

## A Competition Model for a Seasonally Fluctuating Nutrient

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**Abstract.** A model of two species consuming a single, limited, periodically added resource is discussed. The model is based on chemostat-type equations, which differ from the classical models of Lotka and Volterra. The model incorporates nonlinear 'functional response' curves of the Holling or Michaelis–Menten type to describe the dependence of the resource-exploitation rate on the amount of resource. Coexistence of two species due to seasonal variation is indicated by numerical studies.

**Key words:** Exploitative competition — Holling's type-2 functional response — Seasonal variations — Coexistence — Chemostat.

### 1. Introduction

In a previous paper [8], the author analyzed an  $(n + 1)$ -dimensional dynamical system which corresponds to the competition of  $n$  species for a single, essential nutrient in limited supply. The system modeled a chemostat, a laboratory apparatus used for the production and physiological study of microorganisms. In the chemostat model, the limiting nutrient is supplied at a constant rate. The input flow of medium contains all other factors for growth in excess. The output flow equals the input flow, and carries with it cells, waste products, and unused nutrients. The system also approximates conditions for plankton growth in lakes, with the input of limiting nutrients such as silica and phosphate from streams draining the surrounding watershed.

An important advance of this model over classical Lotka–Volterra formulations of competition is that the limiting resource for which competition is being expressed is represented explicitly by an equation in the system. In the Lotka–Volterra model, only the numbers of competing organisms are represented. The result of leaving out an equation for the resource is that the outcome of competition cannot be predicted before the organisms are actually grown together. In the present formulation, the

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outcome of competition can be predicted before the organisms compete, from measurements of growth parameters of the organisms when grown alone on the resource. This advance brings the theory of competition one step closer to being truly predictive rather than merely descriptive *ex post facto*.

In this paper, we continue this approach. We now modify the assumptions in [8], valid for the chemostat, in order to better simulate the ecological situation in natural lakes. First of all, instead of a constant input of limiting nutrient, the resource is permitted to vary periodically, to account for changing pattern in the watershed as the seasons vary. This changes the system of equations to non-autonomous ones. In addition, the death rates – washout rates in the chemostat – are allowed to be different for different species. Due to the complexity of this seasonal variation problem, we treat only the case of one resource and two competing species. The seasonal effect is assumed to be  $b \sin wt$ . Two new variables are present – the amplitude  $b$  and the frequency  $w$  of the input nutrient concentration. We note that it is also possible to perform the laboratory experiment for this seasonal model.

Our purpose in this paper is to examine the seasonal effect of the competition outcome and to examine whether the known ‘competitive exclusion principle’ [5] holds or not.

In Section 3, we attempt to determine regions of the parameter space where the competitive exclusion principle does hold. By extensive numerical studies, we show in Section 4 that coexistence is possible with certain suitable amplitudes and frequencies. The proofs of theorems in Section 3 are given in Section 6, and the model itself is described in Section 2. Section 5 is the discussion section.

## 2. Statement of the Model

The present analysis concerns the behavior of a species-resource system consisting of two species,  $x_1$  and  $x_2$ , and a single nutrient,  $S$ . We specifically assume that the species compete purely exploitatively, with no interference between rivals (no toxins are produced, for example). Both species have access to the resource and compete only by lowering the population of shared resource. For death rates it is assumed that the number dying is proportional to the number currently alive. We also assume that there are no significant time lags in the system and that the functional response of the species obeys the Holling ‘nonlearning’ curve [6, 7]. With the seasonal effect  $b \sin wt$ ,  $0 < b < S^{(0)}$ , the model is given by

$$\begin{aligned}
 S'(t) &= (S^{(0)} + b \sin wt - S(t))D - \left(\frac{m_1}{y_1}\right)\left(\frac{x_1(t)S(t)}{a_1 + S(t)}\right) - \left(\frac{m_2}{y_2}\right)\left(\frac{x_2(t)S(t)}{a_2 + S(t)}\right) \\
 x_1'(t) &= \frac{m_1 x_1(t) S(t)}{a_1 + S(t)} - D_1 x_1(t) \\
 x_2'(t) &= \frac{m_2 x_2(t) S(t)}{a_2 + S(t)} - D_2 x_2(t) \\
 S(0) &> 0, \quad x_1(0) > 0, \quad x_2(0) > 0,
 \end{aligned} \tag{2.1}$$

where  $S^{(0)} + b \sin wt$  is the input concentration at time  $t$ ,  $D$  is the dilution rate,  $x_i(t)$  is the number of the  $i$ th species at time  $t$ ,  $S(t)$  is the concentration of the nutrient at time  $t$ ,  $m_i$  is the maximum growth ('birth') rate of the  $i$ th species,  $D_i$  is the death rate for the  $i$ th species,  $y_i$  is the yield factor for the  $i$ th species feeding on the nutrient,  $a_i$  is the half-saturation constant for the  $i$ th species, which is the nutrient concentration at which the functional response of the species is half maximal. We analyze the behavior of solutions of this system of ordinary differential equations in order to answer the biological question Under what conditions will neither, one, or both, species survive?

### 3. Statement of Results

In this section we state the principal results of the paper. The proofs and certain technical lemmas are deferred to Section 6. The first lemma is a statement that the system given by (2.1) is as 'well-behaved' as one intuitively from the biological problem.

**Lemma 3.1.** *Solutions of (2.1) are bounded and remain in the positive octant.*

The next lemma provides conditions under which the species cannot survive, even in the absence of competition:

**Lemma 3.2.** *Let*

$$C_i = \frac{m_i - D_i}{a_i m_i} - \frac{1}{\sqrt{(a_i + S^{(0)})^2 - B^2}} \tag{3.1}$$

where

$$B = \frac{bD}{\sqrt{w^2 + D^2}}. \tag{3.2}$$

For each  $i = 1, 2$  if  $C_i < 0$  then  $\lim_{t \rightarrow \infty} x_i(t) = 0$ .

Before we explain Lemma 3.2, we first introduce a very important parameter  $\lambda_i$  where

$$\lambda_i = \frac{a_i D_i}{m_i - D_i}, \tag{3.3}$$

$\lambda_i$  is the product of  $i$ th species' half-saturation constant times the ratio of species death rate to the intrinsic rate of increase  $m_i - D_i$ . From (2.1) the number is the 'break-even' concentration of nutrient for the  $i$ th species'  $dx_i/dt = 0$  isocline in the  $S-x_i$  plane.

