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EFFECTS OF DOMAIN SIZE ON THE PERSISTENCE OF POPULATIONS IN A DIFFUSIVE FOOD-CHAIN MODEL WITH BEDDINGTON-DeANGELIS FUNCTIONAL RESPONSE

ROBERT STEPHEN CANTRELL
Department of Mathematics
University of Miami
Coral Gables, FL 33124, USA
E-mail: rsc@math.miami.edu

CHRIS COSNER
Department of Mathematics
University of Miami
Coral Gables, FL 33124, USA
E-mail: gcc@math.miami.edu

ABSTRACT. A food chain consisting of species at three trophic levels is modeled using Beddington-DeAngelis functional responses as the links between trophic levels. The dispersal of the species is modeled by diffusion, so the resulting model is a three component reaction-diffusion system. The behavior of the system is described in terms of predictions of extinction or persistence of the species. Persistence is characterized via permanence, i.e., uniform persistence plus dissipativity. The way that the predictions of extinction or persistence depend on domain size is studied by examining how they vary as the size (but not the shape) of the underlying spatial domain is changed.

KEY WORDS: Reaction-diffusion, food chains, area effects, predator-prey, Beddington-DeAngelis, persistence, permanence.

1. Introduction. In this article we will examine how the size of the underlying spatial environment affects the persistence or extinction of species in a community consisting of three trophic levels. We use a reaction-diffusion model in which the links between trophic levels are given by functional responses of Beddington-DeAngelis type. This type of model has been used to some extent in theoretical ecology. Some background results on Beddington-DeAngelis type models are given in Beddington [1975], Cantrell and Cosner [1998], Cantrell

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and Cosner [2001], DeAngelis et al. [1975], Ruxton et al. [1992]. We use the idea of permanence, i.e., uniform persistence plus dissipativity, to characterize persistence. Permanence can be interpreted as meaning that the system has a global attractor for nontrivial nonnegative solutions which is bounded away from the boundary of the positive cone. To show permanence in the context of our model requires, among other things, that each species is able to invade the system if the species at lower trophic levels are present. Mathematically, this criterion of invasibility means roughly that points in the ω-limit of certain subsystems are unstable with respect to perturbations in which the density of a species not represented in the subsystem is positive. This instability is characterized by the sign of the principal eigenvalue of an associated elliptic operator being positive. To give explicit criteria for permanence in terms of the coefficients of the system we need estimates on the location of the ω-limit sets of subsystems. These estimates are obtained via methods based on sub- and super-solutions.

The model we study has the form

(1.1)

$$\begin{aligned} u_t &= (d_1/l^2)\Delta u + u(1-u) - \frac{A_1 uv}{1+B_1u+C_1v} \\ v_t &= (d_2/l^2)\Delta v + \frac{E_1 uv}{1+B_1u+C_1v} - \frac{A_2 vw}{1+B_2v+C_2w} - D_2 v \\ w_t &= (d_3/l^2)\Delta w + \frac{E_2 vw}{1+B_2v+C_2w} - D_3 w \qquad &&\text{in } \Omega_0 \times (0,\infty), \\ u &= v = w = 0 &&\text{on } \partial\Omega_0 \times (0,\infty). \end{aligned}$$

(We assume that u and t have been rescaled so that the growth rate and carrying capacity in the logistic term of the first equation are both equal to one).

The system (1.1) is obtained by starting on the domain $\Omega = l\Omega_0$, i.e., $\Omega = \{(lx, ly) : (x,y) \in \Omega_0\}$ or the equivalent in three dimensions, then scaling out the length parameter l by a change of independent variables. Thus, our goal is to study how the dynamics of (1.1) are affected by l. The terms forming the links between the trophic levels are functional responses of the form

$$\frac{Auv}{1+Bu+Cv} \tag{1.2}$$

proposed by DeAngelis et al. [1975] and Beddington [1975]. These responses can be derived from mechanistic consideration (Ruxton et al. [1992]) and are reasonably well known among theoretical ecologists but less so among mathematicians. The term Bu in the denominator reflects the time required to handle a prey item, as in the Holling type II functional response (see Freedman [1980], Ruxton et al. [1992]). The term Cv represents mutual interference by predators. In Cantrell and Cosner [2001], we studied a two-species system using the Beddington-DeAngelis functional response. It turns out that such systems can have periodic orbits (Cantrell and Cosner [2001]), which suggests that in general an analysis of the equilibria of the system (1.1) may not adequately characterize the dynamics. That is one of the reasons why we have taken the viewpoint of permanence in studying persistence in (1.1).

There has been some treatment of diffusive food chain models (Cantrell and Cosner [1996], [1998], Feng [1994]), but these studies do not address the effects of the size of the underlying environment on the interactions. Permanence has been used in the context of models involving three interacting species (Avila and Cantrell [1997], Cantrell et al. [1993b], Cantrell and Ward, Jr. [1997]) and our application of the concept is similar in spirit to that in Cantrell et al. [1993b]. For general background on permanence, see Hutson and Schmitt [1992]. As in Cantrell et al. [1993b], we use ideas based on sub- and super-solutions to obtain estimates on the asymptotic behavior of subsystems.

There have been many studies of the effects of habitat size on the number of species which are expected to be seen in a community; see Cantrell and Cosner [1994] and the references therein. However, almost all such studies are based on models where there are no direct interactions between species. The typical approach is to assume that certain parameters such as the probability of colonizing a habitat patch are distributed among species according to certain rules and then to count the number of species whose presence in the habitat is predicted by their parameter sets; see the discussion in Cantrell and Cosner [1994].

What is new in this paper is the use of models such as (1.1) with specific tight interactions between trophic levels to study area effects in a community. The paper is structured as follows: some mathematical background is given in Section 2, with additional details in the

Appendices; the models are analyzed in Section 3 and our conclusions are summarized in Section 4.

2. Mathematical background. Our approach to the analysis of (1.1) is based on the notion of permanence (i.e., uniform persistence and dissipativity) for dynamical systems (Cantrell et al. [1993a], Hale and Waltman [1989], Hutson and Schmitt [1992]). The system (1.1) can be viewed as generating a semi-dynamical system on appropriate spaces of functions. A dynamical or semi-dynamical system on a space with a positive cone is permanent if all solutions are eventually bounded away from infinity and from the boundary of the positive cone, and the bounds are independent of the initial data. For the system (1.1) (and analogous reaction-diffusion systems) permanence implies that each component is eventually bounded above and below by functions that are positive on Ω. In particular, if (1.1) is permanent, then there exists functions $\underline{u}, \underline{v}, \underline{w}, \bar{u}, \bar{v}, \bar{w}$ of x such that $0 \leq \underline{u}(x) \leq u(x,t) \leq \bar{u}(x)$ on Ω for any solution (u, v, w), provided t is large enough, and similarly $\underline{v}(x) < v(x,t) < \bar{v}(x)$ and $\underline{w}(x) < w(x,t) < \bar{w}(x)$ for large t. (This point is discussed in detail in Cantrell et al. [1993a]; see also Hutson and Schmitt [1992]).

Establishing that a system such as (1.1) is permanent typically requires a stability analysis of equilibria and other steady-states of subsystems where one or more components are zero. For permanence to hold, it is necessary for any steady-state where one or more components are zero to be unstable relative to at least some perturbations where some of those components are positive. This is not sufficient for permanence to hold; that also requires a structural condition on the semiflow restricted to the boundary of the positive cone. A brief discussion of permanence and a theorem giving sufficient conditions for permanence are found in Appendix A; also see Avila and Cantrell [1997], Cantrell et al. [1993a], [1993b], [1996], Hutson and Schmitt [1992] for more detailed discussions. Under reasonable hypotheses, which are met by (1.1), permanence implies the existence of a positive equilibrium. We shall not state a formal result to that effect; see Cantrell et al. [1993a], Hutson and Schmitt [1992] for detailed discussions.

To establish the instability of equilibria we will want to consider eigenvalue problems arising from the linearization of (1.1) or its subsystems.

The solution $u \equiv 0$ to a reaction-diffusion equation

$$
\begin{aligned}
&u_t = d\Delta u + p(x)u \ + \ \text{(higher order terms in } u) && \text{in } \Omega \times (0,\infty) \\
&u = 0 && \text{on } \partial\Omega \times (0,\infty)
\end{aligned}
\tag{2.1}
$$

is linearly unstable if $\sigma_1(d, p(x)) > 0$ where $\sigma_1(d, p(x))$ is the principal eigenvalue of the problem

$$
\begin{aligned}
d\Delta\psi + p(x)\psi &= \sigma\psi && \text{in } \Omega \\
\psi &= 0 && \text{on } \partial\Omega.
\end{aligned}
\tag{2.2}
$$

If $p(x)$ is continuous and positive on an open subset of Ω, then the eigenvalue problem

$$
\begin{aligned}
-\Delta\phi &= \lambda p(x)\phi && \text{in } \Omega \\
\phi &= 0 && \text{on } \partial\Omega
\end{aligned}
\tag{2.3}
$$

has a positive principal eigenvalue $\lambda_1^+(p(x))$, see Cantrell and Cosner [1989], [1991], DeFigueiredo [1982], Hess and Kato [1980], Manes and Micheletti [1973], Senn [1983]. (Principal eigenvalues are characterized by their associated eigenfunctions being positive on Ω). The eigenvalues in (2.2) and (2.3) are related: $\sigma_1(d, p(x)) > 0$ if and only if $\lambda_1^+(p(x)) < 1/d$. (This is stated formally in Lemma B.4 of Appendix B). The eigenvalue $\lambda_1^+(p(x))$ can be used to give criteria for the existence of a positive equilibrium for a single reaction-diffusion equation. This is done for the diffusive logistic equation in Cantrell and Cosner [1989], [1991]. Analogous results for an equation arising in the analysis of (1.1) are given in Appendix B.

