Table I). For the nutrient-dependent growth rate of algae, another parameter set was used for each algal species (Table II).

As previously stated, it was assumed that the secondary algae, as well as the primary algae, are consumed and can contribute some nutritional benefit to *Daphnia*. The degree of this unknown nutritional value of the secondary algae is represented by changing the assimilation index of the algae, s_2, which must satisfy the condition [inequality (5)], i.e. $0 \leq s_2 < s_1 h_2/h_1$. The situation $s_2 = 0$ corresponds to one of three classes for inedible algae (nutritionally valueless algae) in the model (Grover, 1995).

RESULTS

The stability of the system in equations (1) to (4) was calculated numerically by testing the Routh–Hurwitz criteria [equations (7) to (9) in the Appendix] in the presence of *Daphnia*, either of *S. quadricauda* or *C. meneghiniana* as the primary algae, and either of *A. flos-aquae* or *O. agardhii* as the secondary algae. Results are expressed in a parameter space of the degree of enrichment (T) and the relative nutritional value of the secondary algae to the primary algae, $\gamma = (s_2/h_2)/(s_1/h_1)$, in Figure 1. Total phosphorus concentration is used here as the degree of enrichment, with a plausible range <3 µmol P L^{-1} in most lakes (Grover, 1995).

With *S. quadricauda* versus *A. flos-aquae* (Figure 1a), at low degrees of enrichment the secondary algae ($X_2 = A.$ *flos-aquae*) cannot invade the system because of its nutritional

inferiority. The primary algae ($X_1 = S.$ *quadricauda*) are excluded when the system is sufficiently enriched and the nutritional value of *A. flos-aquae* is high. This would be the result of a relaxation of nutrient competition between the algal species caused by enrichment and the effect of so-called apparent competition (Holt, 1977). The boundary above which the primary algae (X_1) become extinct approaches the nutritional value of the secondary algae (indicated by arrows in Figure 1) attained at large values of T. This nutritional value is given by setting the right-hand side of equation (3) to zero with $X_1 = 0$ and $X_2 = \infty$, hence giving:

$$s_2/h_2 = \varepsilon_3 \tag{6}$$

This nutritional value is the critical one, above which the secondary algae can support the *Daphnia* population by themselves at a certain density and below which they cannot, even at high densities (Genkai-Kato and Yamamura, 2000). With the parameter values used, the critical γ value is 0.39 [= $\varepsilon_3/(s_1/h_1)$] (arrows in Figure 1).
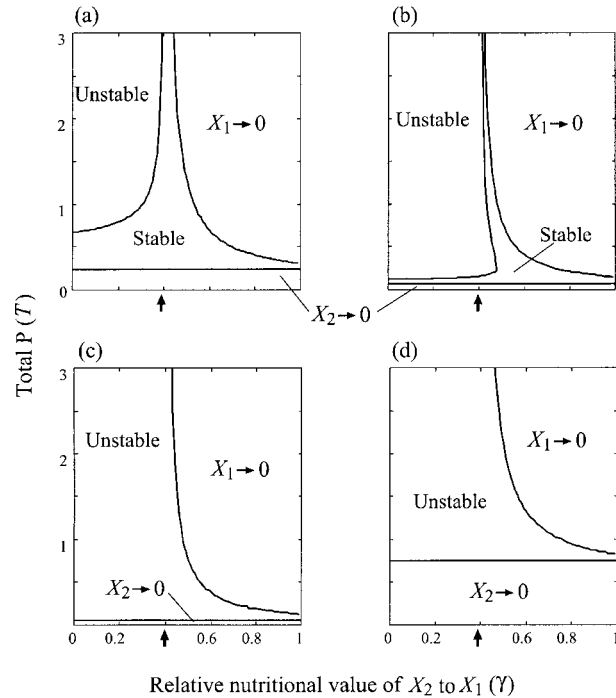

Fig. 1. Numerical analyses of systems with *Daphnia* and algae. The horizontal axes represent the relative nutritional value of the secondary algae to the primary algae, $\gamma = (s_2/h_2)/(s_1/h_1)$ (dimensionless). The vertical axes represent total phosphorus, T (µmol P L^{-1}). Arrows express where the relative nutritional value of the secondary algae takes the critical value given in equation (6) [= $\varepsilon_3/(s_1/h_1)$ = 0.39]. The parameter values used are shown in Tables I and II. Combinations of algal species used are: (**a**) *Scenedesmus quadricauda* and *Anabaena flos-aquae*, (**b**) *Cyclotella meneghiniana* and *A. flos-aquae*, (**c**) *S. quadricauda* and *Oscillatoria agardhii*, (**d**) *C. meneghiniana* and *O. agardhii*.