Secondly we note the following two equivalent statements, namely,

$$C_i < 0 \text{ if and only if } m_i \leq D_i \text{ or } \sqrt{(a_i + \lambda_i)^2 + B^2} - a_i > S^{(0)}, \tag{3.4}$$

and

$$C_i > 0 \text{ if and only if } \sqrt{(a_i + \lambda_i)^2 + B^2} - a_i < S^{(0)}. \tag{3.5}$$

From (3.4) Lemma 3.2 states that if the maximum birth rate  $m_i$  is less than or equal to the death rate  $D_i$  or if the ‘mean’ input concentration  $S^{(0)}$  is less than or equal to the ‘break-even’ concentration  $\lambda_i$ , then the  $i$ th species will die out as time becomes large. Even if  $S^{(0)} > \lambda_i$  the seasonal fluctuation might play some role in driving  $i$ th species extinct provided

$$(\sqrt{a_i + \lambda_i})^2 + B^2 - a_i > S^{(0)} \quad \text{where} \quad B = \frac{bD}{\sqrt{w^2 + D^2}}.$$

We now state the principal results:

**Theorem 3.3.** *If  $C_i < 0$  then  $\lim_{t \rightarrow \infty} x_i(t) = 0$  for  $i = 1, 2$  and  $S(t) = S^{(0)} + B \sin(wt - \beta) + o(1)$  where  $\beta = \tan^{-1} w/D$ .*

From Lemma 3.2 if  $C_i < 0, i = 1, 2$ , then each species will die out as time becomes large. As one expects, the concentration of nutrient will fluctuate periodically. This is the point Theorem 3.3 states.

**Theorem 3.4.** (i) *If  $C_1 > 0$  and  $C_2 < 0$  then  $\limsup_{t \rightarrow \infty} x_1(t) > 0$  and  $\lim_{t \rightarrow \infty} x_2(t) = 0$ .*

(ii) *If  $C_1 < 0$  and  $C_2 > 0$  then  $\lim_{t \rightarrow \infty} x_1(t) = 0$  and  $\limsup_{t \rightarrow \infty} x_2(t) > 0$ .*

Under the hypothesis of theorem 3.4(i), species 2 cannot survive on the nutrient no matter what its rival does, but the rival (species 1) can survive when grown alone on the nutrient. Similar explanation follows for (ii). We note that the notation  $\limsup_{t \rightarrow \infty} x_i(t) > 0$  means  $i$ th species survives. Mathematically, we cannot rule out the possibility that  $\liminf_{t \rightarrow \infty} x_i(t) = 0$ .

For the remainder of the theorems, we assume that  $C_i > 0$ , i.e., (3.5) holds for each  $i$  and the species are labeled such that

$$0 < \lambda_1 < \lambda_2. \tag{3.6}$$

Biologically a species with small half-saturation constant, low death rate, and higher intrinsic rate of increase (small  $\lambda$ ) should be a tough competitor to beat.

**Theorem 3.5.** *Let (3.5) for each  $i = 1, 2$ . Assume (3.6) holds. If  $m_1/D_1 \geq m_2/D_2$ , then  $\limsup_{t \rightarrow \infty} x_1(t) > 0$  and  $\lim_{t \rightarrow \infty} x_2(t) = 0$ .*

Under assumption (3.5) both species can handily survive when grown alone on the nutrient. Theorem 3.5 states that if  $0 < \lambda_1 < \lambda_2$  and species 1 has higher ratio of intrinsic rate of increase to death rate, i.e.,  $(m_1 - D_1)/D_1 \geq (m_2 - D_2)/D_2$  then species 1 outcompetes its rival. It is interesting that under these conditions species 1 also wins even when it has a higher half-saturation constant, so long as  $\lambda_1 < \lambda_2$ . We also note that except (3.5) the result is independent of seasonal fluctuation.

It remains to consider the case  $m_1/D_1 < m_2/D_2$ . This, under the hypothesis  $0 < \lambda_1 < \lambda_2$ , implies  $a_1 < a_2$ . However we were not able to completely analyze the remaining case  $a_1 < a_2, m_1/D_1 < m_2/D_2$ . We have partial results to indicate that any competition outcome is possible, i.e., species 1 wins or both coexist or species 2 wins.

**Theorem 3.6.** *Let (3.5), (3.6) hold. Suppose  $a_1 < a_2, m_1/D_1 < m_2/D_2$ .*

(i) *If*

$$S^{(0)} + B < \frac{(m_1/D_1)a_2 - (m_2/D_2)a_1}{(m_2/D_2) - (m_1/D_1)},$$

*then  $\lim_{t \rightarrow \infty} x_2(t) = 0$  and  $\limsup_{t \rightarrow \infty} x_1(t) > 0$ .*

(ii) *If  $0 < C_1 < C_2$  then  $\lim_{t \rightarrow \infty} x_1(t) = 0$  and  $\limsup_{t \rightarrow \infty} x_2(t) > 0$ .*

We note that the inequalities  $0 < \lambda_1 < \lambda_2, a_1 < a_2, m_1/D_1 < m_2/D_2$ , imply

$$0 < \lambda_1 < \lambda_2 < \frac{(m_1/D_1)a_2 - (m_2/D_2)a_1}{(m_2/D_2) - (m_1/D_1)}.$$

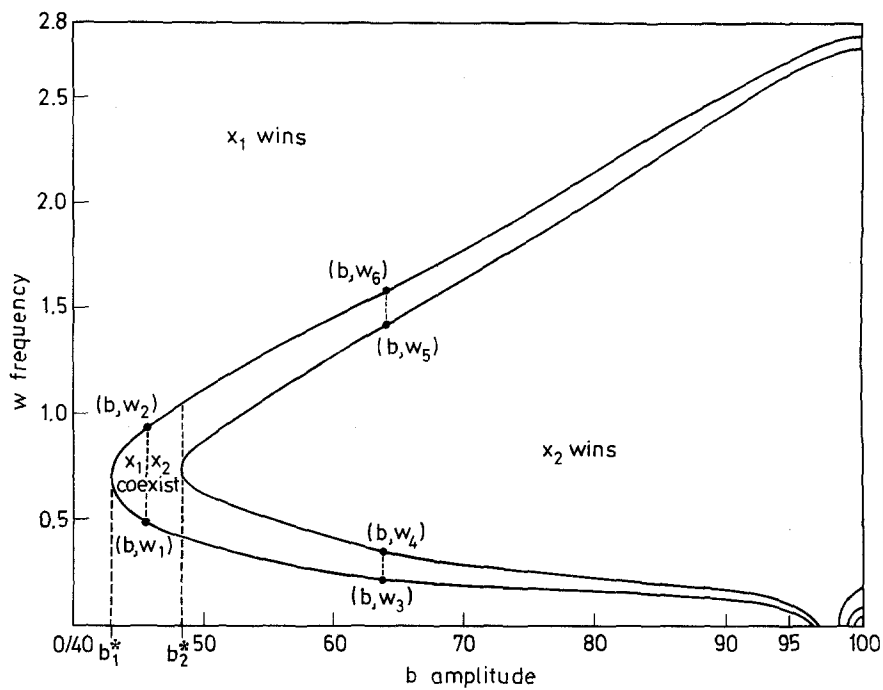
Theorem 3.6 (i) states that under (3.5) if the ‘mean’ input concentration  $S^{(0)}$  and amplitude  $b$  are smaller then species 1 is still a winner. When  $0 < \lambda_1 < \lambda_2$  and  $m_1/D_2 < m_2/D_2$  there is only a very limited range of parameters for which we also have  $0 < C_1 < C_2$ . Usually  $0 < C_1 < C_2$  holds as  $b \approx S^{(0)}$  and  $w \approx 0$ . Then in this case the competition outcome will be reversed.