Determining when solutions to (1.1) are bounded away from zero will be the main goal of the mathematical analysis of the next section. However, it is easy to obtain global asymptotic upper bounds on solutions to (1.1), from which dissipativity follows in stronger norms via parabolic regularity theory, as in Cantrell et al. [1993a], Hutson and Schmitt [1992]. We have

Lemma 2.1. *There are positive constants u_0, v_0, w_0 such that any nonnegative solution of* (1.1) *satisfies $0 \le u \le u_0$, $0 \le v \le v_0$, $0 \le w \le w_0$ for t sufficiently large.*

PROOF. For any solution to (1.1), u is a subsolution to the equation

$$
\begin{aligned}
&y_t = (d_1/l^2)\Delta y + (1-y)y && \text{in } \Omega_0 \times (0,\infty) \\
&y = 0 && \text{on } \partial\Omega_0 \times (0,\infty).
\end{aligned}
\tag{2.1}
$$

By the results of Cantrell and Cosner [1989], all positive solutions of (2.1) either approach zero as $t \to \infty$ or approach a unique positive equilibrium $\bar{y} < 1$. Thus, for large t, $0 \leq u \leq 1$. If $0 \leq u \leq 1$, then v is a subsolution to

(2.2)

$$
\begin{aligned}
&y_t = (d_2/l^2)\Delta y + \big([E_1/(1+B_1+C_1 y)] - D_2\big)y && \text{in } \Omega_0 \times (0,\infty) \\
&y = 0 && \text{on } \partial\Omega_0 \times (0,\infty).
\end{aligned}
$$

By the results in Appendix B, all positive solutions to (2.2) either approach zero or approach a unique positive equilibrium $\bar{\bar{y}}$. By the strong maximum principle $\bar{\bar{y}} < [E_1 - D_2(1+B_1)]/C_1 D_2$ if $\bar{\bar{y}}$ exists. Thus, for large t, $0 \leq v \leq v_0$ where v_0 is any positive number larger than $[E_1 - D_2(1+B_1)]/C_1 D_2$. Finally, if $v \leq v_0$ then w is a subsolution to

(2.3)

$$
\begin{aligned}
&y_t = (d_3/l^2)\Delta y + \big([E_2 v_0/(1+B_2 v_0+C_2 y)] - D_3\big)y && \text{in } \Omega_0 \times (0,\infty) \\
&y = 0 && \text{on } \partial\Omega_0 \times (0,\infty).
\end{aligned}
$$

The same sort of analysis as we used for (2.2) implies that for large t we have $w \leq w_0$ for any sufficiently large positive constant w_0.

3. Analysis of the models.

We shall now analyze how the asymptotic behavior of (1.1) depends on the scaling parameter l. It will turn out that for l sufficiently small none of the populations can persist, but that under suitable conditions on the parameters, persistence will become possible as l increases. If persistence is possible for some of the populations, then as l increases the model will predict persistence of the lowest trophic level first; as l increases further the model will predict persistence of the next lowest trophic level, and so on, up the trophic stack or food chain.

We begin with the observation that (1.1) cannot predict persistence at any given trophic level if it predicts extinction at a lower level. The reason for this is that the only growth terms in the equations for the populations v and w at the higher trophic levels are those arising from predation on the population at the next lowest level. This can be described mathematically as follows:

Lemma 3.1. *Suppose that*

$$l^2 \leq d_1 \lambda_1^+(1). \tag{3.1}$$

Then all components of all nonnegative solutions of (1.1) *tend to zero as* $t \to \infty$.

PROOF. (Recall that $\lambda_1^+(1)$ is the principal eigenvalue of

$$\begin{aligned} -\Delta\phi &= \lambda\phi \quad \text{in } \Omega_0 \\ \phi &= 0 \quad\ \ \text{on } \partial\Omega_0.) \end{aligned}$$

If $l^2 \leq d_1\lambda_1^+(1)$, then by the results in Cantrell and Cosner [1989], all nonnegative solutions to

$$\begin{aligned} z_t &= (d_1/l^2)\Delta z + z(1-z) && \text{in } \Omega_0 \times (0,\infty) \\ z &= 0 && \text{on } \partial\Omega_0 \times (0,\infty) \end{aligned} \tag{3.2}$$

must approach zero as $t \to \infty$. If u satisfies (1.1) then u is a subsolution to (3.2), so choosing z so that $z(x,0) = u(x,0)$ in (3.2) yields $0 \leq u(x,t) \leq z(x,t)$ so, since $z \to 0$ as $t \to \infty$, we must have $u \to 0$ as $t \to \infty$. Hence, for large t, we have $u < D_2/2E_1$ so that $E_1u/(1 + B_1u + C_1v) < E_1(D_2/2E_1) = D_2/2$, and hence v is a subsolution to

$$\begin{aligned} y_t &= (d_2/l^2)\Delta y - (D_2/2)y && \text{in } \Omega_0 \times (0,\infty) \\ y &= 0 && \text{on } \partial\Omega_0 \times (0,\infty). \end{aligned} \tag{3.3}$$

Since the coefficient of y in (3.3) is negative, all solutions must approach zero as $t \to \infty$. Thus, if we choose y to satisfy (3.3) with $y(x,0) = v(x,0)$, then $0 \leq v(x,t) \leq y(x,t)$ for all t. Since $y \to 0$ as $t \to \infty$, we see that $v \to 0$ as well. A similar argument shows that since $v \to 0$ as $t \to \infty$, then $w \to 0$ as $t \to \infty$.

If $l^2 > d_1\lambda_1^+(1)$, then (3.2) has a unique positive equilibrium which is globally attracting among positive solutions; see Cantrell and Cosner [1989]. If $v = w = 0$, then u satisfies (3.2), so in that case the species on the lowest trophic level can persist by itself. We now consider whether the species on the second trophic level can persist. Thus we consider the subsystem

(3.4)
$$\begin{aligned} u_t &= (d_1/l^2)\Delta u + u(1-u) - \frac{A_1uv}{1+B_1u+C_1v} \\ v_t &= (d_2/l^2)\Delta v + \left(\frac{E_1u}{1+B_1u+C_1v} - D_2\right)v \quad && \text{in } \Omega_0 \times (0,\infty) \\ u &= v = 0 && \text{on } \partial\Omega_0 \times (0,\infty). \end{aligned}$$

We have the following.

Lemma 3.2. *If*

$$d_1\lambda_1^+(1) < l^2 \tag{3.5}$$

and $(u,0,0)$ *is a solution to* (1.1) *with* $u \geq 0$, $u \not\equiv 0$ *at* $t = 0$, *then* $u \to \bar{u}$ *as* $t \to \infty$ *where* $\bar{u}$ *is the unique positive equilibrium of* (3.2).

If (3.5) *holds, then* (3.4) *is permanent if and only if*

$$\sup_{\Omega_0}\big([E_1\bar{u}/(1+B_1\bar{u})] - D_2\big) > 0 \tag{3.6}$$

and

$$d_2\lambda_1^+\big([E_1\bar{u}/(1+B_1\bar{u})] - D_2\big) < l^2. \tag{3.7}$$

If inequality (3.6) *fails to hold or if* (3.6) *holds but* (3.7) *is reversed, then* $v \to 0$ *as* $t \to \infty$.

Remark. Since $\bar{u}$ is an equilibrium of (3.2), it follows from the strong maximum principle that $\bar{u} < 1$ so (3.6) holds only if

$$[E_1/(1+B_1)] - D_2 > 0. \tag{3.8}$$

If (3.6) holds, then eigenvalue comparison results imply

$$\begin{aligned} \lambda_1^+\big([E_1\bar{u}/(1+B_1\bar{u})] - D_2\big) &> \lambda_1^+([E_1/(1+B_1)] - D_2) \\ &= \lambda_1^+(1)/\{[E_1/(1+B_1)] - D_2\}, \end{aligned}$$

so (3.7) holds only if

(3.9)
$$\frac{d_2\lambda_1^+(1)}{[E_1/(1+B_1)]-D_2} < l^2.$$

Hence (3.8) and (3.9) are necessary for permanence.

