Two Species Competition in a Periodic Environment*

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Abstract. The classical Lotka-Volterra equations for two competing species have constant coefficients. In this paper these equations are studied under the assumption that the coefficients are periodic functions of a common period. As a generalization of the existence theory for equilibria in the constant coefficient case, it is shown that there exists a branch of positive periodic solutions which connects (i.e. bifurcates from) the two nontrivial periodic solutions lying on the coordinate axes. This branch exists for a finite interval or "spectrum" of bifurcation parameter values (the bifurcation parameter being the average of the net inherent growth rate of one species). The stability of these periodic solutions is studied and is related to the theory of competitive exclusion. A specific example of independent ecological interest is examined by means of which it is shown under what circumstances two species, which could not coexist in a constant environment, can coexist in a limit cycle fashion when subjected to suitable periodic harvesting or removal rates.

Key words: Competition – Periodic environment – Competitive exclusion – Bifurcation.

1. Introduction

The vast majority of mathematical models which have been used in theoretical ecology to study the dynamics of population growth are autonomous, which is to say that they attempt to describe the growth and interaction of species with constant vital parameters living in a constant environment. This is true, for example, of the classical predator-prey and competition models of Volterra and Lotka. While it might be the case that this hypothesis of constant environmental and vital parameters is justifiable under some circumstances, a more realistic model would certainly allow for the temporal variation of these parameters. It is undoubtedly true that such temporal variation is a common and, in many cases, an important component in determining the dynamics of the growth and interaction of species.

Much of the temporal variation in the environment of a species could naturally be assumed to be cyclic or periodic due to seasonal (or daily or other periodic) effects of food availability, weather conditions, temperature, mating habits, contact

with predators and other resource or physical environmental quantities. In previous papers the author has mathematically investigated the equations obtained from the most commonly used differential equations in mathematical ecology when the coefficients are allowed to be periodic functions of time (see Cushing (1976, 1977a, 1977b)). It is shown in these papers that under certain conditions there exist positive periodic solutions of these periodic differential equations. These periodic solutions play the role played by positive equilibria in the autonomous theory and in fact they reduce to such equilibria when the coefficients become constant. Stability of the periodic solutions was also investigated. These results were obtained for n-species interactions by Cushing (1976) and the special cases of one species growth models and two species predator-prey interactions were investigated in more detail by Cushing (1977a, 1977b).

The purpose of this paper is to investigate the case of two-species competition in a periodic environment. In Section 2 we will describe results for two-species competition which extend those obtainable from those for the more general case of n-species interactions studied by Cushing (1976). It will be shown that for averaged (over one season or period) inherent growth rates lying in appropriate intervals the periodic version of the classical Lotka-Volterra competition model will possess a positive periodic solution. The stability of this solution will be discussed. These results will be briefly related to the principle of competitive exclusion. Formal proofs appear in Section 4.

In Section 3 a specific example is studied in detail. Besides illustrating the theorems of Section 2 this example is meant to demonstrate an interesting biological phenomenon: namely, that two competing species, one of which in a *constant* environment would be doomed to extinction in keeping with the principle of competitive exclusion, can under certain circumstances coexist in a *periodic* environment in a limit cycle sense. This theoretical point is made and numerically studied by computer simulation by Koch (1974). Our results in Section 3 establish analytically and rigorously the existence and stability of such limit cycles and describe precisely the conditions under which they exist.

2. The Periodic Lotka-Volterra Model

The classical two-species competition model of Lotka-Volterra can be written

$$N_1' = N_1(b_1 - a_{11}N_1 - a_{12}N_2),$$
$$N_2' = N_2(b_2 - a_{21}N_1 - a_{22}N_2), \tag{1}$$

where the b_i and a_{ij} are positive constants. There are three nontrivial equilibria $E = (N_1, N_2)$ given by

$$((b_1a_{22} - b_2a_{12})/\varDelta, (b_2a_{11} - b_1a_{21})/\varDelta), (b_1/a_{11}, 0), (0, b_2/a_{22})$$

$$\varDelta := a_{11}a_{22} - a_{12}a_{21}$$

which we will denote by E_1, E_2 and E_3, respectively. Only nonnegative equilibria are of interest, of course. Treating these equilibria as functions of the parameter b_2 (the inherent net growth rate of species N_2), we see that equilibrium E_1 is positive if and only if

$$b_1 a_{21}/a_{11} < b_2 < b_1 a_{22}/a_{12} \qquad \text{when} \qquad \Delta > 0,$$

$$b_1 a_{22}/a_{12} < b_2 < b_1 a_{21}/a_{11} \qquad \text{when} \qquad \Delta < 0 \qquad (2)$$

and that as b_2 ranges over this interval the equilibrium E_1 passes from E_2 to E_3 (or vice versa). Thus E_1 is a "branch" of equilibria connecting the equilibrium E_2 with the "branch" E_3. Such intersecting branches are referred to as "bifurcations" and it is this fundamental observation that motivates the mathematical approach taken by Cushing (1976, 1977a, 1977b) for the case of nonconstant, periodic coefficients b_i, a_{ij}.

We also note that a positive equilibrium E_1 is stable if and only if $\Delta > 0$. That is to say, E_1 is stable if and only if the "direction" of bifurcation of E_1 from E_2 at the critical value $\mu_1 = b_1 a_{21}/a_{11}$ is to the right ($b_2 > \mu_1$), in which case there is an *exchange of stability* from E_1 to E_2. In the opposite case $\Delta < 0$ the bifurcation of E_1 from E_2 at μ_1 is to the left ($b_2 < \mu_1$) and E_1 is unstable. The equilibrium E_2 (or E_3) is stable if and only if

$$b_2 < a_{21} b_1 / a_{11} \qquad (\text{or} \quad b_2 > a_{22} b_1 / a_{12}) \qquad (3)$$

respectively. They are otherwise unstable. All of these facts are illustrated in the accompanying Bifurcation Diagram.