#### 4. Numerical Study on the Coexistence of the Species

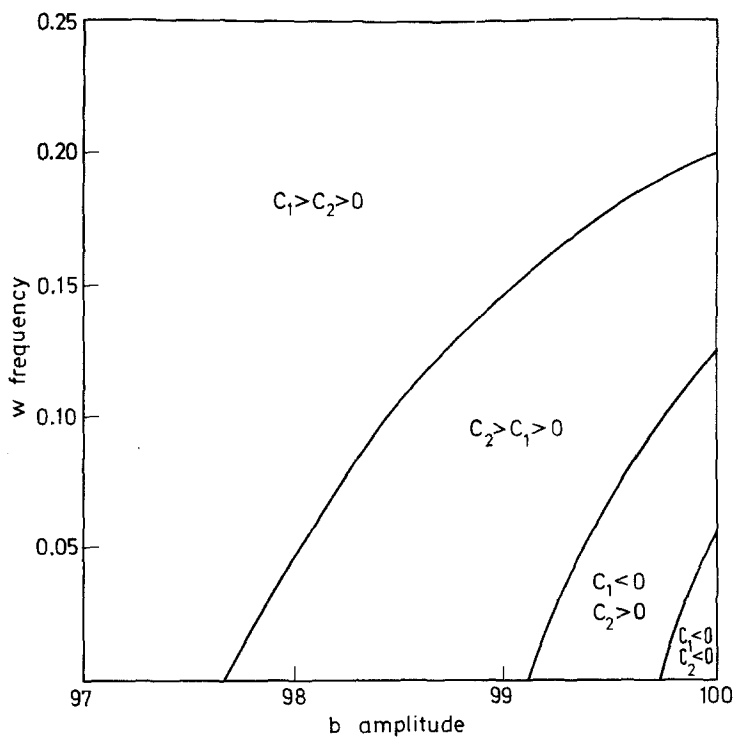
The principal goal of this paper is to investigate the effect of seasonal nutrient fluctuation on the competition outcomes. When the nutrient is supplied at constant rate, that is,  $b = 0$ , the species with the smallest  $\lambda$  wins the competition. However, when the nutrient is allowed to vary periodically and  $\lambda_1 < \lambda_2$ , the numerical study show that any competition outcome is possible, i.e., species 1 wins or both coexist or species 2 wins. In Lemma 3.2, Theorem 3.3, Theorem 3.4, Theorem 3.5, we determined some regions of parameter space where the competition exclusion principle does hold. In the discussion of this section, we assume  $C_i > 0, i = 1, 2, \lambda_1 < \lambda_2, a_1 < a_2, m_1/D_1 < m_2/D_2$ . The condition  $\lambda_1 < \lambda_2$  in the absence of seasonality means species 1 is favored to win the competition. From the result of Theorem 3.6(ii), it indicates that due to the seasonal effect the species  $x_1, x_2$  may coexist or the species  $x_2$  may even win the competition.

In the following numerical study we fix the following data:  $a_1 = 1, a_2 = 2, m_1 = 2.111111, m_2 = 1.6578, y_1 = 2m_1, y_2 = 2m_2/3, D = 1, D_1 = 2, D_2 = 1.5, S^{(0)} = 100$ , which satisfy  $a_1 < a_2, \lambda_1 = 18.0000018 < \lambda_2 = 19.01140684, m_1/D_1 = 1.055555 < m_2/D_2 = 1.105200$ . Let amplitude  $b$  and frequency  $w$  be variables. Figure 1 is the principal result of our numerical simulation. Except for a very small region (see Fig. 2) at the right corner of the bottom of Figure 1, we have three regions in the amplitude-frequency space, namely, species 1 wins, both coexist, species 2 wins.

First, in Figure 1 there exists a point  $b_1^* \approx 42.5$  such that for all  $b < b_1^*$  and  $w > 0$  species 1 is always a winner. That is, species 1 outcompetes species 2 provided  $b$  is smaller. As we increase  $b$  from  $b_1^*$  to  $b_2^* \approx 49$ , then either  $x_1$  wins or  $x_1, x_2$  coexist. We note that for each  $b, b_1^* < b < b_2^*$  there exist  $w_1, w_2$  such that  $x_1$  wins for  $0 < w < w_1$  or  $w > w_2$  and  $x_1, x_2$  coexist for  $w_1 < w < w_2$ . Furthermore the interval  $(w_1, w_2)$  becomes larger as we increase  $b$ . Next, if we increase  $b$  further, then



**Fig. 1**



**Fig. 2**

for each  $b > b_2^*$ , there exist  $w_3 < w_4 < w_5 < w_6$  such that  $x_1$  wins for  $w \in (0, w_3)$  or  $(w_6, \infty)$  and  $x_1, x_2$  coexist for  $w \in (w_3, w_4)$  or  $(w_5, w_6)$  and  $x_2$  wins for  $w \in (w, w_5)$ . We note that the intervals  $(w_3, w_4)$  and  $(w_5, w_6)$  become smaller and the interval  $(w_4, w_5)$  becomes larger as  $b$  increases.

### 5. Discussion

This paper is a mathematical analysis of the behavior of a model of two species competing exploitatively for a shared nutrient. The input concentration of the nutrient varies periodically, and the species consume resources according to a saturating functional response. The analysis has dealt principally with parameters:  $S^{(0)}, b, w, D$  of the resource part and parameters of the  $i$ th species;  $a_i$ , the half-saturation constant;  $m_i/D_i$  ratio of maximal birth rate to death rate; and  $\lambda_i$ .  $\lambda_i$  is a particularly important parameter. Recall that  $\lambda_i$  is the product of the half-saturation constant times the ratio of the death rate to the intrinsic rate of increase of the  $i$ th species:  $\lambda_i = a_i(D_i/r_i)$ . This number is the ‘break-even’ concentration of nutrient for the  $i$ th species, and it defines the position of the  $i$ th species’  $dx_i/dt = 0$  isocline in the  $S-x_i$  plane. A species with a small half-saturation constant, low death rate, and high intrinsic rate of increase (small  $\lambda$ ) should be a tough competitor to beat. In fact, if  $n$  species are competing for a single, limiting nutrient that is supplied at a constant rate, the species with the smallest  $\lambda$  wins the competition and all other species go extinct [8, 9]. The surviving species and its resource approach constant values; there is no limiting periodic behavior.

When the nutrient is allowed to vary periodically and the consumers also have saturating functional responses, the number of possible outcomes is increased to include periodic solutions and dynamic coexistence between species. As in the constantly supplied nutrient case, the  $\lambda$  parameters are important; but, in addition,  $S^{(0)}, b, w, D, a_i$ , and  $m_i/D_i$  must be considered to determine the outcomes of inter-specific competition between the species.

We have been concerned with answering the question: Under what conditions will neither, one, or both species survive or die out? What is the effect of seasonal variation to the competition outcome? We divide our results into three general cases: case I, neither species can survive (even without competition) on this resource; case II, the first species can survive on the nutrient but the second cannot; case III, each species can, in the absence of competition, survive on the nutrient.