Proof of Lemma 3.2. If (3.5) holds, then $\bar{u}$ exists and any solution $(u,0,0)$ with $u \geq 0$, $u \not\equiv 0$ has $u \to \bar{u}$ as $t \to \infty$ by results from Cantrell and Cosner [1989]. If (3.6) holds, then $\lambda_1^+([E_1\bar{u}/(1+B_1\bar{u})]-D_2)$ exists. If (3.5) and (3.7) hold, then Lemma B.4 implies $\sigma_1(d_1/l^2,1) > 0$ and $\sigma_1(d_2/l^2,[E_1\bar{u}/(1+B_1\bar{u})]-D_2) > 0$, so that the equilibria $(0,0)$ and $(\bar{u},0)$ of (3.4) are locally unstable and permanence follows for (3.4) as in Theorem 5.3 of Cantrell et al. [1993a]. Alternatively, since the set $\omega(\partial Y_0)$ for (3.4) consists of $(0,0)$ and $(\bar{u},0)$ with all solutions of the form $(0,v)$ approaching $(0,0)$ and all solutions of the form $(u,0)$ with $u \neq 0$ approaching $(\bar{u},0)$, permanence follows from acyclicity via Theorem A1.

If (u,v) satisfies (3.4), then u is a subsolution to (3.2), so for any $\varepsilon > 0$, we have $u < (1+\varepsilon)\bar{u}$ for sufficiently large t. Thus, for large enough t, v is a subsolution to

(3.10)
$$\begin{aligned} &y_t = (d_2/l^2)\Delta y + \left[\frac{E_1(1+\varepsilon)\bar{u}}{1+B_1(1+\varepsilon)\bar{u}+C_1y} - D_2\right]y && \text{in } \Omega_0 \times (0,\infty) \\ &y = 0 && \text{on } \partial\Omega_0 \times (0,\infty), \end{aligned}$$

for any given $\varepsilon > 0$. If (3.6) is reversed, then $[E_1(1+\varepsilon)\bar{u}/(1+B_1(1+\varepsilon)\bar{u})]-D_2 < 0$ for $\varepsilon > 0$ sufficiently small, so $y \to 0$ as $t \to \infty$ for any solution of (3.10), and hence $v \to 0$ as $t \to \infty$. If equality holds in (3.6), then for any $\delta > 0$ we can choose ε so that $[E_1(1+\varepsilon)\bar{u}/(1+B_1(1+\varepsilon)\bar{u})]-D_2 < \delta$, so $d_2\lambda_1^+([E_1(1+\varepsilon)\bar{u}/(1+\beta_1(1+\varepsilon)\bar{u})]-D_2) > d_2\lambda_1^+(\delta) = (d_2/\delta)\lambda_1^+(1)$. For δ small enough, we will have

(3.11)
$$d_2\lambda_1^+\big([E_1(1+\varepsilon)\bar{u}/(1+B_1(1+\varepsilon)\bar{u})]-D_2\big) > l^2.$$

Similarly, if (3.6) holds but (3.7) is reversed, then continuity of λ_1^+ with respect to the weight function (i.e., the potential) implies (3.11) for ε

small. If (3.11) holds, then by Lemma B.4 $\sigma_1(d_2/l^2, [E_1(1+\varepsilon)\bar{u}/(1+B_1(1+\varepsilon)\bar{u})] - D_2) < 0$. It follows that the solution $y \equiv 0$ to (3.10) is asymptotically stable. Since v is a subsolution to (3.10) and $v \geq 0$, we must have $v \to 0$ as $t \to \infty$.

Finally if equality holds in (3.7) we still cannot have permanence. Permanence implies the existence of a positive equilibrium (u^*, v^*) (see Cantrell et al. [1993a], Hutson and Schmitt [1992]). If (u^*, v^*) is a positive equilibrium to (3.4), then u^* is a strict subsolution to the equilibrium equation for (3.2). Since any large constant is a supersolution and there is a unique positive equilibrium $\bar{u}$ for (3.2) we must have $u^* < \bar{u}$. Also, $v^* > 0$ on Ω_0. The equation for v^* is

$$(d_2/l^2)\Delta v^* + \left(\frac{E_1 u^*}{1 + B_1 u^* + C_1 v^*} - D_2\right) v^* = 0 \quad \text{in } \Omega_0$$
$$v^* = 0 \quad \text{on } \partial\Omega_0.$$

Since $v^* > 0$ on Ω_0, the principal eigenvalue $\sigma_1(d_2/l^2, [E_1 u^*/(1 + B_1 u^* + C_1 v^*)] - D_2)$ must be zero. (The eigenfunction would be a multiple of v^*). But $\bar{u} > u^*$ and $v^* > 0$, so $E_1\bar{u}/(1+B_1\bar{u}) > E_1 u^*/(1+B_1 u^* + C_1 v^*)$ in Ω_0. Thus, standard eigenvalue comparison results imply

$$\begin{aligned} 0 &= \sigma_1\big(d_2/l^2, [E_1 u^*/(1 + B_1 u^* + C_1 v^*)] - D_2\big) \\ &< \sigma_1\big(d_2/l^2, [E_1\bar{u}/(1+B_1\bar{u})] - D_2\big); \end{aligned}$$

by Lemma B.4 this last inequality implies that (3.7) must hold.

We now consider the relations between hypotheses (3.5), (3.6) and (3.7).

Lemma 3.3. *There is a number* $l^* > \sqrt{d_1\lambda_1^+(1)}$ *such that* (3.6) *and* (3.7) *cannot hold (so* (3.4) *cannot be permanent) unless* $l > l^*$. *If* (3.8) *holds and* l *is sufficiently large, then* (3.6) *and* (3.7) *are satisfied so that* (3.4) *is permanent.*

Remark. For $l \leq \sqrt{d_1\lambda_1^+(1)}$, none of the components of (1.1) can persist. For $\sqrt{d_1\lambda_1^+(1)} < l < l^*$, u will persist but v and hence w will not. Only for $l > l^*$ can v persist. Thus, as the size of the habitat increases, we should first expect no population to persist, then only the population on the first trophic level, then perhaps the populations on the first two trophic levels.

PROOF. We know that for any fixed $l > \sqrt{d_1\lambda_1^+(1)}$ the problem (3.2) has a unique equilibrium $\bar{u}(l)$. By the results of Cantrell and Cosner [1989], $\bar{u}(l)$ depends continuously on the parameter l, is increasing with respect to l, and satisfies $\bar{u}(l) \to 0$ in $C^{1+\alpha}(\overline{\Omega}_0)$ as $l \downarrow \sqrt{d_1\lambda_1^+(1)}$. (The last result follows from the bifurcation theoretic analysis in Cantrell and Cosner [1989]. If $l \leq \sqrt{d_1\lambda_1^+(1)}$, then $u \to 0$ as $t \to \infty$ so $v \to 0$ as $t \to \infty$ also). Thus, there is a number $\varepsilon^* > 0$ such that if $\sqrt{d_1\lambda_1^+(1)} < l < \sqrt{d_1\lambda_1^+(1)} + \varepsilon^*$, then $\bar{u}(l) < D_2/2E_1$ so that (3.6) fails. Hence we may take l^* to be any number in the interval $(\sqrt{d_1\lambda_1^+(1)}, \sqrt{d_1\lambda_1^+(1)} + \varepsilon^*)$. By the results of Cantrell and Cosner [1989], $\bar{u}(l) \to 1$ as $l \to \infty$, uniformly on any subdomain Ω' of Ω_0 with $\overline{\Omega'} \subset \Omega_0$. Thus, if (3.8) holds, then (3.6) holds for l large. If (3.6) holds for some value of l, then it holds for all larger values of l since $\bar{u}(l)$ is increasing in l. The eigenvalue $\lambda_1^+([E_1\bar{u}(l)/(1 + B_1\bar{u}(l))] - D_2)$ thus exists for l sufficiently large, and it is decreasing in l since $[E_1\bar{u}(l)/(1 + B_1\bar{u}(l))] - D_2$ is increasing in l. Since the left side of (3.7) decreases in l while the right side increases without bound as $l \to \infty$, (3.7) must hold for l sufficiently large.

We have an analogous result relating the conditions for permanence in (1.1) for those needed in (3.4).

Lemma 3.4. *Suppose that, for some l,* (3.6) *and* (3.7) *hold. There is a number l^{**} satisfying $l^{**} > \inf\{l :$ inequalities* (3.6) *and* (3.7) *are satisfied$\}$ so that for $l < l^{**}$, $w \to 0$ as $t \to \infty$ in* (1.1).

Remark. It follows that (1.1) cannot be permanent unless l exceeds the threshold value needed for permanence in (3.4) by some positive amount.