The main result of this section is that a similar set of bifurcating branches of solutions exists when $b_i = b_i(t)$, $a_{ij} = a_{ij}(t)$ are p-periodic functions of time t. The branches consist now of p-periodic solutions and the "bifurcation parameter" b_2 is replaced by its average

$$\mu = [b_2] := p^{-1} \int_0^p b_2(t)\, dt.$$
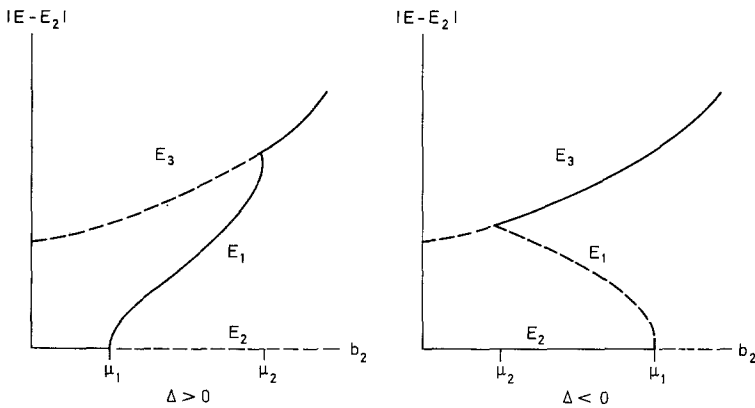
Bifurcation diagram

The distance of a positive equilibrium of (1) from E_2 is plotted against the net growth rate b_2, all other parameters being held fixed. The solid lines denote stable equilibria while the dotted lines denote unstable equilibria. When $\Delta > 0$ the bifurcation of E_1 from E_2 at $b_2 = \mu_1$ is to the right and shows an exchange of stability from E_2 to E_1. If $\Delta < 0$ this bifurcation at $b_2 = \mu_1$ is to the left and the bifurcating branch E_1 is unstable. Theorems $1-3$ show that these bifurcation diagrams are qualitatively unchanged when the coefficients in (1) are periodic functions of time. In this case $|E - E_2|$ is replaced by $|N - N^0|_\infty$ and b_2 is replaced by $[b_2]$ while $\mu_1 = [a_{21} N_1^0]$ and Δ is replaced by Δ_p

This bifurcating branch is stable if and only if bifurcation is to the right in which case there is an exchange of stability.

Let $P(p)$ denote the Banach space of continuous p-periodic functions under the supremum norm $|\cdot|_\infty$. Let $B(p) := P(p) \times P(p)$ and let R denote the reals. The positive reals will be denoted by $R^+ = (0, +\infty)$. By a *continuum* we mean a set which cannot be written as the union of two disjoint, nonempty open sets. By a *positive continuum* $C^+ \subset B(p) \times R$ we mean a continuum such that if $(N_1, N_2, \mu) \in C^+$ then the p-periodic functions $N_i(t)$ are positive for all t. Let the "spectrum" be the set $M := \{\mu \in R: (N_1, N_2, \mu) \in C^+ \text{ for some } N_i \in P(p)\}$.

The periodic logistic equations

$$N' = N(b_i - a_{ii}N), \qquad i = 1, 2 \tag{4}$$

have unique positive (stable) p-periodic solutions $N_i^0 \in P(p)$ for $b_i, a_{ii} \in P(p)$ provided $[b_i] > 0$ and $a_{ii}(t) > 0$ for $0 \leqslant t \leqslant p$. This can be seen by direct integration (or see Cushing (1977b)).

The existence of a bifurcating branch of positive solutions of (1) is contained in the following theorem.

Theorem 1. *Suppose that $b_1(t), a_{ij}(t), p_2(t) \in P(p)$ are given functions of a common period p which satisfy $[p_2] = 0$, $[b_1] > 0$ and $a_{ij}(t) > 0$ for all t. Then there exists a positive continuum $C^+ \subset B(p) \times R$ with the following properties*:

(a) $(N_1, N_2, \mu) \in C^+$ *implies that N_1 and N_2 are positive solutions of the periodic competition equations* (1) *with $b_2(t) = \mu + p_2(t)$*;

(b) C^+ *is bounded and its closure contains $(N_1^0, 0, \mu_1)$ and $(0, N_2^0, \mu_2)$ where*

$$\mu_1 := [a_{21}N_1^0] > 0$$

and N_i^0 solve the periodic logistics (4) *(with $b_2 = \mu_2 + p_2(t)$ when $i = 2$) for some real $\mu_2 > 0$. Thus*

(c) *the spectrum M is a finite interval in R^+ whose closure contains μ_1 and μ_2*.

The positive continuum of periodic solutions whose existence is asserted by this theorem has the basic properties of the equilibrium E_1 when (1) is autonomous. In fact, if all b_i and a_{ij} are constants then $N_i^0 = b_i/a_{ii}$; $\mu_1 = a_{21}b_1/a_{11}$ and $\mu_2 = a_{22}b_1/a_{12}$ are the endpoints of the intervals in (2); $\mu = b_2$; and the continuum C^+ reduces to the equilibrium E_1.

It is of course important in the theory of competing species to determine the stability of the equilibria E_i. Likewise the stability of the positive solutions on the continuum C^+ as well as the periodic solutions $(N_1^0, 0)$ and $(0, N_2^0)$ is of interest in the case of periodic coefficients in (1). (It is easy to see that the trivial solutions $(0, 0)$ is locally unstable when $[b_1] > 0$ and/or $[b_2] > 0$.) The stability of a periodic solution of a periodic system of differential equations is more difficult to ascertain than is the stability of an equilibrium of an autonomous system. We have not obtained necessary and sufficient conditions for the stability of all of the above positive periodic solutions of (1) in the periodic case. We expect, however, that in keeping with the principle of competitive exclusion the solutions $(N_1^0, 0)$ and/or $(0, N_2^0)$ should be stable under conditions of "strong" interspecific competition (i.e. a_{ij} for $i \neq j$ are "large" compared to a_{ii}) but unstable under the opposite conditions of "strong" intraspecific competition. In the latter case the positive solutions on C^+

should be stable so as to indicate coexistence. The periodicity of the coefficients a_{ij} in time, however, complicate this expectation and make it unclear what is meant by "strong" competition.

With regard to the stability of the periodic solutions $(N_1^0, 0)$ and $(0, N_2^0)$ of (1) we have Theorem 2.

Theorem 2. *Suppose that the b_i and a_{ij} satisfy the conditions in Theorem 1. The periodic solution $(N_1^0, 0)$ is (locally uniformly asymptotically) stable as a solution of the periodic system (1) if and only if $\mu = [b_2] < \mu_1 = [a_{21}N_1^0]$ and is unstable if*

$$\mu > \mu_1. \tag{5}$$

Likewise, the periodic solution $(0, N_2^0)$ of the periodic system (1) is stable if and only if $[b_1] < [a_{12}N_2^0]$ and is unstable if

$$[b_1] > [a_{12}N_2^0]. \tag{6}$$

These stability results correspond exactly to those (3) for the equilibria E_2 and E_3 in the case of constant coefficients.