*Case I:* This represents the case in which neither species can survive on the nutrient, regardless of the presence or absence of its rival. This situation can arise for one of two reasons: either the intrinsic rate of increase is negative or zero ( $m_i \leq D_i$ ) or the ‘mean’ input concentration  $S^{(0)}$  is too small such that  $\sqrt{(a_i + S^{(0)})^2 - B^2} - a_i$  is below the ‘break-even’ density  $\lambda_i$  for the species. In either event, both species go extinct, and the nutrient concentration approaches  $S^{(0)} + B \sin(\omega t + \beta)$ . We note that if the amplitude  $b = 0$ , then (3.4) becomes

$$\lambda_i > S^{(0)}$$

which is consistent with the results in [8, 9]. Generally speaking, from (3.4) with the oscillatory input,  $S^{(0)}$  should be higher in order to keep the species from dying out as compared to the nonoscillatory case.

*Case II:* This situation is readily understood from the outcome in Case I. One of the species (say, species 2) cannot survive on the resource no matter what its rival does, but the rival (species 1) can survive when grown alone on the nutrient. In the limit, this case becomes a one-species single-nutrient system.

We conjecture that the trajectory tends to a unique  $2\pi/w$ -period orbit which is globally asymptotically stable.

*Case III:* This case represents the most interesting and potentially complex situation of the two-species one-resource system. In this case, both species can handily survive when grown alone on the nutrient. This condition is met when the 'mean' input concentration rate  $S^{(0)}$  exceeds the value of  $\sqrt{(a + \lambda)^2 + B^2} - a$  for each species. Consider first the case in which  $\lambda_1$  is less than  $\lambda_2$ . In the case of a nutrient supplied at a constant rate, we have proven that  $\lambda_1 < \lambda_2$  would be sufficient to guarantee that species 1 wins and species 2 dies out. However, when the nutrient varies periodically, this relationship between the  $\lambda$ 's is neither a necessary nor a sufficient condition for survival of species 1 and extinction of species 2.

Under the hypothesis of Theorem 3.5, species 1 wins. Species 1 wins because it has higher ratio of intrinsic rate of increase to death rate of the two competitors. It is interesting that species 1 also wins even when it has a higher half-saturation constant, so long as  $\lambda_1$  is less than  $\lambda_2$ .

The results in Theorem 3.6 are incomplete. Part (i) says that when  $a_1 < a_2$ ,  $m_1/D_1 < m_2/D_2$ ,  $\lambda_1 < \lambda_2$ ,  $C_1, C_2 > 0$  and

$$S^{(0)} + B < \frac{a_2(m_1/D_1) - a_1(m_2/D_2)}{(m_2/D_2) - (m_1/D_1)}$$

then species 1 wins and species 2 dies out. For smaller  $S^{(0)}$  and  $b$ , species 1 should win. Note that these conditions imply that

$$\lambda_1 < \lambda_2 < \frac{a_2(m_1/D_1) - a_1(m_1/D_2)}{(m_2/D_2) - (m_1/D_1)}.$$

We usually designate species 1 the winner in our discussion. Part (ii) is a very interesting result. It says that if  $0 < C_1 < C_2$  then species 2 wins! This result indicates that there may exist a coexistence region in certain parameter space. Although the condition  $0 < C_1 < C_2$  is very special, it holds when  $w$  is small and  $b$  is closed to  $S^{(0)}$ .

For the case  $b = 0$ , the equilibrium  $(\lambda_1, x_1^*, 0)$  is globally stable provided  $0 < \lambda_1 < \lambda_2 < S^{(0)}$  [8, 9]. It is easy to show that (see [3] pp. 348–350 or [2]) there exists an asymptotically stable  $2\pi/w$ -periodic solution  $(S(t), x_1(t), x_2(t))$  such that  $\lim_{b \rightarrow \infty} (S(t), x_1(t), x_2(t)) = (\lambda_1, x_1^*, 0)$  for all sufficiently small  $b$ . We note that  $C_1 > C_2$  provided  $b = 0$ ,  $0 < \lambda_1 < \lambda_2 < S^{(0)}$ ,  $a_1 < a_2$  and  $m_1/D_1 < m_2/D_2$ . Hence Theorem 3.6 part (ii) is consistent with the above small parameter result.



In Section 4 we demonstrate our numerical study to show that any competition outcome is possible. It should be noted that this result strongly depends on both the seasonal effect  $b \sin wt$  and the characteristics of the functional response of the species. Without the season effect, then the species with lowest  $\lambda$  wins [8, 9]. With the season effect, it is easy to show that if the species' functional response is linear, then only one species survives!

It is interesting to relate these results to published speculations and conclusions about competitive coexistence between species. Stewart and Levin [11] shows analytically that coexistence is possible for two species sharing a common limiting resource in a periodic environment in which resources fluctuate from high to low levels. The resource was depleted at the end of each season, and the populations of plankton were restarted in the next season by means of small seed populations.

Armstrong and McGehee [1] also construct an example showing that coexistence is possible for  $n$  species sharing a single conservative resource in a periodic environment.

On a final note, system (2.1) can be generalized as following (5.1):

$$\begin{aligned}
 S'(t) &= p(t) + \sum_{i=1}^n \left( \frac{m_i}{y_i} \right) g_i(S)x_i \\
 x'_i(t) &= (g_i(S) - D_i)x_i, \quad i = 1, 2, \dots, n,
 \end{aligned}
 \tag{5.1}$$

where  $g_i(S)$  is bounded for  $S \geq 0$ ,  $g_i(0) = 0$  and  $g'_i(S)$  is positive, continuous, monotone decreasing,  $p(t) > 0$ ,  $p(t + w) = p(t)$ .

Even the simplest autonomous case,  $p(t) \equiv \text{constant} > 0$ , which we expect competitive exclusion occurs, difficulties still arise. The interested reader may consult with the counterexample demonstrated in McGehee and Armstrong [10].

### 6. Proof

*Proof of Lemma 3.1.* Since  $x_i(0) > 0$ , then from the representation

$$x_i(t) = x_i(0) \exp \int_0^t \left( \frac{m_i S(\xi)}{a_i + S(\xi)} - D_i \right) d\xi,
 \tag{6.1}$$

we have  $x_i(t) > 0$  provided  $S(\xi) > -a_i$  for  $0 \leq \xi \leq t$ . Suppose  $S(t)$  is not positive for all  $t \geq 0$ . Since  $S(0) > 0$ , there exists a point  $T_0$  with  $S(T_0) = 0$  and  $S(t) > 0$  for  $0 \leq t \leq T_0$ . For  $0 \leq t \leq T_0$ ,

$$S'(t) > [S^{(0)} - b - S(t)]D - \sum_{i=1}^2 \frac{m_i}{y_i} \frac{x_i(t)S(t)}{a_i + S(t)}$$

or

$$S'(t) > -S(t)D - \sum_{i=1}^2 \frac{m_i}{y_i} \frac{x_i(t)S(t)}{a_i + S(t)}$$

or

$$\frac{S'(t)}{S(t)} > -D - \sum_{i=1}^2 \frac{m_i}{y_i} \frac{x_i(t)}{a_i + S(t)}.$$

Integrating from 0 to  $T_0$  and taking the exponentials of both sides, it follows that

$$S(T_0) > S(0) \exp \int_0^{T_0} \left( -D - \sum_{i=1}^2 \frac{m_i}{y_i} \frac{x_i(\xi)}{a_i + S(\xi)} \right) d\xi > 0.$$

This is a contradiction and hence  $S(t)$ ,  $x_i(t)$ ,  $i = 1, 2$  are positive for all  $t \geq 0$ .