PROOF. Note that if (3.6) fails or (3.7) is reversed, then $v \to 0$ as $t \to \infty$, so $w \to 0$ as $t \to \infty$, by essentially the same arguments used to show $v \to 0$ as $t \to \infty$ in Lemma 3.1. Suppose that (3.6) holds and (3.7) is satisfied for at least some value of l. Note that the analysis in Cantrell and Cosner [1989] implies that the equilibrium $\bar{u}(l)$ of (3.2) is increasing with respect to l, so $[E_1\bar{u}/(1+B_1\bar{u})] - D_2$ is also increasing in l, so $\lambda_1^+([E_1\bar{u}/(1+B_1\bar{u})] - D_2)$ is decreasing. Hence (3.7) holds for $l > l_1$ but fails for $l \leq l_1$ where l_1 satisfies

$$d_2\lambda_1^+([E_1\bar{u}(l_1)/(1+B_1\bar{u}(l_1)] - D_2) = l_1^2. \tag{3.12}$$

Recall that for any $\varepsilon > 0$ and t sufficiently large, v is a subsolution to (3.10). By Theorems B.1 and B.2, the problem (3.10) has a unique positive equilibrium $\bar{y}(l,\varepsilon)$. Multiparameter bifurcation theory, e.g. as in Alexander and Antman [1981], implies that $\bar{y}(l,\varepsilon)$ will depend continuously on l and ε. A bifurcation analysis of the type used in Cantrell and Cosner [1989] shows that $\bar{y}(l,0)$ branches from 0 at $l = l_1$. Thus, if (l,ε) is sufficiently close to $(l_1,0)$, we have $\bar{y}(l,\varepsilon) < D_3/3E_2$. Hence we may choose $l^{**} > l_1$ and $\varepsilon > 0$ so that $\bar{y}(l,\varepsilon) < D_3/3E_2$ for $l_1 \leq l < l^{**}$. If $\bar{y}(l,\varepsilon) < D_3/3E_2$, then since v is a subsolution to (3.10) for large t, we have $v < (1+\delta)\bar{y}(l,\varepsilon)$ for any $\delta > 0$ if t is sufficiently large. For $\delta = 1/2$ we get $v < D_3/2E_2$ for large t. It then follows that for large t, w is a subsolution to

$$\begin{aligned} z_t &= (d_3/l^2)\Delta z - (D_3/2)z \quad &&\text{in } \Omega_0 \times (0,\infty) \\ z &= 0 &&\text{on } \partial\Omega_0 \times (0,\infty). \end{aligned} \tag{3.13}$$

Since the coefficient of the zero order term in (3.13) is negative, all solutions of (3.13) must approach zero as $t \to \infty$. Since $w \geq 0$ is a subsolution, $w \to 0$ as $t \to \infty$ provided $l < l^{**}$.

Remark. We have established that there are numbers l^* and l^{**} such that (3.4) cannot be permanent if $l < l^*$ and (1.1) cannot be permanent for $l < l^{**}$. (If in fact (3.4) is permanent for some l, then we have $l^{**} > l^*$). We will devote the remainder of the analysis to finding conditions under which (1.1) is necessarily permanent for large l. We already know that (3.6) and (3.7) must hold for the system to be permanent. (Note that (3.7) is equivalent to $l > l_1$ where l_1 satisfies (3.12)). In this case the subsystem (3.4) is permanent and hence admits a compact global attractor (for initial data (u_0, v_0) with $u_0(x) \overset{>}{\not\equiv} 0$, $v_0(x) \overset{>}{\not\equiv} 0$) in the interior of the positive cone in $[C_0^1(\overline{\Omega}_0)]^2$ which is bounded away from the boundary of the cone. Let us denote this attractor by $\mathcal{A}(l)$. The omega limit set of the boundary of the positive cone in $[C_0^1(\overline{\Omega}_0)]^3$ under solution trajectories for (1.1), $\omega(\partial Y_0)$ in the notation of Appendix A, is then given by $\{(0,0,0), (\bar{u}(l), 0, 0), \mathcal{A}(l) \times \{0\}\}$ and consequently is acyclic. Moreover, the semiflow in $[C_0^1(\overline{\Omega}_0)]^3$ corresponding to (1.1) is dissipative and hence Theorem A.1 is in principle applicable. The condition $W^s(\mathcal{A}(l) \times \{0\}) \cap Y_0 = \varnothing$ will be sufficient to assert that (1.1) is permanent, and we have the following result.

Theorem 3.5. *Suppose that* (3.5), (3.6) *and* (3.7) *hold. Let* $\mathcal{A}(l)$ *be the compact global attractor whose existence is guaranteed by permanence in Lemma* 3.2. *Then* (1.1) *is permanent provided there is a constant* $c > 0$ *with the property that if* $(u, v, 0) \in \mathcal{A}(l) \times \{0\}$ *and* $\sigma \in \mathbf{R}$ *are such that*

$$(3.14) \qquad \begin{aligned} (d_3/l^2)\Delta\psi + \left(\frac{E_2 v}{1 + B_2 v} - D_3\right)\psi &= \sigma\psi \quad \text{in } \Omega_0 \\ \psi &= 0 \qquad \text{on } \partial\Omega_0 \end{aligned}$$

admits a solution $\psi > 0$ *in* Ω_0, *then* $\sigma \geq c$.

Proof. The condition $\sigma \geq c$ in the statement of the result may be interpreted as uniform invasibility of the w component of solutions to (1.1) over $\mathcal{A}(l) \times \{0\}$. We may establish $W^s(\mathcal{A}(l) \times \{0\}) \cap Y_0 = \varnothing$ by exploiting Lemma 4.2 of Cantrell and Cosner [2001] in much the same way as was done in the proof of Theorem 4.1 in Avila and Cantrell [1997]. A more formal treatment of the concept of a uniformly repelling set is given in Freedman and Ruan [1995].

Our goal is to identify conditions on the system parameters under which (1.1) becomes permanent as $l \to \infty$. In order to verify the hypotheses of Theorem 3.5 to assert the permanence of (1.1), we will need lower bounds on the v component of $(u, v, 0) \in \mathcal{A}(l) \times \{0\}$ that we can track as $l \to \infty$. Our approach to establishing such bounds is as follows. Start with arbitrary initial data of the form $(u_0, v_0, 0)$, with $u_0(x) \overset{>}{\not\equiv} 0$, $v_0 \overset{>}{\not\equiv} 0$, and let $(u, v, 0)$ denote the corresponding solution of (1.1). (Note that (u, v) is then a solution of (3.4)). Establish an asymptotic upper bound on u. Use this bound to establish an asymptotic upper bound on v from which an asymptotic lower bound on u can be derived under appropriate conditions on the system parameters. Then employ the asymptotic lower bound on u to obtain a corresponding asymptotic lower bound on v under appropriate conditions on the system parameters. Since u_0 and v_0 are arbitrary, this last provides a lower bound for v if $(u, v, 0) \in \mathcal{A}(l) \times \{0\}$ for some u. Finally we may employ Theorem B.3 to track the corresponding σ in (3.14) as l increases to satisfy the hypotheses of Theorem 3.5 under suitable conditions on the parameters of the system (1.1).

We have observed that u is a lower solution to (3.2) so that for any $\varepsilon > 0$, we have $u < (1+\varepsilon)\bar{u}$ for large t, where $\bar{u}$ is the positive equilibrium of (3.2), and hence $\bar{u} < 1$ by the strong maximum principle. Also, for large t, v is a subsolution of (3.10) and hence of

$$
(3.15)\quad \begin{aligned} z_t &= \left(\frac{d_2}{l^2}\right)\Delta z + \frac{E_1(1+\varepsilon)z}{1+B_1(1+\varepsilon)+C_1 z} - D_2 z && \text{in } \Omega_0 \times (t,\infty) \\ z &= 0 && \text{on } \Omega_0 \times (t,\infty) \end{aligned}
$$

for t large. Since

$$
\frac{E_1}{1+B_1} - D_2 > 0
$$

and

$$
l > \sqrt{d_2\lambda_1^+\left(\frac{E_1\bar{u}(l)}{1+B_1\bar{u}(l)} - D_2\right)} > \sqrt{d_2\lambda_1^+\left(\frac{E_1}{1+B_1} - D_2\right)},
$$

all nonnegative nontrivial solutions to (3.15) converge to the unique positive equilibrium solution of (3.15). The maximum principle guarantees that the equilibrium solution is less than $[(E_1 - B_1D_2)(1+\varepsilon) - D_2]/D_2C_1$ everywhere in $\overline{\Omega}_0$. As a consequence, $v < (1+\delta)([(E_1 - B_1D_2)(1+\varepsilon) - D_2]/D_2C_1)$ for any $\delta > 0$ and $\varepsilon > 0$ for t sufficiently large. Hence for any $\eta > 0$, we have $v < (1+\eta)[(E_1 - B_1D_2 - D_2)/D_2C_1]$ for t sufficiently large.