The stability of the periodic solutions $(N_1^0, 0)$ and $(0, N_2^0)$ deals of course with the question of the extinction of one of the species and the survival of the other. Thus, a necessary condition for the coexistence of the two species would seem to be, first of all, the existence of a positive periodic solution of (1) and secondly the inequalities (5) and (6). These conditions are in fact sufficient in the constant coefficient case as can be seen from the first case in (2) to which they reduce when the coefficients are constant. For the periodic case, however, the sufficiency of these conditions is not obvious.

For bifurcation phenomena such as is being considered here in Theorem 1 the rule of thumb concerning stability is the so-called principle of the "exchange of stability". This principle asserts that if bifurcation occurs as a parameter is increased through a critical value, if this bifurcation is "to the right" and if the "trivial solution" off which the bifurcation occurs passes from stable to unstable as this parameter passes through the critical value, then locally near the bifurcation point the bifurcating branch consists of stable solutions (e.g. see Sattinger (1973)). We saw this principle at work in the case of constant coefficients (see the Bifurcation Diagram above). Theorem 3 below establishes, at least locally near the critical value μ_1, this exchange of stability for the bifurcating branch of periodic solutions in Theorem 1.

Let

$$y_2(t) := \exp\left(\int_0^t (\mu_1 + p_2(s) - a_{21}(s)N_1^0(s))\, ds\right) \in P(p)$$

and let $y_1(t)$ be the unique p-periodic solution of the linear equation

$$y_1' = (r_1 - 2a_{11}N_1^0)y_1 - N_1^0 a_{12}y_2.$$

Thus

$$y_1(t) := -\int_0^p G(t, s)N_1^0(s)a_{12}(s)y_2(s)\, ds$$

where the Green's function is given by

$$G(t,s) = \begin{cases} Y(t)(1 - Y(p))^{-1}/Y(s), & 0 \leqslant s \leqslant t \leqslant p, \\ Y(t + p)(1 - Y(p))^{-1}/Y(s), & 0 \leqslant t < s \leqslant p, \end{cases}$$

$$Y(t) = \exp\left(\int_0^t (r_1(s) - 2a_{11}(s)N_1^0(s))\,ds\right).$$

Note that $y_2(t) > 0$ for all t. Also since $[r_1 - 2a_{11}N_1^0] = - [a_{11}N_1^0] < 0$ we see that the Green's function $G(t, s) > 0$ and hence $y_1(t) < 0$ for all t.

Finally define the quantity

$$\Delta_p := [a_{21}(t)y_1(t) + a_{22}(t)y_2(t)].$$

Theorem 3. *Suppose that b_i and a_{ij} satisfy the conditions in Theorem 1. In a sufficiently small neighborhood of $(N_1^0, 0, \mu_1)$ the positive continuum (N_1, N_2, μ) described in Theorem 1 has the form*

$$N_1(t) = N_1^0(t) + \varepsilon y_1(t) + z_1(t, \varepsilon), \qquad N_2(t) = \varepsilon y_2(t) + z_2(t, \varepsilon),$$

$$\mu = \mu_1 + \varepsilon\Delta_p + \beta(\varepsilon)$$

for small $\varepsilon > 0$ where $z_i(\cdot, \varepsilon) \in P(p)$ and $|z_i|_\infty$, $\beta(\varepsilon)$ are $0(\varepsilon^2)$ near $\varepsilon = 0$. Moreover the Floquet exponents e_i of the system (1) *linearized at $N_i(t)$ have the form*

$$e_1(\varepsilon) = - [a_{11}N_1^0] + \gamma_1(\varepsilon), \qquad e_2(\varepsilon) = - \varepsilon\Delta_p + \gamma_2(\varepsilon)$$

where γ_1 and γ_2 are respectively $0(\varepsilon)$ and $0(\varepsilon^2)$ near $\varepsilon = 0$. Thus, the bifurcation at μ_1 is to the right if $\Delta_p > 0$, in which case the positive solutions on this branch are stable, and to the left if $\Delta_p < 0$ in which case these solutions are unstable. Also $N_1(t) \leqslant N_1^0(t)$ for all t and small ε.

From Theorem 3 we see that Δ_p is the quantity which measures the "strength" of interspecific competition and the possibility of (limit cycle) coexistence. It is easy to show that if all coefficients in (1) are constants then $\Delta_p = \Delta$.

Whether the solutions along the entire branch given in Theorem 1 are stable when $\Delta_p > 0$ is an open question. Our final theorem gives sufficient, but not necessary conditions for which this is true.

Theorem 4. *Suppose that $b_i \in P(p)$ and, in addition to the conditions in Theorem 1, the coefficients $a_{ij} \in P(p)$ satisfy*

$$a_{11}(t) > a_{21}(t), \qquad a_{22}(t) > a_{12}(t) \qquad (7)$$

for all t. Then any positive p-periodic solution of (1) *is (locally uniformly asymptotically) stable.*

These results and observations support the expectation that two competing species can coexist if and only if interspecific competition is "weaker" than intraspecific competition and hence support the principle of competitive exclusion in a periodic or seasonally fluctuating environment. The stability results above are, however, incomplete. Those in Theorem 3 are only local while the strong conditions in (7) require that intraspecific competition be pointwise for all time greater than interspecific competition and is not necessary for stability even in the case of

constant coefficients. Further study of this question of coexistence in a periodic environment could prove interesting.

As a simple illustration of the above consider the case when the competition coefficients a_{ij} are positive constants while the inherent net growth rates $b_i(t)$ are p-periodic functions. If the logistic equation (4) is divided by N and integrated over one period, one finds that $[N_i^0] = [b_i]/a_{ii}$ and $\mu_1 = a_{21}[b_1]/a_{11}$. Moreover, division of the equations in (1) by N_1 and N_2 respectively followed by an integration over one period shows that for any positive solution of (1)

$$[b_i] = [a_{ii}N_i] + [a_{ij}N_j], \qquad 1 \leqslant i \neq j \leqslant 2. \tag{8}$$

For constants a_{ij} we find in the limit as we approach $(0, N_2^0, \mu_2)$ along the continuum C^+ in Theorem 1 that

$$[b_1] = a_{12}[N_2^0], \qquad \mu_2 = a_{22}[N_2^0]$$

so that $\mu_2 = a_{22}[b_1]/a_{12}$. Consequently, the spectrum of those $\mu = [b_2]$ for which positive p-periodic solutions exist when the a_{ij} are constants contains the interval with endpoints $\mu_1 = a_{21}[b_1]/a_{11} > 0$ and $\mu_2 = a_{22}[b_1]/a_{12} > 0$. Compare this with (2).