Multiplying the equations for  $x_i$  in (2.1) by  $1/y_i$  and adding yields

$$S'(t) + \sum_{i=1}^2 \frac{x_i'(t)}{y_i} = (S^{(0)} + b \sin wt - S(t))D - \sum_{i=1}^2 \frac{D_i x_i(t)}{y_i}. \quad (6.2)$$

Let  $\eta = \min(D, D_1, D_2)$ . Then

$$S'(t) + \sum_{i=1}^2 \frac{x_i'(t)}{y_i} \leq (S^{(0)} + b \sin wt)D - \eta \left[ S(t) + \sum_{i=1}^2 \frac{x_i(t)}{y_i} \right].$$

Comparing the solutions

$$S(t) + \sum_{i=1}^2 \frac{x_i(t)}{y_i}$$

of the above inequality with solutions of

$$z'(t) = (S^{(0)} + b \sin wt)D - \eta z(t)$$

$$z(0) = S(0) + \sum_{i=1}^2 \frac{x_i(0)}{y_i}$$

it follows that

$$S(t) \leq z(t) \quad \text{for all } t \geq 0,$$

or

$$S(t) + \sum_{i=1}^2 \frac{x_i(t)}{y_i} \leq A e^{-\eta t} + \frac{S^{(0)}D}{\eta} + \frac{bD}{\sqrt{\eta^2 + w^2}} \sin(wt - \varphi), \quad (6.3)$$

where

$$A = S(0) + \left( \sum_{i=1}^2 \frac{x_i(0)}{y_i} \right) + \frac{bDw}{\sqrt{\eta^2 + w^2}} - \frac{S^{(0)}D}{\eta} \quad \text{and} \quad \varphi = \tan^{-1} \frac{w}{\eta}.$$

Since

$$|\sin(wt - \varphi)| \leq 1 \quad \text{and} \quad \lim_{t \rightarrow \infty} A e^{-\eta t} = 0,$$

the sum on the left side is bounded, and since each term is positive, each term is bounded.

Before we prove the main results, we note the following lemmas.

**Lemma 6.1.** *Let  $S(t)$ ,  $x_i(t)$ ,  $i = 1, 2$  be solutions of (2.1). Then*

$$S(t) = A e^{-Dt} + S^{(0)} + B \sin(wt - \beta) + \frac{h_1(t)}{y_1} + \frac{h_2(t)}{y_2}. \quad (6.4)$$

where

$$\begin{aligned}
 A &= S(0) + \frac{x_1(0)}{y_1} + \frac{x_2(0)}{y_2} + \frac{bDw}{D^2 + w^2} - S^{(0)} \\
 B &= \frac{bD}{\sqrt{D^2 + w^2}}, \quad \beta = \tan^{-1} \frac{w}{D} \\
 h_i(t) &= (D - D_i) \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi - x_i(t), \quad i = 1, 2.
 \end{aligned} \tag{6.5}$$

*Proof.* From (6.2) it follows that

$$S'(t) + DS(t) = (S^{(0)} + b \sin wt)D - \sum_{i=1}^2 \frac{1}{y_i} [x_i'(t) + D_i x_i(t)]$$

or

$$\frac{d}{dt} [S(t) e^{Dt}] = (S^{(0)} + b \sin wt)D e^{Dt} - \sum_{i=1}^2 \frac{e^{Dt}}{y_i} [x_i'(t) + D_i x_i(t)]$$

or

$$\begin{aligned}
 S(t) &= S(0) e^{-Dt} + \int_0^t (S^{(0)} + b \sin w\xi)D e^{-D(t-\xi)} d\xi \\
 &\quad - \sum_{i=1}^2 \frac{1}{y_i} \int_0^t [x_i'(\xi) + D_i x_i(\xi)] e^{-D(t-\xi)} d\xi.
 \end{aligned}$$

Then (6.4) follows after an integration.  $\square$

**Lemma 6.2.** *If  $\lim_{t \rightarrow \infty} x_i(t) = 0$ , then  $\lim_{t \rightarrow \infty} h_i(x) = 0$ .*

*Proof.* If  $D_i = D$  then by (6.5) we have  $\lim_{t \rightarrow \infty} x_i(t) = 0$  if and only if  $\lim_{t \rightarrow \infty} h_i(t) = 0$ . Suppose  $D_i \neq D$  and suppose first

$$\int_0^\infty x_i(\xi) e^{D\xi} d\xi < \infty.$$

Then

$$\lim_{t \rightarrow \infty} \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi = 0.$$

Hence by (6.5)

$$\lim_{t \rightarrow \infty} h_i(t) = 0.$$

If

$$\int_0^\infty x_i(\xi) e^{D\xi} d\xi = \infty$$

then L'Hospital's rule yields

$$\lim_{t \rightarrow \infty} \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi = \lim_{t \rightarrow \infty} \frac{\int_0^t x_i(\xi) e^{D\xi} d\xi}{e^{Dt}} = \lim_{t \rightarrow \infty} \frac{x_i(t) e^{Dt}}{De^{Dt}} = 0.$$

Hence, again by (6.5), we have  $\lim_{t \rightarrow \infty} h_i(t) = 0$ .  $\square$

**Lemma 6.3.**  $h_i(t) \leq -x_i(0) e^{-Dt} < 0$ ,  $i = 1, 2$ .

*Proof.* From (6.5) one has

$$\begin{aligned} h'_i(t) &= (D - D_i) \left[ x_i(t) - D \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi \right] - x_i(t) \\ &= -D \left[ (D - D_i) \int_0^t x_i(\xi) e^{-D(t-\xi)} d\xi - x_i(t) \right] \\ &\quad - D_i x_i(t) - \left[ (m_i - D_i) x_i(t) - \frac{a_i m_i x_i(t)}{a_i + S(t)} \right] \\ &= -D h_i(t) - m_i x_i(t) + \frac{a_i m_i x_i(t)}{a_i + S(t)} \\ &\leq -D h_i(t) - m_i x_i(t) + m_i x_i(t) = -D h_i(t). \end{aligned}$$

Comparing the solutions  $h_i(t)$  of the above inequality with the solutions of

$$\begin{aligned} Z'(t) &= -DZ(t) \\ Z(0) &= h_i(0) = -x_i(0), \end{aligned}$$

it follows that

$$h_i(t) \leq -x_i(0) e^{-Dt} < 0. \quad \square$$

We note the following lemma which provides the necessary condition for both organisms  $x_1, x_2$  to become extinct.

**Lemma 6.4.** *Let*

$$C_i = \frac{m_i - D_i}{a_i m_i} - \frac{1}{\sqrt{(a_i + S^{(0)})^2 - B^2}}, \quad i = 1, 2$$

where

$$B = \frac{bD}{\sqrt{D^2 + w^2}}.$$

If  $\lim_{t \rightarrow \infty} x_i(t) = 0$ ,  $i = 1, 2$ , then  $C_i \leq 0$ ,  $i = 1, 2$ .