Returning to the u equation we now find that, for t sufficiently large,

u is an upper solution to

(3.16)

$$y_t = \left(\frac{d_1}{l^2}\right)\Delta y + y(1-y) - \frac{A_1 y\big((1+\eta)[(E_1 - B_1 D_2 - D_2)/D_2 C_1]\big)}{1 + C_1\big((1+\eta)[(E_1 - B_1 D_2 - D_2)/D_2 C_1]\big)} \quad \text{in } \Omega_0 \times (t,\infty)$$

$$y = 0 \quad \text{on } \partial\Omega_0 \times (t,\infty).$$

Now

$$\frac{A_1\big((1+\eta)[(E_1 - B_1 D_2 - D_2)/D_2 C_1]\big)}{1 + C_1\big((1+\eta)[(E_1 - B_2 D_2 - D_2)/D_2 C_1]\big)} = \frac{(1+\eta)A_1(E_1 - B_1 D_2 - D_2)}{C_1(D_2 + (1+\eta)(E_1 - B_1 D_2 - D_2))}$$

and hence

$$y(1-y) - \frac{A_1 y[(1+\eta)((E_1 - B_1 D_2 - D_2)/D_2 C_1)]}{1 + C_1[(1+\eta)((E_1 - B_1 D_2 - D_2)/D_2 C_1)]} = y\left(1 - \frac{(1+\eta)A_1(E_1 - B_1 D_2 - D_2)}{C_1(D_2 + (1+\eta)(E_1 - B_1 D_2 - D_2))} - y\right).$$

It follows from Cantrell and Cosner [1989], for example, that (3.16) admits a globally attracting positive equilibrium solution which we will denote by $\bar{y}(l,\eta)$ provided

$$l^2 > d_1 \lambda_1^+ \left(1 - \frac{(1+\eta)A_1(E_1 - B_1 D_2 - D_2)}{C_1(D_2 + (1+\eta)(E_1 - B_1 D_2 - D_2))}\right). \tag{3.17}$$

To have

$$\lambda_1^+ \left(1 - \frac{(1+\eta)A_1(E_1 - B_1 D_2 - D_2)}{C_1(D_2 + (1+\eta)(E_1 - B_1 D_2 - D_2))}\right)$$

exist as a positive number for small $\eta > 0$ requires

$$\frac{A_1(E_1 - B_1 D_2 - D_2)}{C_1(E_1 - B_1 D_2)} < 1.$$

An elementary calculation shows that this inequality is equivalent to $(A_1 - C_1)/A_1 < D_2/(E_1 - B_1 D_2)$. Now (3.6) implies (3.8), which implies $D_2/(E_1 - B_1 D_2) < 1$. It follows that we must require

$$\frac{C_1}{A_1} > 1 - \frac{D_2}{E_1 - B_1 D_2} \tag{3.18}$$

in order to have (3.17) hold for l large enough. Assuming (3.17) and (3.18), we may assert that $u > (1-\gamma)\bar{y}(l,\eta)$ for $0 < \gamma < 1$ for t sufficiently large. Recall that by Lemma 3.3, inequality (3.8) implies that (3.6) and (3.7) hold for l sufficiently large.

We now have imposed (3.17) and (3.18), in addition to the assumptions (3.6) and (3.7), as being required for the permanence of the (u, v) subsystem of (1.1). Under these assumptions, we now find v is an upper solution to

(3.19)
$$\begin{aligned} &\frac{\partial z}{\partial t} = \frac{d_2}{l^2}\Delta z + \frac{E_1(1-\gamma)\bar{y}(l,\eta)z}{1 + B_1(1-\gamma)\bar{y}(l,\eta) + C_1 z} - D_2 z \quad && \text{in } \Omega_0 \times (t, \infty) \\ &z = 0 && \text{on } \partial\Omega_0 \times (t,\infty) \end{aligned}$$

for t sufficiently large. Nonnegative nontrivial solutions to (3.19) will converge to a unique positive equilibrium solution provided that

$$\frac{E_1(1-\gamma)\max\bar{y}(l,\eta)}{1 + B_1(1-\gamma)\max\bar{y}(l,\eta)} > D_2 \tag{3.20}$$

and

$$l^2 > d_2\lambda_1^+\left(\frac{E_1(1-\gamma)\bar{y}(l,\eta)}{1 + B_1(1-\gamma)\bar{y}(l,\eta)} - D_2\right). \tag{3.21}$$

(Note that (3.20) guarantees that

$$\lambda_1^+\left(\frac{E_1(1-\gamma)\bar{y}(l,\eta)}{1 + B_1(1-\gamma)\bar{y}(l,\eta)} - D_2\right)$$

exists as a positive number). It follows from Section 4 of Cantrell and Cosner [1989] that if Ω' is an open subdomain of Ω_0 such that $\overline{\Omega}' \subset \Omega_0$, then $\bar{y}(l,\eta)$ converges uniformly to

$$1 - \frac{(1+\eta)A_1(E_1 - B_1D_2 - D_2)}{C_1(D_2 + (1+\eta)(E_1 - B_1D_2 - D_2))} \quad \text{on } \overline{\Omega}' \quad \text{as } l \to \infty.$$

In order for (3.20) to hold for small γ and η and large enough l, we must have

$$(3.22)\qquad \frac{E_1[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]}{1+B_1[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]} > D_2.$$

A calculation will show that (3.22) holds if and only if

$$(3.23)\qquad C_1 > A_1.$$

(Notice that (3.23) implies (3.18)).

Now assume (3.23). Let Ω' be a subdomain of Ω_0 with $\overline{\Omega}' \subset \Omega_0$. Choose $\delta \in (0,1)$ so that

(3.24)

$$\frac{E_1(\delta)[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]}{1+B_1(\delta)[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]} > D_2.$$

Choose $\delta' \in (\delta, 1)$ so that $(\delta')^3 > \delta$. Then choose $\eta' > 0$ so that if $0 \le \eta < \eta'$,

$$1-\frac{(1+\eta)A_1(E_1-B_1D_2-D_2)}{C_1(D_2+(1+\eta)(E_1-B_1D_2-D_2))} > \delta'\left(1-\frac{A_1(E_1-B_1D_2-D_2)}{C_1(E_1-B_1D_2)}\right).$$

Next pick l' large enough so that

$$(3.25)\qquad \bar{y}(l,\eta') > \delta'\left(1-\frac{(1+\eta')A_1(E_1-B_1D_2-D_2)}{C_1(D_2+(1+\eta')(E_1-B_1D_2-D_2))}\right)$$

on $\overline{\Omega}'$ if $l > l'$. Since $\bar{y}(l,\eta)$ decreases in η, it follows from (3.25) that if $\gamma < 1-\delta'$,

$$(3.26)\qquad (1-\gamma)\bar{y}(l,\eta) > \delta\left(1-\frac{A_1(E_1-B_1D_2-D_2)}{C_1(E_1-B_1D_2)}\right)$$

on $\overline{\Omega}'$ for $l > l'$ and $0 \le \eta < \eta'$. It follows from (3.24) and (3.26) that (3.20) holds if $l > l'$, $0 \le \eta < \eta'$ and $\gamma < 1-\delta'$.

We may now assert that there is a number $l'' > l'$ so that if $l > l''$, $0 \le \eta < \eta'$ and $0 \le \gamma < 1-\delta'$, (3.21) holds. It follows that for $l > l''$, $0 \le \eta < \eta'$ and $0 \le \gamma < 1-\delta'$, (3.19) admits a unique globally attracting positive equilibrium solution $\bar{z}(l,\eta,\gamma)$. Multiparameter global bifurcation theory (Alexander and Antman [1981]) and the uniqueness of positive equilibrium solutions to (3.19) guarantee that $(l,\eta,\gamma) \to \bar{z}(l,\eta,\gamma)$ is continuous as a map from $(l'',\infty) \times [0,\eta'] \times [0,1-\delta') \to C_0^1(\overline{\Omega}_0)$. Since v is an upper solution to (3.19) for sufficiently large t under the assumptions (3.6), (3.7), (3.17) and (3.18), we have for any $\beta \in (0,1)$ that $v \geq \beta\bar{z}(l,\eta,\gamma)$ provided $l > l''$, $0 \leq \eta < \eta'$, $0 \leq \gamma < 1-\delta'$ and t is sufficiently large. By (3.26), $\bar{z}(l,\eta,\gamma)$ is an upper solution to the elliptic problem

(3.27)

$$0 = \frac{d_2}{l^2}\Delta\rho + \frac{E_1\delta[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]\rho}{1+B_1\delta[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]+C_1\rho} - D_2\rho \quad \text{in } \Omega'$$

$$\rho = 0 \quad \text{on } \partial\Omega'$$

for $l > l''$, $0 \leq \eta < \eta'$ and $0 \leq \gamma < 1-\delta'$. By (3.24), there is $l''' > l''$ so that if $l > l'''$, (3.27) admits a unique positive solution, which we denote by $\rho(l)$, with $\bar{z}(l,\eta,\gamma) > \rho(l)$ on $\overline{\Omega}'$. Theorem B.3 implies that if Ω'' is an open subdomain of Ω' such that $\overline{\Omega}'' \subset \Omega'$, $\rho(l)$ converges uniformly on $\overline{\Omega}''$ to the root of

(3.28)

$$\frac{E_1\delta[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]}{1+B_1\delta[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))]+C_1\rho} - D_2 = 0$$

as $l \to \infty$. It is easy to calculate that the root of (3.28) is given by

$$K = \frac{(E_1-B_1D_2)\delta[1-(A_1(E_1-B_1D_2-D_2)/C_1(E_1-B_1D_2))] - D_2}{D_2C_1}.$$

We may conclude that there is a number $l^{(\text{iv})} > l'''$ so that if $l > l^{(\text{iv})}$, $v > \beta K$ on $\overline{\Omega}''$ for t sufficiently large. We have now established the following result.