By Theorem 2 the solution $(N_1^0, 0)$ (or $(0, N_2^0)$) is stable if and only if $\mu = [b_2] < a_{21}[b_1]/a_{11}$ (or $[b_2] > a_{22}[b_1]/a_{12}$). By Theorem 4 the positive solutions on C^+ are stable if $a_{11} > a_{21}$ and $a_{22} > a_{12}$, a condition stronger than the condition $\Delta > 0$ needed when the b_i are also constant. Thus, these results are nearly, but not exactly identical with those for (1) with constant coefficients.

3. Avoiding Competitive Exclusion by Means of Environmental Periodicities

Although the generalization is not complete, the main thrust of the results in Section 2 is that qualitatively, in so far as coexistence versus competitive exclusion is concerned, the theory of competition is to a large extent the same in a periodic environment as it is in a constant environment. This does not mean, however, that interesting and unusual phenomena cannot occur because of environmental periodicities. To illustrate this point we will show in this section that it is possible for two species to coexist in a periodic environment when in a constant environment they could not coexist.

This possibility, besides serving as an illustrative example of the results of Section 2, is of independent ecological interest. It was raised and studied in an interesting paper by Koch (1974), who attributes the original idea to Hutchinson (1961). The idea is that at low population densities when resources are abundant competition between two species is low and consequently both species increase (roughly exponentially) as they would in isolation. If one species is the superior competitor, then this increase will continue until population densities are such that the increased competition causes a decline in the density of the inferior competitor. However, should both species at this point in time suffer a significant loss in density for some reason (such as seasonal harvesting or a seasonal "kill") so that both densities return to approximately the same previously low levels, then the cycle is renewed. If this common loss in density is repeated periodically, it seems possible

that the inferior species will not suffer competitive exclusion, but that the species will coexist in a periodically fluctuating (limit cycle) fashion.

Using differential equations as theoretical models (including the Lotka-Volterra system) Koch (1974) shows by means of computer studies that this possibility is indeed born out. The results of Section 2 above can be used to prove rigorously the existence of the limit cycles observed by Koch and to establish conditions under which they are stable.

The Lotka-Volterra equations for two-species competition are frequently written

$$N_1' = r_1 N_1 (K_1 - N_1 - \alpha N_2)/K_1,$$
$$N_2' = r_2 N_2 (K_2 - \beta N_1 - N_2)/K_2 \tag{9}$$

where $r_i > 0$, $K_i > 0$, α and $\beta > 0$ are constants. Here r_i is the inherent, unrestrained growth rate of species N_i, K_i is the carrying capacity of species N_i in isolation from N_j and α, β are constants which measure the amount of competition between the species. We suppose here throughout that

$$K_1/K_2 > \max\{\alpha, 1/\beta\}. \tag{10}$$

This implies in (9) that the equilibrium $(N_1, N_2) = (K_1, 0)$ is a global attractor (in the first quadrant). Thus (10) implies that N_2 will go extinct in competition with the "superior" species N_1.

Suppose now that each species suffers an additional periodic, per unit rate of change in density as modeled by the modified system

$$N_1' = r_1 N_1 (K_1 - N_1 - \alpha N_2)/K_1 - p_1(t)N_1,$$
$$N_2' = r_2 N_2 (K_2 - \beta N_1 - N_2)/K_2 - hp_2(t)N_2. \tag{11}$$

Here

$$p_1(t), p_2(t) \in P(p), \qquad [p_2] = 1, \qquad h \in R \tag{12}$$

and the p-periodic functions p_1 and hp_2 describe this periodic, per unit rate of change of N_1 and N_2 respectively. We wish to show that (11) can, under the right circumstances, possess a stable positive p-periodic solution even when (10) holds. We are particularly interested in this possibility when $p_i(t) \geqslant 0$ and $h > 0$, that is when the species suffer a periodic removal or kill rate.

In the notation of Section 2

$$b_1 = r_1 - p_1(t), \qquad b_2 = r_2 - hp_2(t), \qquad a_{ii} = r_i/K_i,$$
$$a_{12} = \alpha r_1/K_1, \qquad a_{21} = \beta r_2/K_2.$$

Thus in order to apply Theorem 1 it is necessary to assume

$$r_1 > [p_1]. \tag{13}$$

Theorem 1 then implies that positive p-periodic solutions of (11) exist and bifurcate from $(N_1^0, 0, \mu_1)$ where N_1^0 is the positive p-periodic solution of the periodic logistic growth equation

$$N_1' = N_1(r_1 - p_1(t) - r_1 N_1/K_1)$$

and $\mu_1 = \beta r_2 [N_1^0]/K_2 > 0$. But $[N_1^0] = K_1(r_1 - [p_1])/r_1$ so that

$$\mu_1 = \beta r_2 K_1(r_1 - [p_1])/r_1 K_2 > 0. \tag{14}$$

As far as the stability of these p-periodic solutions is concerned we content ourselves with an application of Theorem 4 even though (7), as pointed out above, is only sufficient and not necessary for stability. The inequalities (7) are equivalent to

$$(r_1/r_2)\alpha < K_1/K_2 < (r_1/r_2)/\beta. \tag{15}$$

Under these conditions we have positive p-periodic solutions for $\mu = [b_2] = r_2 - h$ lying in an interval whose closure contains μ_1 as given by (14) (and in particular near μ_1), that is to say for h in an interval whose closure contains the critical bifurcation value $h_{cr} := (r_2 - \mu_1)$ or

$$h_{cr} = r_2(1 - \beta K_1(r_1 - [p_1])/r_1 K_2). \tag{16}$$

Since we wish h to be positive we require $h_{cr} > 0$, or in other words

$$K_1/K_2 < r_1/(r_1 - [p_1])\beta. \tag{17}$$

An investigation of the required inequalities (10), (13), (15) and (17) leads to the following conclusion: *suppose that the parameters of the systems* (9) *and* (11) *satisfy the inequalities*

$$\alpha < K_1 r_2/K_2 r_1 < 1/\beta < K_1/K_2. \tag{18}$$

If the p-periodic removal rates $p_i(t) \in P(p)$ *satisfy* (12) *and*

$$r_1(1 - K_2/\beta K_1) < [p_1] < r_1 \tag{19}$$

then all positive solutions of (9) *tend to the equilibrium* $(K_1, 0)$ *as* $t \to +\infty$ *while the system* (11) *possesses a stable, positive p-periodic limit cycle for h lying in an interval whose closure contains the positive number* h_{cr} *given by* (16).