*Proof.* From the assumption and Lemma 6.2, it follows that  $\lim_{t \rightarrow \infty} h_i(t) = 0$ ,  $i = 1, 2$ . By the representation (6.4), we have  $S(t) = S^{(0)} + B \sin(wt - \beta) + o(1)$ . Since  $S^{(0)} > b \geq 0$ , then

$$B = \frac{bD}{\sqrt{w^2 + D^2}} < S^{(0)},$$

given  $\varepsilon > 0$ , satisfying  $a_i + S^{(0)} - \varepsilon > B$ , there exists  $t_0 > 0$  such that

$$S^{(0)} - \varepsilon + B \sin(wt - \beta) < S(t) < (S^{(0)} + \varepsilon) + B \sin(wt - \beta),$$

for  $t \geq t_0$ .

A rearrangement of (6.1) yields

$$x_i(t) = x_{i0} \exp \int_0^t \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi. \tag{6.1}'$$

From the assumption  $\lim_{t \rightarrow \infty} x_i(t) = 0$ , it follows that

$$\lim_{t \rightarrow \infty} \int_0^t \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi = -\infty. \quad \text{For } t \geq t_0, \tag{6.6}$$

$$\begin{aligned} & \int_0^t \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi \\ &= \int_0^{t_0} \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi + \int_{t_0}^t \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi \\ &\geq \int_0^{t_0} \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi \\ &\quad + \int_{t_0}^t \left[ (m_i + D_i) - \frac{a_i m_i}{(a_i + S^{(0)} - \varepsilon) + B \sin(w\xi - \beta)} \right] d\xi. \end{aligned}$$

By (6.6) we have

$$\lim_{t \rightarrow \infty} \int_{t_0}^t \left[ (m_i - D_i) - \frac{a_i m_i}{(a_i + S^{(0)} - \varepsilon) + B \sin(w\xi - \beta)} \right] d\xi = -\infty.$$

The integrand of the above integral is a periodic function of period  $2\pi/w$ . Hence we have

$$\Delta = \int_{t_0}^{t_0 + 2\pi/w} \left[ (m_i - D_i) - \frac{a_i m_i}{(a_i + S^{(0)} - \varepsilon) + B \sin(w\xi - \beta)} \right] d\xi < 0.$$

From the following integral formula (e.g. [4], p. 147),

$$\int \frac{dx}{a + b \sin x} = \frac{2}{\sqrt{a^2 - b^2}} \tan^{-1} \frac{a \tan x/2 + b}{\sqrt{a^2 - b^2}}, \quad a^2 < b^2,$$

it follows that

$$\begin{aligned} \Delta &= (m_i - D_i) \frac{2\pi}{w} - a_i m_i \int_{t_0}^{t_0 + 2\pi/w} \frac{d\xi}{(a_i + S^{(0)} - \varepsilon) + B \sin(w\xi - \beta)} \\ &= (m_i - D_i) \frac{2\pi}{w} - \frac{a_i m_i}{w} \int_{t_0 - \beta}^{t_0 + 2\pi/w - \beta} \frac{d\xi}{(a_i + S^{(0)} - \varepsilon) + B \sin \xi} \\ &= (m_i - D_i) \frac{2\pi}{w} - \frac{a_i m_i}{w} \left[ \frac{2}{\sqrt{(a_i + S^{(0)} - \varepsilon)^2 - B^2}} \tan^{-1} \right. \\ &\quad \left. \times \frac{(a_i + S^{(0)} - \varepsilon) \tan(\xi/2) + B}{\sqrt{(a_i + S^{(0)} - \varepsilon)^2 - B^2}} \right] \Big|_{t_0 - \beta}^{t_0 + 2\pi/w - \beta} \\ &= (m_i - D_i) \frac{2\pi}{w} - \frac{a_i m_i}{w} \frac{2}{\sqrt{(a_i + S^{(0)} - \varepsilon)^2 - B^2}} \cdot \pi \\ &= \frac{2\pi}{w} a_i m_i \left[ \frac{(m_i - D_i)}{a_i m_i} - \frac{1}{\sqrt{(a_i + S^{(0)} - \varepsilon)^2 - B^2}} \right] < 0. \tag{6.7} \end{aligned}$$

Since  $\varepsilon$  is arbitrarily small and  $\Delta$  is independent of  $t_0$ , it follows that

$$\frac{m_i - D_i}{a_i m_i} - \frac{1}{\sqrt{(a_i + S^{(0)})^2 - B^2}} \leq 0. \quad \square$$

The following lemma is similar to Lemma 4.3 of Hsu, Hubbell, and Waltman [8].

**Lemma 6.5.** *Let (3.5) and (3.6) hold. If  $m_1/D_1 \geq m_2/D_2$  then*

$$\lim_{t \rightarrow \infty} x_2(t) = 0.$$

*Proof.* If there exists  $t_0$  such that  $S(t) \geq \lambda_2$  or  $S(t) \leq \lambda_1$  for  $t \geq t_0$  then, from (2.1),  $x_1(t)$  becomes unbounded or  $\lim_{t \rightarrow \infty} x_2(t) = 0$ . Hence we may assume there exists a point  $t_0$  such that  $\lambda_1 < S(t_0) < \lambda_2$ . Let  $\xi > 0$ ,  $\alpha_i = m_i/D_i - 1$ ,  $i = 1, 2$ . Then

$$\xi \frac{x_2'(t)}{D_2 x_2(t)} - \frac{x_1'(t)}{D_1 x_1(t)} = \frac{1}{(a_1 + S(t))(a_2 + S(t))} P_\xi(S(t)) \tag{6.8}$$

where

$$P_\xi(z) = z^2(\xi\alpha_2 - \alpha_1) + z[\xi\alpha_2(a_1 - \lambda_2) - \alpha_1(a_2 - \lambda_1)] + (\alpha_1\lambda_2 a_2 - \xi\alpha_2\lambda_2 a_1) \tag{6.9}$$

$$P_\xi[S(t_0)] < 0 \quad \text{if } \xi > 0. \tag{6.10}$$

The lemma will be proved by obtaining a representation of  $x_2(t)/x_1(t)$ . To analyze this representation, information is needed about the quadratic  $P_\xi(z)$ . The technical arguments in the proof involve selection of a proper value of  $\xi$ . To do this we first analyze this quadratic in some detail.