There is a region in which all three species coexist (Figure 1a). Similar to previous models of one predator and one prey [e.g. (Rosenzweig, 1971)], coexisting equilibria tend to be stable at low degrees of enrichment. It is noticeable that when the nutritional value of the secondary algae is close to the critical value given in equation (6) (γ = 0.39 in Figure 1), coexisting equilibrium points remain stable even at considerably high degrees of enrichment. An explanation for why the unstable region occurs at large T and low γ values would be as follows. When the nutritional value of the secondary algae is low, the density of the primary algae increases more sensitively to an increase in the total amount of nutrient than the secondary algae (Genkai-Kato and Yamamura, 2000). Thus, the stabilizing effect of the secondary algae, by decreasing the net grazing rate on the primary algae, diminishes with enrichment. With intermediate values of γ [close to the critical value given in equation (6)], the secondary algae do not yield sufficient energy to enhance the *Daphnia* population, while at the same time *Daphnia* spends so much time handling the secondary algae that it cannot graze down the primary algae. Thus the secondary algae stabilize the system by providing an effective refuge for the primary algae.

With *C. meneghiniana* versus *A. flos-aquae* (Figure 1b), there is a stable coexisting region similar to the case of *S. quadricauda* versus *A. flos-aquae* (Figure 1a). It is notable that although the region is much smaller than that in Figure 1a, it lies around the critical nutritional value of the secondary algae. Combinations of either species of the primary algae with *O. agardhii* yield an unstable state (Figures 1c,d).

Finally, a numerical simulation was conducted to examine the dependency of presence (as Figures 1a,b) or absence (as Figures 1c,d) of the region in the γ–T space where all three species can coexist stably upon the parameters for the nutrient-dependent growth rate of algae (Figure 2). Given that one of two algal species is *S. quadricauda* (and the other is an imaginary algal species), the region of stably coexisting equilibria appears over a wide range of parameter values for the nutrient-dependent growth rate of the imaginary algae (Figure 2a), reflecting the coexistence of *S. quadricauda* with the secondary algae shown in Figure 1. Although *O. agardhii* is unable to have stable equilibria with either of the primary algae chosen (Figures 1c,d), there still exist parameter values that have stable equilibria with an imaginary algal species, but the region is considerably smaller (Figure 2b) than for *S. quadricauda* (Figure 2a). In systems with parameter sets in the region of the stable equilibria in Figure 2, there was a common tendency, similar to Figures 1a and b, that coexisting equilibrium points were likely to be stable with the nutritional value
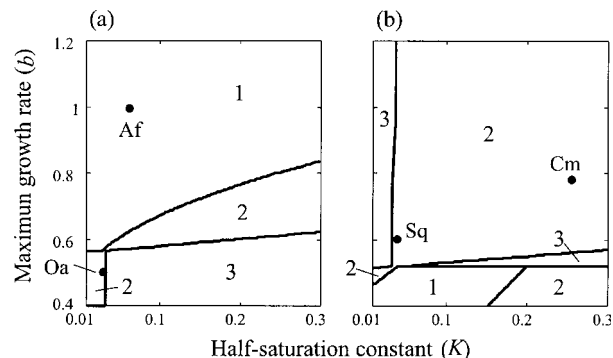

Fig. 2. Dependency of the presence or absence of a stably coexisting region in the γ–T space on the nutrient-dependent growth rate of algae, b and K, in systems consisting of *Daphnia* and two algal species. One of the two algal species is given and the other is an imaginary algal species with various b and K values. (**a**) *Scenedesmus quadricauda* is given. (**b**) *Oscillatoria agardhii* is given. Region 1, there are stably coexisting equilibria (results qualitatively similar to Figures 1a and b are obtained with the b and K parameters within this region); region 2, coexisting equilibria are always unstable (similar to Figures 1c and d); region 3, there is no equilibrium for all three species to coexist. The parameter sets for the nutrient-dependent growth rate of *S. quadricauda* (Sq), *Cyclotella meneghiniana* (Cm), *Anabaena flos-aquae* (Af), and *O. agardhii* (Oa) are also indicated.

of the secondary algae around the critical one given in equation (6) even at high degrees of enrichment.