Remarks. (1) The conditions $r_1 > [p_1]$ and (17) are the only conditions required for the existence assertion in the above statement (including $h_{cr} > 0$). The added constraint (10) guarantees that species N_2 goes extinct in the constant environment case modeled by (9). The remaining parameter constraints are sufficient, but not known to be necessary for the stability assertion above as it is based on Theorem 4.

(2) Note that it is required by (18) that the superior species N_1 have a larger inherent growth rate: $r_1 > r_2$. In view of Remark 1 it is not clear that this constraint is necessary for the conclusions drawn above.

(3) Also note that it is required by (18) that $\alpha\beta < 1$. Again it is not clear that this is necessary for the stability of the periodic solution, but Koch (1974) reports that he was numerically unable to find limit cycles when $\alpha\beta = 1$, the so-called case of "perfect competition" (as was originally considered by Volterra).

(4) It is interesting to note that only the averages of the periodic per unit removal rates appear in the above analysis. Thus, if for example one takes the point of view that a removal program for both species is to be instigated in order to save the inferior competitor N_2 from competitive extinction as based on the ideas above, then for the application of the above theory the amplitudes and phases of the periodic removal rates $p_i(t)$ are irrelevant per se as far as success defined by the

existence of a stable limit cycle is concerned. But one must exercise care, however, because of the many constraints needed above. The species must be "eligible" in the sense that their parameter values r_i, K_i and α, β are restricted by (18). Moreover the averages of the removal rates over one period must be carefully chosen: $[p_1]$ must satisfy (19) and h must be "close to" h_{cr}.

(5) It is easy to see that (18) and (19) imply

$$0 < h_{cr} < [p_1]. \tag{20}$$

In particular $[p_1] > 0$, which is to say that some removal of the superior species N_1 is required. Furthermore this means that, at least near the occurrence of bifurcation, $h < [p_1]$ or in other words the superior species must be removed at a greater rate than the inferior species. While we have not proved that $h < [p_1]$ on the entire bifurcating branch of Theorem 1, this would seem to be the expected situation as based, if nothing else, on the constant coefficient case and the author speculates that this in fact is true in general. If this is indeed true then it is necessary for the limit cycle coexistence of these two species that the superior species be removed at an average rate greater than that for the inferior species.

(6) It is allowed in the above considerations and conclusions that both $p_i(t) \equiv$ constant. In this case, however, the conclusions are not very interesting. It is a trivial observation that if the constant growth rates r_i in (9) are decreased by a constant amount then there can possibly result a positive stable equilibrium.

Also it is not difficult to see that if the general system (1) has a positive periodic solution when all the interaction coefficients a_{ij} are *constants*, then the competition system obtained from (1) by replacing the periodic growth rates b_i by their averages $[b_i]$ results in an autonomous system which possesses a positive equilibrium (equal, in fact, to the averages $([N_1], [N_2])$). This can be seen by dividing the equations in (1) by N_1 and N_2 respectively and integrating over one period.

This observation applies to the system (11) being considered in this section. Thus while, as we have shown above, system (11) can have a stable positive periodic solution when (9) has no positive equilibrium, it is nonetheless true that system (9) will have in this event a stable positive equilibrium if r_1 and r_2 are replaced by the averages $r_1 - [p_1]$ and $r_2 - h$ respectively. One might then be tempted to say that it is no surprise that the species coexist in the periodic environment since their averaged parameter values indicate the existence of a stable equilibrium. This would be, however, beside the point and in view of the first sentence above in this remark (6) would be a trivial observation anyway. The point being made here (and I believe it is the point made in Koch's paper) is that coexistence is possible in a periodic limit cycle sense in a genuinely periodic environment in which species suffer a strictly seasonal reduction in numbers or density. Obviously the dynamics of such a case would not be adequately described by averaged parameters and a study of equilibrium states. Thus, the emphasis in the above analysis is on the case when the $p_i(t)$ are nonconstant, periodic functions (for example with rather narrowly defined support intervals as in the numerical examples below) as opposed to when they are simply taken to be constants.

A numerical study of system (11) was carried out in order to demonstrate not only the existence and stability of the periodic solutions described above, but to study other features of the solutions of these periodic competition equations. The

numerical integrations, carried out by high speed computer, where performed for the removal rate functions defined on the unit interval $0 \leqslant t \leqslant 1$ by

$$0 \leqslant p_i(t) = \begin{cases} \sin \pi(t - d_i)/w_i & \text{for } d_i \leqslant t \leqslant d_i + w_i \\ 0 & \text{for all other } t \end{cases} \tag{21}$$

and extended periodically with period $p = 1$. Here the constants $d_i \geqslant 0$ and $w_i > 0$, which satisfy

$$0 \leqslant d_i < d_i + w_i \leqslant 1,$$

allow variation in the phase and duration of the removal rates. In this case $[p_i] = 2w_i/\pi$.