The Discriminant  $D(\xi)$  of  $P_\xi(z)$  is given by

$$D(\xi) = \xi^2(\alpha_2(a_1 + \lambda_2))^2 - 2\xi \cdot \alpha_1\alpha_2[(a_1 + \lambda_2)(a_2 + \lambda_1) + 2(\lambda_2 - \lambda_1)(a_1 - a_2)] + [\alpha_1(a_2 + \lambda_1)]^2. \tag{6.11}$$

Under the assumptions of the Lemma,  $m_1/D_1 \geq m_2/D_2 > 1$ ,  $\lambda_1 < \lambda_2$ , we have three cases, namely  $a_1 > a_2$ ,  $a_1 = a_2$ ,  $a_2 > a_1$ . If  $a_1 > a_2$ , the discriminant  $D^*$  of  $D(\xi)$  is

$$D^* = 4\alpha_1^2\alpha_2^2(\lambda_2 - \lambda_1)(a_1 - a_2)(a_1 + \lambda_1)(\lambda_2 + a_2) > 0. \tag{6.12}$$

It follows that  $D(\xi) = 0$  has two real roots  $\xi_1, \xi_2$ . Furthermore,  $\xi_1, \xi_2$  are positive. If  $\xi^*$  is chosen between  $\xi_1, \xi_2$ , then  $D(\xi^*) < 0$ . Hence  $P_{\xi^*}(z) = 0$  has no real roots and by (6.10),  $P_{\xi^*}(z) < 0$  for all  $z$ . Put  $\xi = \xi^*$  in (6.8) it follows that

$$\begin{aligned} \xi^* \frac{x_2'(t)}{D_2 x_2(t)} - \frac{x_1'(t)}{D_1 x_1(t)} &= \frac{1}{[a_1 + S(t)][a_2 + S(t)]} P_{\xi^*}(S(t)) \\ &\leq \frac{1}{(a_1 + S_{\max})(a_2 + S_{\max})} \max_{0 \leq \xi \leq S_{\max}} P_{\xi^*}(z) = \zeta < 0, \end{aligned} \tag{6.13}$$

where  $S_{\max} = \sup_{0 \leq t < \infty} S(t)$ . Integrating from 0 to  $t$  and taking exponentials on both sides of (6.13) yields

$$\left(\frac{x_2(t)}{x_2(0)}\right)^{\xi^*/D_2} \leq \left(\frac{x_1(t)}{x_1(0)}\right)^{1/D_1} e^{\zeta t} \leq M e^{\zeta t}.$$

It follows that  $\lim_{t \rightarrow \infty} x_2(t) = 0$ , since  $x_1(t)$  is positive and bounded and  $\zeta$  is negative.

If  $a_2 = a_1$ , then from the assumption  $\lambda_1 < \lambda_2$  we have  $m_1/D_1 > m_2/D_2$ . From (2.1), it follows that

$$\frac{x_2'(t)}{x_2(t)} - \frac{m_2 x_1'(t)}{m_1 x_1(t)} = \frac{D_1 D_2}{m_1} \left( \frac{m_2}{D_2} - \frac{m_1}{D_1} \right) = \eta < 0.$$

Again we have  $\lim_{t \rightarrow \infty} x_2(t) = 0$ .

If  $a_2 > a_1$ , then from (6.12) we have  $D^* < 0$ . Hence  $D(\xi) > 0$  for all  $\xi$ . Rewrite (6.9) for this case as

$$P_\xi(z) = \xi \alpha_2 (z - \lambda_2)(z + a_1) - \alpha_1 (z - \lambda_1)(z + a_2). \tag{6.14}$$

Let  $z_0 > \max(S_{\max}, \lambda_2)$  and choose

$$\xi^* = \frac{\alpha_1 (z_0 - \lambda_1)(z_0 + a_2)}{\alpha_2 (z_0 - \lambda_2)(z_0 + a_1)}.$$

Since  $\alpha_1 \geq \alpha_2, \lambda_2 > \lambda_1, a_2 > a_1$ , it follows that  $\xi^* > 1$ . From (3.3) we have  $a_i = \lambda_i \alpha_i, i = 1, 2$ . Consider the coefficients of polynomial  $P_{\xi^*}(z)$  in (6.9). Then

$$\xi^* \alpha_2 - \alpha_1 = \alpha_1 \left[ \frac{(z_0 - \lambda_1)(z_0 + a_2)}{(z_0 - \lambda_2)(z_0 + a_1)} - 1 \right] > 0$$

and

$$\alpha_1 \lambda_1 a_2 - \xi^* \alpha_2 \lambda_2 a_1 = a_1 a_2 (1 - \xi^*) < 0.$$

Hence  $P_{\xi^*}(z)$  has one positive and one negative root. However, from (6.16),  $P_{\xi^*}(z_0) = 0$  and  $P_{\xi^*}(\lambda_2) < 0$ , so  $P_{\xi^*}(S(t)) < 0$  on  $0 < S(t) \leq S_{\max}$ . The argument is complete as before using (6.8).  $\square$

*Proof of Lemma 3.2.* From (6.4) and Lemma 6.3, it follows that

$$\begin{aligned} S(t) &\leq S^{(0)} + B \sin (wt - \beta) + A e^{-Dt} + \left( -\frac{x_1(0)}{y_1} - \frac{x_2(0)}{y_2} \right) e^{-Dt} \\ &= S^{(0)} + B \sin (wt - \beta) + A_1 e^{-Dt} = Q(t), \end{aligned} \tag{6.15}$$

where

$$A_1 = S^{(0)} + \frac{bDw}{D^2 + w^2} - S^{(0)}.$$

Since

$$Q(t) = S^{(0)} + B \sin (wt - \beta) + 0(1),$$

given  $\epsilon > 0$  there exists  $t_0$  such that for  $t \geq t_0$

$$S^{(0)} + B \sin (wt - \beta) - \epsilon < Q(t) < S^{(0)} + B \sin (wt - \beta) + \epsilon. \tag{6.16}$$

From (6.1)', it suffices to show that

$$\lim_{t \rightarrow \infty} \int_0^t \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi = -\infty.$$

Since

$$\int_0^t \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi = \left( \int_0^{t_0} + \int_{t_0}^t \right) \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi,$$

by (6.15) and (6.16) we have

$$\begin{aligned} & \int_{t_0}^t \left[ (m_i - D_i) - \frac{a_i m_i}{a_i + S(\xi)} \right] d\xi \\ & \leq \int_{t_0}^t \left[ (m_i - D_i) - \frac{a_i m_i}{(a_i + S^{(0)} + \varepsilon) + B \sin(\omega \xi - \beta)} \right] d\xi. \end{aligned}$$

The integrand of the above integral is a periodic function of period  $2\pi/\omega$ , hence it suffices to show

$$\Delta^* = \int_{t_0}^{t_0 + 2\pi/\omega} \left[ (m_i - D_i) - \frac{a_i m_i}{(a_i + S^{(0)} + \varepsilon) + B \sin(\omega \xi - \beta)} \right] d\xi < 0.$$

Since  $C_i < 0$ , or

$$\frac{m_i - D_i}{a_i m_i} < \frac{1}{\sqrt{(a_i + S^{(0)})^2 - B^2}},$$

let  $\varepsilon > 0$  be so small that

$$\frac{m_i - D_i}{a_i m_i} < \frac{1}{\sqrt{(a_i + S^{(0)} + \varepsilon)^2 - B^2}}.$$

Using the same computation method for  $\Delta$  in Lemma 6.4 yields

$$\Delta^* = \frac{2\pi}{\omega} a_i m_i \left[ \frac{(m_i - D_i)}{a_i m_i} - \frac{1}{\sqrt{(a_i + S^{(0)} + \varepsilon)^2 - B^2}} \right] < 0. \quad \square$$