DISCUSSION

In the Grover model (Grover, 1995) there were no stable equilibria when the secondary algae were nutritionally valueless (s_2 = 0, b_1 = 0.93, K_1 = 0.02, b_2 = 0.9, K_2 = 0.06 were used). I preliminarily re-examined the stability of the model with nutritionally valueless algae (Grover, 1995), but no stable equilibria appeared even when the nutritional value of the secondary algae, which had been assumed zero, or 'valueless', could take positive values. In my *Daphnia*–two-algae systems, all three species were able to coexist stably in two out of four possible combinations of algae, whereas there were no stable equilibria for the other two combinations, which always involved the species *O. agardhii* (Figures 1c,d). It was, however, shown that in theory a species such as *O. agardhii* could coexist stably with another phytoplankter ('imaginary algae'), depending on the nutrient-dependent growth rate of its competitor (Figure 2b). This indicates that in a *Daphnia*–two-algae system every algal species in nature might coexist stably with a certain algal species. Furthermore, an algal species has the potential to coexist stably with many algal species because parameter values for the algal growth rate are variable depending on temperature (Ahlgren, 1987), light intensity (Schlesinger and Shuter, 1981), and probably the conditions of other nutrients, such as nitrogen and silicon.

When all three species were able to coexist stably, equilibria were always stable around the critical nutritional value of the secondary algae [equation (6)], even in the face of sufficient enrichment. Genkai-Kato and Yamamura (Genkai-Kato and Yamamura, 2000) suggested that the unknown nutritional value of secondary algae in nature may be close to the critical one. They showed that the primary algae did not change in density with enrichment when the nutritional value of the secondary algae took the critical value. According to compiled empirical data (Watson and McCauley, 1988; Watson *et al.*, 1992), the biomass of the primary algae (nano-phytoplankton) scarcely varies, while that of the secondary algae (micro-phytoplankton) increases, with increased total phosphorus loading. Thus the theoretical prediction and the compiled empirical data on the population response to enrichment lead to an estimation of the unknown nutritional value of the secondary algae in nature that is close to the critical value given in equation (6). Together with this estimation, my results with plausible parameter values imply that natural *Daphnia*–algal systems maintain stable equilibria with no increase in the biomass of the primary algae against enrichment, without any specific assumptions such as spatial heterogeneity [e.g. (Ruxton, 1995; Krivan, 1998)].

A system with inedible algae (Kretzschmar *et al.*, 1993) showed similar predictions for the stability and density response of the primary algae to enrichment. However, they did not find a possible mechanism to account simultaneously for stability at high nutrient levels (McCauley and Murdoch, 1990) and little or no change in the density of the primary algae (Watson and McCauley, 1988; Watson *et al.*, 1992) in natural systems. Grover and Holt (Grover and Holt, 1998) analysed a similar system of *Daphnia* with different species of algae (with a certain nutritional value for each algal species) to explore the means by which algal species could coexist or not. Within the range of 0.1–0.6 μmol P L^{-1} (corresponding to oligotrophic to mesotrophic), their system exhibited unstable equilibria under nutrient-rich conditions.

Gragnani *et al.* (Gragnani *et al.*, 1999) extensively analysed the stability of a specific *Daphnia*–algal system in which green algae and *Oscillatoria* were competing for a common resource. They used two different nutritional values for *Oscillatoria* (secondary algae) and showed that the possibility of algal coexistence was higher in the system with the lower nutritional value for *Oscillatoria*. However, general relationships between the nutritional value and the possibility of coexistence (such that the possibility decreases with increasing nutritional value) are not clear from the result (Gragnani *et al.*, 1999) because only two nutritional values were analysed. The coexistence was not possible in their system including *Oscillatoria* with either of the nutritional values

under extremely nutrient-rich conditions (>3 μmol P L^{-1}). None of these account simultaneously for the stability in enriched systems (McCauley and Murdoch, 1990) and the response of the plankton populations to enrichment (Watson and McCauley, 1988; Watson *et al.*, 1992), observed in natural environments. To my knowledge, the present paper is the first possible theoretical explanation for the stability, along with the plankton community response.