Figure 1 illustrates the competitive exclusion of the inferior species N_2 for h larger than the critical bifurcation value $h_{cr} > 0$ and the coexistence of the two species when $0 < h < h_{cr}$. The parameter values for both graphs in Fig. 1 are such that in the absence of the periodic removal of both species (i.e. for system (9)) species N_2 would go extinct. Fig. 1(b) is one of many numerical integrations for $h < h_{cr}$ which resulted in limit cycle coexistence. In all cases observed, the variation in species N_1 was greater than that of the inferior species N_2. Fig. 1(b) shows a case when the densities of both species have roughly the same averages; this was not always seen to be the case, however. As is to be expected, for $h < h_{cr}$ near h_{cr} the species N_1 was considerably larger (pointwise for all t) than N_2 while as h was decreased towards zero the opposite was true. Limit cycles were also observed for $h < 0$, which is to say that the spectral interval contains zero in its interior, but this means of course that species N_2 is not removed, but added to the population. If h
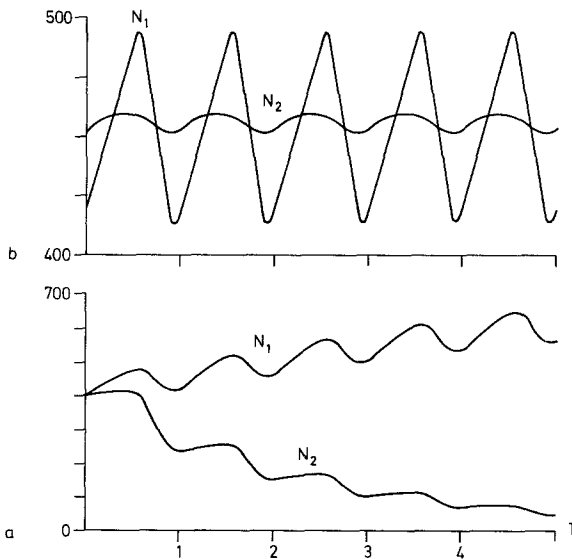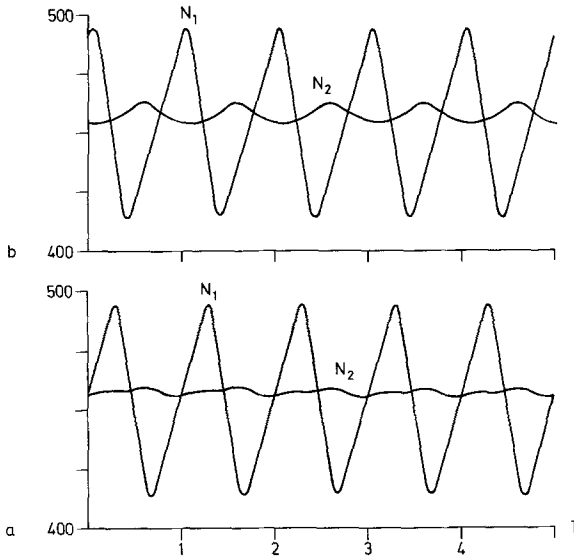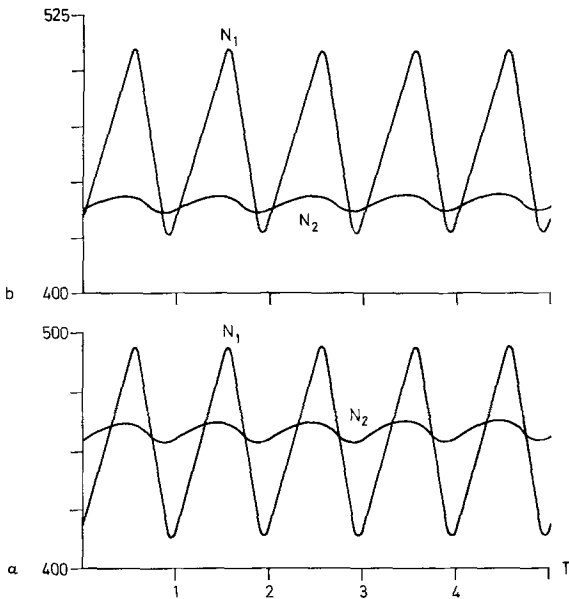

Fig. 1. Solutions of the competition system (11) are shown for $K_1 = K_2 = 1000$, $\alpha = \frac{1}{2}$, $\beta = \frac{10}{9}$, $d_i = w_i = \frac{1}{2}$. Figure **a** shows the extinction of species N_2 for $h = 2.0 > h_{cr} \sim 0.60964$ while **b** shows limit cycle coexistence for $h = 0.1 < h_{cr}$

Fig. 2. Shown here are solutions of (11) with the same parameter values $K_1 = K_2 = 1000$, $\alpha = \frac{1}{2}$, $\beta = \frac{10}{9}$, $d_2 = w_1 = w_2 = \frac{1}{2}$ as in Fig. 1. Figure **a** is for $d_1 = 0$ while **b** is for $d_1 = \frac{1}{4}$ and hence illustrate the effects of one-half cycle and one-quarter cycle phase shifts in the removal rate function $p_1(t)$ respectively

Fig. 3. These solutions are for the competition system (11) with parameter values $K_1 = K_2 = 1000$, $\alpha = \frac{1}{2}$, $\beta = \frac{10}{9}$, $d_i = \frac{1}{2}$ as in Fig. 1. Figure **a** is for $w_1 = 0.50$ and $w_2 = 0.49$ while Fig. **b** is for $w_1 = 0.49$ and $w_2 = 0.50$ and show the effects of a two percent change in the duration of actual removal of species N_2 or N_1 respectively

was decreased sufficiently, then as predicted above the superior species goes extinct, but in no case was this observed for $h > 0$.

Figure 2 shows the effect of phase shifts in the removal rates. In Fig. 1 both species are removed in phase while in Fig. 2 they are removed one-half cycle out of phase or one-quarter cycle out of phase in (b) or (a) respectively. The main effect of these phase differences was a resulting similar phase shift in the density oscillations. Also noticable are changes in amplitude and "shape" in the oscillation of the inferior species N_2. Fig. 2 is to be compared with Fig. 1(b).

In both Figs. 1 and 2 the species removals were performed for the same duration of time (i.e. $w_1 = w_2$). Fig. 3 illustrates the effect of changes in relative lengths of the duration of actual removal (or what amounts to the same thing here, of changes in the relative averages $[p_i]$ and $[p_2]$). It is perhaps no surprise that a shortening of w_1 causes a pointwise increase in the superior species N_1 accompanied by a decrease in N_2 while a shortening of w_2 has the opposite effect. These changes are more sensitive to changes in w_1 than in w_2. Fig. 3 is to be compared to Fig. 1(b).

4. Proofs

Many of the results described in Section 2 are special cases of those proved in an earlier paper by the author concerning n-species interactions to which the reader is referred (Cushing (1976)).

Proof of Theorem 1. (a) By direct application of Theorem 1 and the Remark following the Corollary in Cushing (1976) we have the existence of an unbounded continuum $C = \{(N_1, N_2, \mu) \in B(p) \times R\}$ such that (N_1, N_2) solves (1) with $b_2 = \mu + p_2$. This continuum contains $(N_1^0, 0, \mu_1)$ in its closure and in a neighborhood of $(N_1^0, 0, \mu_1)$ consists of positive solutions $N_i(t) > 0$. Let C^+ be the maximal positive subcontinuum of C whose closure contains $(N_1^0, 0, \mu_1)$.