*Proof of Theorem 3.3.* Theorem 3.3 follows directly from Lemma 3.2, Lemma 6.2 and Lemma 6.1.  $\square$

*Proof of Theorem 3.4.* Theorem 3.4 follows directly from Lemma 3.2 and Lemma 6.4.  $\square$

*Proof of Theorem 3.5.* Theorem 3.5 follows directly from Lemma 6.5 and Lemma 6.4.  $\square$

*Proof of Theorem 3.6.* For convenience we adopt the notation  $b_i = m_i/D_i$ ,  $i = 1, 2$ . We note that  $b_i$  is different from amplitude  $b$ . Choose  $\varepsilon > 0$  such that  $S^{(0)} + B + \varepsilon < (b_1 a_2 - b_2 a_1)/(b_2 - b_1)$  and choose  $t_0$  such that  $S(t) \leq S^{(0)} + B + \varepsilon$  for  $t \geq t_0$ . Then one has

$$\begin{aligned} \frac{x_2'(t)}{D_2 x_2(t)} - \frac{x_1'(t)}{D_1 x_1(t)} &= \frac{b_2 S(t)}{a_2 + S(t)} - \frac{b_1 S(t)}{a_1 + S(t)} \\ &= S(t) \frac{(b_2 - b_1)S(t) - (b_1 a_2 + b_2 a_1)}{[a_1 + S(t)][a_2 + S(t)]} \\ &\leq S(t) \frac{(b_2 - b_1)(S^{(0)} + B + \varepsilon) - (b_1 a_2 + b_2 a_1)}{(a_1 + S^{(0)} + B + \varepsilon)(a_2 + S^{(0)} + B + \varepsilon)} \end{aligned}$$

for  $t \geq t_0$ .



Since  $\limsup_{t \rightarrow \infty} S(t) = \bar{S} > 0$  (a consequence of Lemma 3.1) and since  $S'(t)$  is uniformly bounded, there are constants  $\delta > 0$  and  $\varepsilon^* > 0$  and a sequence of disjoint intervals  $I_n = (t_n - \delta, t_n + \delta)$ ,  $t_n \rightarrow \infty$ , such that  $S(t) > \varepsilon^*$  for  $t \in I_n$ . In particular,  $\lim_{t \rightarrow \infty} \int_{t_0}^t S(\eta) d\eta = +\infty$ . Integrating the above inequality gives

$$\left(\frac{x_2(t)}{x_2(t_0)}\right)^{1/D_2} \leq \left(\frac{x_1(t)}{x_1(t_0)}\right)^{1/D_1} \exp \left[ -C \int_{t_0}^t S(\eta) d\eta \right], \text{ for some } C > 0.$$

Hence it follows that  $\lim_{t \rightarrow \infty} x_2(t) = 0$  and (i) follows directly from Lemma 6.4.

Let

$$\xi = \frac{a_1 b_1 C_1}{a_2 b_2 C_2} + \varepsilon_1$$

where  $\varepsilon_1$  is a small, positive number. Let  $\varepsilon > 0$  by a sufficiently small number satisfying

$$a_1 b_1 \left[ \frac{b_1 - 1}{a_1 b_1} - \frac{1}{\sqrt{(a_1 + S^{(0)} + \varepsilon)^2 - B^2}} \right] - \xi a_2 b_2 \left[ \frac{b_2 - 1}{a_2 b_2} - \frac{1}{\sqrt{(a_2 + S^{(0)} + \varepsilon)^2 - B^2}} \right] < 0.$$

From Lemma 6.1 and Lemma 6.4, there exist  $t_0 > 0$  such that  $S(t) \leq S^{(0)} + B \sin(\omega t - \beta) + \varepsilon$ , for  $t \geq t_0$ . Then one has

$$\Delta = \frac{x_1'(t)}{D_1 x_1(t)} - \xi \frac{x_2'(t)}{D_2 x_2(t)} = \left( \frac{b_1 S(t)}{a_1 + S(t)} - 1 \right) - \xi.$$

$$\left( \frac{b_2 S(t)}{a_2 + S(t)} - 1 \right) = g[S(t)].$$

It is easy to verify  $g(S)$  is strictly increasing for  $S \geq 0$  provided  $a_1 < a_2$ ,  $C_1 < C_2$  and  $\varepsilon_1$  is sufficiently small. Then

$$\Delta \leq g[S^{(0)} + B \sin(\omega t - \beta) + \varepsilon].$$

Integrating the above inequality gives

$$\left(\frac{x_1(t)}{x_1(t_0)}\right)^{1/D_1} \leq \left(\frac{x_2(t)}{x_2(t_0)}\right)^{\xi/D_2} \cdot \exp \left( \int_{t_0}^t g[S^{(0)} + B \sin(\omega s - \beta) + \varepsilon] ds \right).$$

Using the same computational method in Lemma 6.4 yields

$$\int_{t_0}^{t_0 + 2\pi/\omega} g[S^{(0)} + B \sin(\omega s - \beta) + \varepsilon] ds$$

$$= \frac{2\pi}{\omega} \left[ a_1 b_1 \left( \frac{b_1 - 1}{a_1 b_1} - \frac{1}{\sqrt{(a_1 + S^{(0)} + \varepsilon)^2 - B^2}} \right) - a_2 b_2 \left( \frac{b_2 - 1}{a_2 b_2} - \frac{1}{\sqrt{(a_2 + S^{(0)} + \varepsilon)^2 - B^2}} \right) \right] < 0.$$

Hence  $\lim_{t \rightarrow \infty} x_1(t) = 0$  and (ii) follows from Lemma 6.4.

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## References

- [1] Armstrong, R. A., McGehee, R.: Coexistence of species competing for shared resource. *Theor. Pop. Biol.* **9**, 317–328 (1976)
- [2] Brauer, F.: Periodic solutions of some ecological models. *J. Theor. Biol.* **69**, 143–152 (1977)
- [3] Coddington, E. A., Levinson, N.: *The theory of ordinary differential equation*. New York: McGraw-Hill 1955
- [4] Gradshteyn, I. S., Ryzhik, I. M.: *Table of Integrals, Series and Products*. New York and London: Academic Press 1965
- [5] Hardin, G.: The competitive exclusion principle. *Science* **131**, 1292–1298 (1960)
- [6] Holling, C. S.: The functional response of predators to prey density and its role in mimicry and population regulation. *Me. Entomol. Soc. Canada* **45**, 5–60 (1965)
- [7] Holling, C. S.: The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Canada* **48**, 1–85 (1966)
- [8] Hsu, S. B., Hubbell, S. P., Waltman, P. E.: A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *Siam J. Appl. Math.* **32**, 366–383 (1977)
- [9] Hsu, S. B.: Limiting behavior for competing species. *Siam J. Appl. Math.* **34**, 760–763 (1978)
- [10] McGehee, R., Armstrong, R. A.: Some mathematical problems concerning the ecological principle of competitive exclusion. *J. Differential Equation* **23**, 30–52 (1977)
- [11] Stewart, F. M., Levin, B. R.: Partitioning of resources and the outcome of interspecific competition: a model and some general consideration. *Amer. Nat.* **7**, 171–198 (1973)

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