Lemma 3.6. *Suppose that* (3.8) *and* (3.23) *hold. For any* $\beta,\delta \in (0,1)$, *if* Ω^* *is an open subdomain of* Ω_0 *such that* $\overline{\Omega}^* \subset \Omega_0$, *then there* *is an* $l^{***} > l_1$ *so that if* $l > l^{***}$ *and* $(u, v, 0) \in \mathcal{A}(l) \times \{0\}$*, then*

$$v \geq \frac{\beta\big((E_1 - B_1D_2)\delta[1 - (A_1(E_1 - B_1D_2 - D_2)/C_1(E_1 - B_1D_2))] - D_2\big)}{D_2C_1}$$
$$> 0 \quad \text{on } \overline{\Omega}^*.$$

Now let $l > l^{***}$. Consider

$$\begin{aligned} &\left(\frac{d_3}{l^2}\right)\Delta\phi + \left(\frac{E_2\underline{v}}{1 + B_2\underline{v}} - D_3\right)\phi = \underline{\sigma}(l)\phi && \text{in } \Omega_0 \\ &\phi = 0 && \text{on } \partial\Omega_0 \\ &\phi > 0 && \text{in } \Omega_0, \end{aligned} \tag{3.29}$$

where

$$\underline{v} = \begin{cases} \dfrac{\beta\big((E_1 - B_1D_2)\delta[1 - (A_1(E_1 - B_1D_2 - D_2)/C_1(E_1 - B_1D_2))] - D_2\big)}{D_2C_1} & \text{on } \overline{\Omega}^* \\ 0 & \text{on } \Omega_0 \setminus \overline{\Omega}^*. \end{cases}$$

We may apply Lemma B.4 to (3.29) and, moreover, $\lambda_1^+[(E_2\underline{v}/(1 + B_2\underline{v})) - D_3]$ exists as a positive number provided that

$$\frac{E_2\underline{v}}{1 + B_2\underline{v}} - D_3 > 0 \tag{3.30}$$

on an open subset of Ω_0. By the formulation of $\underline{v}$, (3.30) will be satisfied on Ω^* if δ and β are close enough to 1, provided

$$\frac{(E_1 - B_1D_2)[1 - (A_1(E_1 - B_1D_2 - D_2)/C_1(E_1 - B_1D_2))] - D_2}{D_2C_1} > \frac{D_3}{E_2 - B_2D_3}. \tag{3.31}$$

Inequality (3.31) may be rewritten as

$$(E_1 - B_1D_2 - D_2)\left(1 - \frac{A_1}{C_1}\right) > \frac{C_1D_2D_3}{E_2 - B_2D_3}. \tag{3.32}$$

We may now establish our main result.

Theorem 3.7. *Suppose that* (3.8), (3.23) *and* (3.31) *hold. Then* (1.1) *is permanent for* l *sufficiently large.*

PROOF. By (3.30) and (3.31), there is an $l^{****} > l^{***}$ so that

$$l > \sqrt{d_3\lambda_1^+\left[(E_2\underline{v}/(1+B_2\underline{v}) - D_3\right]} \quad \text{if } l > l^{****}.$$

For such an l, $\underline{\sigma}(l) > 0$ by Lemma B.4. Since $l > l_1$, (3.4) is permanent. Let $(u, v, 0) \in \mathcal{A}(l) \times \{0\}$. Then $v > \underline{v}$ on Ω_0. So

$$l > \sqrt{d_3\lambda_1^+\left[(E_2v/(1+B_2v)) - D_3\right]}$$

and σ in (3.14) is positive. Moreover, comparison via integration by parts yields $\sigma > \underline{\sigma}(l) > 0$ if $(u, v, 0) \in \mathcal{A}(l) \times \{0\}$. Consequently, Theorem 3.5 implies that (1.1) is permanent.

Biological interpretation. Recall that in (1.1) the growth rate and carrying capacity of the species on the lowest trophic level are rescaled to equal one. The terms A_1 and A_2 represent the rates at which the predators on the second and third trophic levels find their prey. When predator and prey densities are low, these are the effective rates of predation. At higher densities the predation rates are affected by the time required to handle prey, which is represented by the coefficients B_i, and by the extent to which predators interfere with each other, which is represented by the coefficients C_i. The interference described by the C_i terms is the only mechanism of self-limitation on the second and third trophic levels. The coefficients E_i describe the efficiency of the predators in converting consumed prey into new predators. Finally, the coefficients D_i represent the density-independent death rates for the predators. (These terms do not produce any direct self-limiting effects).

Condition (3.8) says that the net local population growth rate at low densities for the species on the second trophic level must be positive when the species on the first trophic level is at its carrying capacity, which has been scaled to be 1. If the density of the species on the first trophic level is held equal to its carrying capacity, then the maximum density of the species on the second trophic level is given by the expression on the left side of (3.31). Condition (3.31) requires that if the density of the species on the second trophic level were held at that maximum value, then the net local population growth rate at low densities for the species on the third trophic level must be positive. Conditions (3.8) and (3.31) are thus natural. They essentially require that the species on the second and third trophic levels have low enough death rates D_2 and D_3 relative to the size of the ratios E_1/B_1 and E_2/B_2 which describe the maximum rates of conversion of prey into new predators. (The units of E_i are predators/prey; those of B_i are time/prey since the B_i's represent handling times, so the units of E_i/B_i are predators/time). Thus, conditions (3.8) and (3.31) are natural, since for the system (1.1) to be permanent it is necessary that each species in the food chain be efficient enough to sustain itself under ideal conditions.

The condition (3.23) requires that the coefficient C_1, describing the extent that the species on the second trophic level limits its own density via intraspecific interference, must be relatively large compared with the maximum rate of prey consumption described by A_1. It is not clear to us whether this condition is natural or whether it is an artifact of the analysis. Superficially, it seems surprising that self-limitation of the species on the second trophic level would be needed for persistence of the species on the third trophic level, since a higher density of the population on the second level could be expected to benefit the species on the third. However, the self-regulation term associated with C_1 can have a "stabilizing effect" on the interaction between the species on the first two trophic levels by making it less likely that limit cycles can occur, i.e., by preventing the "paradox of enrichment" from occurring. Eliminating the C_1 term might in some cases lead to oscillations in the densities of the populations on the first and second trophic levels, which might cause the density of the population on the second trophic level to temporarily dip below the density needed to sustain the species on the third trophic level. Thus it is possible (but not clear) that some degree of self-regulation by the species on the second trophic level might be needed for persistence of the species on the third. It does not appear to be necessary for the species on the third trophic level to be self-limiting since the coefficient C_2 does not enter into any of the hypotheses required for (1.1) to be permanent on large domains.

Determining whether or not self-limitation on the second trophic level is truly relevant for persistence of the entire food chain is an interesting topic for further research.

4. Conclusions. We have obtained conditions for persistence or extinction in a model for populations at three trophic levels diffusing through a region with a lethal boundary in the case where the links between trophic levels are of Beddington-DeAngelis type. Our essential conclusion is that in those cases where populations at all three levels can persist in a sufficiently large region, there will be a critical size for the region below which no population can persist, and above which the population on the lowest level can persist; there is then a larger critical size below which the population on the second trophic level cannot persist but above which the first and second level will persist together; finally, there is a third still larger critical size below which the third level cannot persist but above which all three levels persist together. Thus, the number of species that will be seen increases with the size of the region. This is consistent with numerous empirical and theoretical studies in ecology, see Cantrell and Cosner [1994]. The empirical study described in Fraser and Grime [1997] gives evidence that the length of food chains may increase in response to increases in primary productivity, that is, increases in the productivity of the species or resource on the lowest trophic level of the food chain. In our models the average density at equilibrium and the intrinsic rate of growth from low densities both increase with patch size for the species on the lowest trophic level if the consumer species on the higher levels are not present. Since these quantities measure primary productivity in one sense or another, our theoretical results are consistent with the empirical observations of Fraser and Grime [1997].