(b) To begin we will argue that any sequence $S = \{(N_{1,n}, N_{2,n}, \mu_n)\}_{n=1}^{\infty}$ from C^+ is bounded in $B(p) \times R$. This will show that C^+ is bounded.

The assumption $0 < a_{ij}(t) \in P(p)$ implies that $a_{ij}(t) \geqslant \delta > 0$ for all t and some constant $\delta > 0$. First we show that the sequence of first components $N_{1,n} \in P(p)$ is bounded. Let $t_n \in [0, p]$ be such that $N_{1,n}(t_n) = |N_{1,n}|_{\infty}$, $N'_{1,n}(t_n) = 0$. Then from (1) we have

$$|b_1|_{\infty} \geqslant b_1(t_n) = a_{11}(t_n)|N_{1,n}|_{\infty} + a_{12}(t_n)N_{2,n}(t_n) \geqslant \delta|N_{1,n}|_{\infty}$$

which shows that $|N_{1,n}|_{\infty}$ is bounded.

Now let t_n^* and $t_n^{**} \in [0, p]$ be such that

$$N'_{2,n}(t^*) = N'_{2,n}(t^{**}) = 0, \qquad N_{2,n}(t^*) = m_n := \min_{[0,p]} N_{2,n}(t),$$

$$N_{2,n}(t^{**}) = |N_{2,n}|_{\infty}.$$

From (1) we get the two equations

$$\mu_n + p_2(t_n^*) = a_{21}(t_n^*)N_{1,n}(t_n^*) + a_{22}(t_n^*)m_n,$$

$$\mu_n + p_2(t_n^{**}) = a_{21}(t_n^{**})N_{1,n}(t_n^{**}) + a_{22}(t_n^{**})|N_{2,n}|_{\infty}.$$

From these equations and the fact that $p_2(t)$ and $N_{1,n}(t)$ are bounded in t and n we

conclude that if the sequence S is unbounded then so must all three sequences μ_n, $|N_{2,n}|_\infty$ and m_n be unbounded. Thus, extracting a subsequence if necessary, $m_n \to +\infty$ and for large enough n we get

$$b_1(t) - a_{11}(t)N_{1,n}(t) - a_{12}(t)N_{2,n}(t) \leqslant b_1(t) - a_{11}(t)N_{1,n}(t) - \delta m_n < 0$$

for all t. This implies $N'_{1,n}(t) < 0$ for all t which contradicts $N_{1,n} \in P(p)$. Consequently S cannot be unbounded and hence C^+ is bounded in $B(p) \times R$.

Solutions of (1) are either never zero or identically zero. Since C is unbounded while $C^+ \subset C$ is bounded it follows that C^+ must "leave" the positive cone of positive solutions at some point other than the bifurcation point $(N_1^0, 0, \mu_1)$. That is, C^+ must contain in its closure either $(0, 0, \mu_2)$ or $(0, N_2^0, \mu_2) \in B(p) \times R$ for some $\mu_2 \in R$. The proof of (b) will be complete if the first case can be ruled out.

If (N_1, N_2) is any positive solution of (1), then division by N_i followed by an integration over one period in (1) shows that

$$[b_i] = [a_{ii}N_i] + [a_{ij}N_j], \qquad 1 \leqslant i \neq j \leqslant 2. \tag{22}$$

Suppose $(N_{1,n}, N_{2,n}, \mu_n) \in C^+$ converges in $B(p) \times R$ to $(0, 0, \mu_2)$ for some $\mu_2 \in R$. Then (22) implies

$$[b_1] = [a_{11}N_{1,n}] + [a_{12}N_{2,n}] \to 0 \qquad \text{as} \qquad n \to +\infty$$

which contradicts the assumption that $[b_1] > 0$.

(c) C^+ is bounded implies that the spectrum M of C^+ is a finite interval in R (which by (b) contains μ_1 and μ_2 in its closure). We need only prove that this interval lies in R^+.

If $(N_1, N_2, \mu) \in C^+$, then (22) implies

$$\mu = [a_{22}N_2] + [a_{21}N_1] \geqslant 0.$$

Clearly $\mu = 0$ if and only if $(N_1, N_2) = (0, 0)$. But in (b) above we ruled out $(0, 0, 0) \in C^+$. Thus, $\mu \in M$ implies $\mu > 0$.

Proof of Theorem 2. If we set $x_i = N_i - N_i^0$, $x_j = N_j$ for $1 \leqslant i \neq j \leqslant 2$ in (1) and ignore higher order terms, then there results the uncoupled, linear periodic system

$$x'_i = (-a_{ii}N_i^0)x_i + (-a_{ij}N_j^0)x_j,$$
$$x'_j = (b_j - a_{ji}N_i^0)x_j, \qquad 1 \leqslant i \neq j \leqslant 2.$$

This uncoupled system is easily seen to be (uniformly asymptotically) stable if and only if $[b_j - a_{ji}N_i^0] < 0$.

Proof of Theorem 3. That the continuum (N_1, N_2, μ) has a parametrization in terms of a small parameter ε follows from standard and very general perturbation or Liapunov-Schmidt methods. For example Theorem 1 of Cushing (1979) applies straightforwardly to the operator formulation of (1) in the proof of Theorem 1 in Cushing (1976). Both N_i and μ are infinitely differentiable in ε. Substituting these expressions for N_i and μ into the system (1) and equating coefficients of ε terms, one finds a linear system

$$y'_1 = (r_1 - 2a_{11}N_1^0)y_1 - N_1^0 a_{12}y_2, \qquad y'_2 = (\mu_1 + p_2 - a_{21}N_1^0)y_2$$

for the p-periodic coefficients $y_i(t)$. The solution of this system yields $y_1(t)$ and $y_2(t)$ as defined prior to Theorem 3.

The adjoint system

$$w_1' = -(r_1 - 2a_{11}N_1^0)w_1, \qquad w_2' = (N_1^0 a_{12})w_1 - (\mu_1 + p_2 - a_{21}N_1^0)w_2$$

has one independent, p-periodic solution given by $w_1 = 0$, $w_2 = 1/y_2$.

The ε^2 terms in (1) lead to a linear, inhomogeneous system

$$z_1' = (r_1 - 2a_{11}N_1^0)z_1 + (-a_{12}N_1^0)z_2 + y_1(-a_{11}y_1 - a_{12}y_2),$$

$$z_2' = (\mu_1 + p_2 - a_{21}N_1^0)z_1 + y_2(\Delta_p - a_{21}y_1 - a_{22}y_2)$$

for a p-periodic solution z_i whose inhomogeneities must be orthogonal to the adjoint solution $w_1 = 0$, $w_2 = 1/y_2$. This yields $\Delta_p = [a_{21}y_1 + a_{22}y_2]$ as desired.