Here it is shown that secondary algae with a nutritional value close to the critical one given in equation (6) could possibly dampen population oscillations, thus supporting stable equilibria in systems involving *Daphnia*, a zooplankter that displays poorly selective grazing because of its filter feeding. In contrast to *Daphnia* (one of the dominant zooplankton in lakes), the feeding mode of many copepods, another dominant zooplankton form, is quite different: they display selective feeding more effectively by detection and active capture of algae (in this sense, *Daphnia* are a non-selective feeding grazer and the copepods are selective feeding grazers). With a grazer with optimally selective feeding, like copepods, the presence of secondary algae with a nutritional value in a range slightly lower than the critical value, which is exactly the same as that given in equation (6), strongly decreases the magnitude of population oscillations (Fryxell and Lundberg, 1994; Krivan, 1996; Genkai-Kato and Yamamura, 1999; van Baalen *et al.*, 2001). These results clearly highlight the importance of secondary algae with regard to their critical nutritional value (i.e. whether or not they can yield sufficient energy by themselves to maintain their grazer populations) as a key to the stability of zooplankton–phytoplankton systems in a recently serious trend of eutrophication, irrespective of the feeding modes of zooplankton.

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APPENDIX: STABILITY ANALYSIS

Though the system described in equations (1) to (4) has four variables, X_1, X_2, Y and N, it can be reduced to a three-dimensional system (X_1, X_2, Y) because of the mass balance equation (4). Standard analysis for stability in this system leads to three conditions expressed by three dummy variables, A_i (where $i = 1, 2, 3$). The system is stable if and only if:

$$A_1 > 0 \tag{7}$$

$$A_3 > 0 \tag{8}$$

$$A_1 A_2 > A_3 \tag{9}$$

These dummy variables are obtained, from the reduced three-dimensional system (X_1, X_2, Y), by derivatives at equilibrium, $\alpha_{ij} = \partial \dot{X}_i / \partial X_j |*$ (where $i, j = 1, 2, 3$; X_3=corresponds to Y, and * denotes a value at equilibrium):

$$A_1 = -\alpha_{11} - \alpha_{22} - \alpha_{33}$$

$$A_2 = \alpha_{11}\alpha_{22} + \alpha_{22}\alpha_{33} + \alpha_{33}\alpha_{11} - \alpha_{12}\alpha_{21} - \alpha_{23}\alpha_{32} - \alpha_{31}\alpha_{13}$$

$$A_3 = -\alpha_{11}\alpha_{22}\alpha_{33} - \alpha_{12}\alpha_{23}\alpha_{31} - \alpha_{32}\alpha_{21}\alpha_{13} + \alpha_{11}\alpha_{23}\alpha_{32} + \alpha_{22}\alpha_{31}\alpha_{13} + \alpha_{33}\alpha_{12}\alpha_{21}.$$

The full expressions of the derivatives, $\alpha_{ij} = \partial \dot{X}_i / \partial X_j$, are

$$\alpha_{11} = X_1^*(-q_1 d\mu_1/dN|_* + h_1 a_1^2 Y^*/D^2)$$

$$\alpha_{12} = X_1^*(-q_2 d\mu_1/dN|_* + h_2 a_1 a_2 Y^*/D^2)$$

$$\alpha_{13} = X_1^*(-q_3 d\mu_1/dN|_* - a_1/D)$$

$$\alpha_{21} = X_2^*(-q_1 d\mu_2/dN|_* + h_1 a_1 a_2 \Upsilon^*/D^2)$$

$$\alpha_{22} = X_2^*(-q_2 d\mu_2/dN|_* + h_2 a_2^2 \Upsilon^*/D^2)$$

$$\alpha_{23} = X_2^*(-q_3 d\mu_2/dN|_* - a_2/D)$$

$$\alpha_{31} = \Upsilon^*[s_1 a_1/D - h_1 a_1(s_1 a_1 X_1^* + s_2 a_2 X_2^*)/D^2]$$

$$\alpha_{32} = \Upsilon^*[s_2 a_2/D - h_2 a_2(s_1 a_1 X_1^* + s_2 a_2 X_2^*)/D^2]$$

$$\alpha_{33} = 0,$$

where

$$D = 1 + h_1 a_1 X_1^* + h_2 a_2 X_2^*.$$