The methods used in this article could also be applied to a Lotka-Voltera model with three trophic levels, provided that the predators have logistic self-limitation terms, and the results would be similar. (Other Lotka-Volterra models are treated in Cantrell and Cosner [1996], Cantrell et al. [1993a], [1993b], [1996]). However, the requirement of predator self-limitation seems necessary for our methods to yield concrete conditions for the persistence of the population at the top trophic level. The reason is that we need quantitative estimates on the asymptotic behavior (equivalently on the location of the positive attractor) of the system describing the first two trophic levels if we want to establish persistence in the third trophic level. It is unclear whether having predator self-limitation is actually necessary or whether it is needed only because of the limitations of our methods. This issue merits further investigation.

APPENDIX

A. Preliminaries. Reaction-diffusion models as dynamical systems: permanence. In this section we shall briefly review ideas from the theory of dynamical systems and describe how they apply to the reaction-diffusion system (1.1). All the topics in this Appendix are discussed in more detail in Avila and Cantrell [1997], Cantrell and Cosner [2001], Cantrell et al. [1993a], [1993b], [1996] and Cantrell and Ward, Jr. [1997] and the references therein; see also Hale and Waltman [1989] and Hutson and Schmitt [1992]. The key idea for us is permanence, i.e., uniform persistence plus dissipativity. Suppose that Y is a complete metric space with $Y = Y_0 \cup \partial Y_0$ for an open set Y_0. We will typically choose Y_0 to be the positive cone in an ordered Banach space. A flow or semiflow on Y under which Y_0 and ∂Y_0 are forward invariant is said to be permanent if it is dissipative and if there is a number $\varepsilon > 0$ such that any trajectory starting in Y_0 will be at least a distance ε from ∂Y_0 for all sufficiently large t. We shall choose Y_0 so that permanence will imply the existence of functions which are positive on Ω and are asymptotic lower bounds on the components of solutions to the model as $t \to \infty$, see Cantrell et al. [1993a], [1993b].

To establish permanence we must choose the space Y and the set Y_0 appropriately and then verify the hypotheses of an abstract result on permanence. A good underlying space for our purposes is $[C_0^1(\overline{\Omega})]^m$ where $m = 1, 2$ or 3 depending on how many components of the system are being considered. It is well known that reaction-diffusion systems with smooth coefficients generate semiflows on such spaces, see Cantrell et al. [1993a], [1993b], Hutson and Schmitt [1992] and Mora [1983]. The reason for working in $[C_0^1(\overline{\Omega}]^m$ is that the model system has homogeneous zero boundary conditions so that no solution could ever be in the interior of the standard positive cone for $[C^0(\overline{\Omega})]^m$. Instead we use the cone $[C_{0+}^1(\overline{\Omega})]^m \equiv \{u \in C_0^1(\overline{\Omega}) : u > 0 \text{ in } \Omega, \partial u/\partial n < 0 \text{ on } \partial\Omega\}^m$. This cone has nonempty interior in $[C_0^1(\overline{\Omega})]^m$. Because every component of the system (1.1) satisfies an equation of the form

$$\frac{\partial y}{\partial t} = D\Delta y + py \tag{A.1}$$

(where p may depend on other components of the system), it follows from the strong maximum principle that, for any component either $y \equiv 0$ or $y > 0$ on Ω and $\partial y/\partial n < 0$ on $\partial\Omega$. Thus, the semiflow generated by (1.1) maps componentwise nonnegative elements of $[C_0^1(\overline{\Omega})]^m$ into $Y \equiv \{u \in [C_0^1(\overline{\Omega})]^m$: for each component u_i of u, either $u_i \in C_{0+}^1(\overline{\Omega})$ or $u_i \equiv 0\}$. We then take $Y_0 = \operatorname{int} Y$ so that by our choice of Y, we have $\partial Y_0 = \{u \in [C_0^1(\overline{\Omega})]^m$: at least one component of u is identically 0, and all nonzero components are in $C_{0+}^1(\overline{\Omega})\}$. The strong maximum principle implies that both Y_0 and ∂Y_0 are forward invariant. To establish dissipativity in Y it suffices to show that nonnegative solutions to the system are uniformly bounded in $[C^0(\overline{\Omega})]^m$ and the system is dissipative on the standard positive cone in $[C^0(\overline{\Omega})]^m$. Dissipativity in $[C_{0+}^1(\overline{\Omega})]^m$ then follows via parabolic regularity. The appropriate formulation of uniform boundedness in $[C^0(\overline{\Omega})]^m$ is that, for any $\beta > 0$, there is a $B(\beta)$ such that all nonnegative solutions of (1.1) whose initial data are bounded by β in the norm of $[C^0(\overline{\Omega})]^m$ must be bounded in the $[C^0(\overline{\Omega})]^m$ norm by $B(\beta)$ for all $t > 0$. For dissipativity there must be a constant $\gamma > 0$ such that the $[C^0(\overline{\Omega})]^m$ norm of any nonnegative solution of (1.1) is bounded by γ for t sufficiently large. A precise statement of the result that $[C^0(\overline{\Omega})]^m$ dissipativity and uniform boundedness imply dissipativity in Y is given in Theorem 2.6 of Cantrell et al. [1993b]. More detailed discussions of why this is true are given in Cantrell et al. [1993a], Hutson and Schmitt [1992]. It will turn out that for (1.1), uniform boundedness and dissipativity in $[C^0(\overline{\Omega})]^m$ can be established via comparison methods based on sub and supersolutions. Once dissipativity is established, it follows from parabolic regularity that the semiflow maps bounded sets in Y into sets that are precompact.

To state the result we will use to establish permanence, we will need a few definitions.

Suppose that $Y = Y_0 \cup \partial Y_0$ is a complete metric space with Y_0 an open subset of Y. Suppose further that a semiflow acts upon Y, leaving both Y_0 and ∂Y_0 forward invariant. An invariant set M for the semiflow is said to be *isolated* if it has a neighborhood U such that M is the maximal invariant subset of U. Let $\omega(\partial Y_0)$ denote the union of the sets

$\omega(u)$ over $u \in \partial Y_0$. (This differs from the standard definition of the ω-limit set of a set but is more convenient for our purposes; see Hale and Waltman [1989] for a discussion). The set $\omega(\partial Y_0)$ is said to be *isolated* if it has a covering $M = \cup_{k=1}^{N} M_k$ of pairwise disjoint sets M_k which are isolated and invariant with respect to both the semiflow on ∂Y_0 and the semiflow on $Y = Y_0 \cup \partial Y_0$. The covering M is then called an *isolated covering.* Suppose that N_1 and N_2 are isolated invariant sets (not necessarily distinct) for some semiflow. The set N_1 is said to be *chained* to N_2 (denoted $N_1 \to N_2$) if there exists $u \notin N_1 \cup N_2$ with $u \in W^u(N_1) \cap W^s(N_2)$. A finite sequence $N_1, N_2, \ldots, N_k$ of isolated invariant sets is a *chain* if $N_1 \to N_2 \to N_3 \cdots \to N_k$. (This is possible for $k = 1$ if $N_1 \to N_1$). The chain is called a *cycle* if $N_k = N_1$. The set $\omega(\partial Y_0)$ is said to be *acyclic* if there exists an isolated covering $\cup_{k=1}^{N} M_k$ such that no subset of $\{M_k\}$ is a cycle. We can now state the theorem that will be used to establish permanence.

Theorem A.1 (Hale and Waltman [1989]). *Suppose that Y is a complete metric space with $Y = Y_0 \cup \partial Y_0$ where Y_0 is open. Suppose that a semiflow on Y leaves both Y_0 and ∂Y_0 forward invariant, maps bounded sets in Y to precompact sets for $t > 0$, and is dissipative. If, in addition,*

i) *$\omega(\partial Y_0)$ is isolated and acyclic*

and

ii) *$W^s(M_k) \cap Y_0 = \phi$ for all k,*

then the semiflow is permanent, i.e., there exists an $\varepsilon > 0$ such that any trajectory with initial data in Y_0 will be bounded away from ∂Y_0 by a distance greater than ε for t sufficiently large.

Remarks. The notation used here is different from that of Hale and Waltman [1989] because of the definition we have given for $\omega(\partial Y_0)$. The key issues in applying the theorem are establishing dissipativity and verifying (i) and (ii). The other hypotheses follow from the general theory of parabolic equations and the structure of the system as described in (A.1). We have already commented on dissipativity. To establish (i) we will need to analyze in some detail the dynamics of the subsystems which arise when one or more components of the original system are identically zero. To establish (ii) we shall examine eigenvalue problems associated with equations of the form (A.1). Suppose that $M_k \subseteq \partial Y_0$ and that y in (A.1) corresponds to a component of the system which is identically zero on M_k. Suppose that for all $u \in M_k$, the coefficient p in (A.1) evaluated at u is bounded below by $p_k(x)$ and that the principal eigenvalue of

$$\text{(A.2)} \qquad \begin{aligned} D\Delta\phi + p_k(x)\phi &= \sigma\phi \quad \text{in } \Omega \\ \phi &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

is positive. In that case a solution y of (A.1) which is sufficiently near M_k will be a supersolution for

$$\text{(A.3)} \qquad \begin{aligned} \frac{\partial z}{\partial t} &= D\Delta z + p_k(x)z \quad \text{in } \Omega \\ z &= 0 \qquad\qquad\qquad \text{on } \partial\Omega, \end{aligned}$$

but (A.3) has solutions of the form $\delta e^{\sigma t}\phi(x)$ which are arbitrarily small initially and grow in time since $\sigma > 0$. These solutions can be used in a comparison argument to show that if $y > 0$ initially, then y is bounded away from M_k. That in turn precludes having $y > 0$ in $W^s(M_k)$, and if we can treat all the components that are zero on M_k in this way, we can establish (ii). This sort of argument is developed in some detail in Cantrell et al. [1993a], [1993b]; see, for example Lemma 4.2 of Cantrell et al. [1993b] and the related discussion.