Finally, we must compute the Floquet exponents e_i of the system (1) linearized at the branch solutions as they are functions of ε. Let

$$N_1 = x_1 + (N_1^0 + \varepsilon y_1 + \varepsilon z_1), \qquad N_2 = x_2 + (\varepsilon y_2 + \varepsilon z_2)$$

in (1) and drop all terms of second or higher order in x_i. This results in the linear homogeneous system

$$x_1' = (r_1 - 2a_{11}N_1^0)x_1 + (-a_{12}N_1^0)x_2$$
$$\qquad + \varepsilon(-2a_{11}y_1 - a_{12}y_2 + \cdots)x_1 + \varepsilon(-a_{12}y_1 + \cdots)x_2,$$

$$x_2' = (\mu_1 + p_2 - a_{21}N_1^0)x_2$$
$$\qquad + \varepsilon(-a_{21}y_2 + \cdots)x_1 + \varepsilon(\Delta_p - a_{21}y_1 - 2a_{22}y_2 + \cdots)x_2$$

where the dots denote terms of order ε or higher. From the general theory of linear, periodic systems we know that the Floquet exponents $e_i = e_i(\varepsilon)$ of this linear system are infinitely differentiable in ε (because the coefficients of the system are). Moreover, when $\varepsilon = 0$ these exponents are easily seen to be $e_1(0) = -[a_{11}N_1^0] < 0$ and $e_2(0) = 0$. Thus,

$$e_i(\varepsilon) = -[a_{11}N_1^0] + \gamma_1(\varepsilon), \qquad e_2(\varepsilon) = \varepsilon\gamma(\varepsilon)$$

for small ε where $\gamma_1(\varepsilon) = 0(\varepsilon)$. We need yet to compute $\gamma(0)$.

It is not difficult to show that $\varepsilon\gamma(\varepsilon)$ is a Floquet exponent if and only if the following linear, homogeneous system has a nontrivial p-periodic solution:

$$x_1' = (r_1 - 2a_{11}N_1^0)x_1 + (-a_{12}N_1^0)x_2$$
$$\qquad + \varepsilon(-2a_{11}y_1 - a_{12}y_2 + \cdots)x_1 + \varepsilon(-a_{12}y_1 + \cdots)x_2 - \varepsilon\gamma(\varepsilon)x_1,$$

$$x_2' = (\mu_1 + p_2 - a_{11}N_1^0)x_2$$
$$\qquad + \varepsilon(-a_{21}y_2 + \cdots)x_1 + \varepsilon(\Delta_p - a_{21}y_1 - 2a_{22}y_2 + \cdots)x_2 - \varepsilon\gamma(\varepsilon)x_2. \qquad (23)$$

It is again a straightforward application of perturbation or Liapunov-Schmidt techniques to show that there indeed exists a function $\gamma(\varepsilon)$ for which this system has a nontrivial p-periodic solution $x_i = y_i + \varepsilon\zeta_i + \cdots$, $\zeta_i(t) \in P(p)$ where the dots denote terms of order $0(\varepsilon^2)$ and the $y_i(t)$ are as defined in Theorem 3. We are here not so interested in the details of this standard proof, but rather are interested in

finding $\gamma(0)$. This we can do by equating coefficients of ε terms in (23), a procedure which results in a linear inhomogeneous system for the coefficients $\zeta_i(t)$:

$$\zeta_1' = (r_1 - 2a_{11}N_1^0)\zeta_1 + (-a_{12}N_1^0)\zeta_2 + (-2a_{11}y_1 - a_{12}y_2 - \gamma(0))y_1 - a_{12}y_1y_2,$$

$$\zeta_2' = (\mu_1 + p_2 - a_{11}N_1^0)\zeta_2 - a_{21}y_1y_2 + (\Delta_p - a_{21}y_1 - 2a_{22}y_2 - \gamma(0))y_2$$

whose inhomogeneous terms must be orthogonal to the adjoint solution $w_1 = 0$, $w_2 = 1/y_2$. This orthogonality condition implies

$$\gamma(0) = -[a_{21}y_1] + \Delta_p - [a_{21}y_1 - 2a_{22}y_2] = -\Delta_p$$

as was to be proved.

Proof of Theorem 4. Let (N_1^*, N_2^*) be a positive periodic solution of (1) and set $x_i = (N_i - N_i^*)/N_i^*$. Substituting into (1) and ignoring higher order terms we obtain the linearized system

$$x_i' = (-a_{ii}N_i^*)x_i + (-a_{ij}N_j^*)x_j, \qquad 1 \leqslant i \neq j \leqslant 2.$$

This system is (uniformly asymptotically) stable if

$$\max_{1 \leqslant i \neq j \leqslant 2} \{-a_{ii}(t)N_i^*(t) + a_{ji}(t)N_i^*(t)\} \leqslant -\varepsilon < 0$$

for all t (see Coppel (1965), pages 41 and 59). Since the positive periodic solutions $N_i^*(t)$ are bounded away from zero we see that this stability condition is equivalent to (7).

References

Coppel, W. A.: Stability and asymptotic behavior of differential equations. Boston: D. C. Heath and Company 1965

Cushing, J. M.: Stable limit cycles of time dependent multispecies interactions. Math. Biosci. **31**, 259–273 (1976)

Cushing, J. M.: Periodic time-dependent predator-prey systems. SIAM J. Appl. Math. **32**, No. 1, 82–95 (1977a)

Cushing, J. M.: Stable positive periodic solutions of the time-dependent logistic equation under possible hereditary influences. J. Math. Anal. Appl. **60**, No. 3, 747–754 (1977b)

Cushing, J. M.: Nontrivial periodic solutions of integrodifferential equations. J. Integral Equations **1**, 165–181 (1979)

Hutchinson, G. E.: The paradox of the plankton. American Naturalist **95**, 137–143 (1961)

Koch, A. L.: Coexistence resulting from an alternation of density dependent and density independent growth. J. Theor. Biol. **44**, 373–386 (1974)

Sattinger, D. H.: Topics in stability and bifurcation theory. Lec. Notes in Math. **309**. New York: Springer 1973