B. Results on single equations. In this section we collect some basic facts regarding the equation

$$\text{(B.1)} \qquad v_t = \mu\Delta v + \left(\frac{Ah(x)}{1 + Bh(x) + Cv} - D\right)v \quad \text{in } \Omega_0 \times (0, \infty)$$

subject to the homogeneous boundary condition

$$\text{(B.2)} \qquad v = 0 \quad \text{on } \partial\Omega_0 \times (0, \infty).$$

The analogous results for the diffusive logistic equation are derived in Cantrell and Cosner [1989], [1991]. In (B.1) μ, A, B, C and D are positive constants and $h(x)$ is a continuously differentiable function on $\overline{\Omega}_0$ which is positive in Ω_0. If $\bar{h} = \max_{\overline{\Omega}_0} h(x)$ and $A\bar{h}/(1 +$

$B\bar{h}) \le D$, then it follows from Hess and Kato [1980] or Manes and Micheletti [1973] that 0 is the only nonnegative equilibrium solution to (B.1)–(B.2). It follows as in Section 2 of Cantrell and Cosner [1989] that any solution $v(x,t)$ to (B.1)–(B.2) corresponding to nonnegative initial data when viewed as a map from $(0,\infty)$ to $C_0^1(\overline{\Omega}_0)$ converges to 0 as $t \to \infty$. As a result we make the additional requirement upon h that

$$\text{(B.3)} \qquad \frac{Ah(x_0)}{1+Bh(x_0)} > D$$

for some $x_0 \in \Omega_0$. Under assumption (B.3), it follows from Hess and Kato [1980] or Manes and Micheletti [1973] that the linear eigenvalue problem

$$\text{(B.4)} \qquad \begin{aligned} -\Delta z &= \lambda\left(\frac{Ah(x)}{1+Bh(x)} - D\right)z \quad \text{in } \Omega_0 \\ z &= 0 \quad \text{on } \partial\Omega_0 \end{aligned}$$

admits a unique positive eigenvalue $\lambda_1 = \lambda_1^+[Ah(x)/(1+Bh(x)) - D]$ for which (B.4) has a solution z which is of one sign in Ω_0. (λ_1 is referred to as the positive principal eigenvalue for (B.4). It follows from DeFigueiredo [1982] that $\lambda_1^+[Ah(x)/(1+Bh(x))-D]$ is continuous in h, relative to the $C^1(\overline{\Omega}_0)$ topology). Moreover, under assumption (B.3), if we define $f(x,v)$ by

$$f(x,v) = \frac{Ah(x)}{1+Bh(x)+Cv} - D$$

it is easy to verify that $f(x,v)$ satisfies

(i) $f(x_0,0) > 0$ for some $x_0 \in \Omega_0$;

(ii) $(\partial f/\partial v)(x,v) < 0$ for $x \in \Omega_0$ and $v > 0$;

(iii) $f(x,v) \le 0$ for $x \in \overline{\Omega}$ and $v \ge [(A-DB)\bar{h} - D]/Cd$.

Theorem 2.3 of Cantrell and Cosner [1989] is now applicable and enables us to describe the dynamics for (B.1)–(B.2) as follows.

Theorem B.1. *Consider* (B.1)–(B.2) *and assume that* (B.3) *holds. Let* $\lambda_1^+[Ah(x)/(1+Bh(x))-D]$ *denote the positive principal eigenvalue* *for* (B.4). *Then* (B.1)–(B.2) *admits a positive equilibrium solution if and only if*

$$\mu \in \left(0, \left(\lambda_1^+\left(\frac{Ah(x)}{1+Bh(x)} - D\right)\right)^{-1}\right).$$

Moreover, we have

(i) *if*

$$\mu \in \left(0, \left(\lambda_1^+\left(\frac{Ah(x)}{1+Bh(x)} - D\right)\right)^{-1}\right),$$

there is precisely one positive equilibrium solution to (B.1)–(B.2) *and it is globally asymptotically stable with respect to nonnegative nontrivial solutions of* (B.1)–(B.2) *when viewed as a steady-state to* (B.1)–(B.2).

(ii) *If*

$$\mu \geq \left(\lambda_1^+\left(\frac{Ah(x)}{1+Bh(x)} - D\right)\right)^{-1},$$

the 0 *solution to* (B.1)–(B.2) *is globally asymptotically stable with respect to nonnegative solutions of* (B.1)–(B.2).

Suppose now that

$$\mu \in \left(0, \left(\lambda_1^+\left(\frac{Ah(x)}{1+Bh(x)} - D\right)\right)^{-1}\right),$$

and let $v^* = v^*(h,\mu)$ denote the globally attracting positive equilibrium of (B.1)–(B.2) whose existence is guaranteed by Theorem B.1. Then v^* satisfies

$$\text{(B.5)} \qquad \begin{aligned} -\mu\Delta w &= \left(\frac{Ah(x)}{1+Bh(x)+Cw} - D\right)w \quad \text{in } \Omega_0 \\ w &= 0 \qquad\qquad\qquad\qquad\qquad \text{on } \partial\Omega_0. \end{aligned}$$

We have the following monotonicity result on $v^*(h,\mu)$.

Theorem B.2. *Suppose* h_1 *and* h_2 *are continuously differentiable on* $\overline{\Omega}_0$ *with* $0 < h_1(x) \leq h_2(x)$ *on* Ω_0, *and suppose that* h_1 *(and hence* h_2*) satisfy* (B.3). *Then*

(i)

$$\lambda_1^+\left(\frac{Ah_1(x)}{1+Bh_1(x)} - D\right) \geq \lambda_1^+\left(\frac{Ah_2(x)}{1+Bh_2(x)} - D\right)$$

with strict inequality whenever $h_1 \not\equiv h_2$.

(ii) *If*

$$\mu \in \left(0, \left(\lambda_1^+\left(\frac{Ah_1(x)}{1+Bh_1(x)} - D\right)\right)^{-1}\right),$$

then $v^*(h_1, \mu) \leq v^*(h_2, \mu)$ *with strict inequality in* Ω_0 *whenever* $h_1 \not\equiv h_2$.

(iii) *If* $\bar{h}_i$ *denotes* $\max_{\overline{\Omega}_0} h_i(x)$ *and*

$$\mu_1 \in \left(0, \left(\lambda_1^+\left(\frac{A\bar{h}_1}{1+B\bar{h}_1} - D\right)\right)^{-1}\right),$$

then for any $\mu_2 \in (0, \mu_1]$, $v^*(\bar{h}_1, \mu_1) \leq v^*(\bar{h}_2, \mu_2)$ *with strict inequality in* Ω_0 *if* $\bar{h}_1 < \bar{h}_2$ *or* $\mu_2 < \mu_1$.

PROOF. Part (i) is known from Hess and Kato [1980] or Manes and Micheletti [1973]. K is an upper solution for (B.5) for any constant $K \geq [(A - BD)\bar{h} - D]/CD$, and the maximum principle implies that $v^*(h, \mu) \leq [(A-BD)\bar{h} - D]/CD$ on $\overline{\Omega}_0$. As a result, parts (ii) and (iii) follow directly from the method of upper and lower solutions.

Applying a singular perturbation result of DeSanti [1986] as formulated in Cantrell and Cosner [1989], we may also track the behavior of $v^*(\bar{h}, \mu)$ as μ tends to 0. Our result is as follows.

Theorem B.3. *Suppose that* h *satisfies* (B.3) *and that*

$$\varepsilon < \sqrt{\left(\lambda_1^+\left(\frac{A\bar{h}}{1+B\bar{h}} - D\right)\right)^{-1}}.$$

Consider (B.5) *for* $\bar{h}$ *with* $\mu = \varepsilon^2$, *i.e.,*

$$\begin{aligned} -\varepsilon^2 \Delta w &= \left(\frac{A\bar{h}}{1+B\bar{h}+Cw} - D\right) w \quad && \text{in } \Omega_0 \\ w &= 0 && \text{on } \partial\Omega_0. \end{aligned}$$

Then if Ω' *is any subdomain of* Ω_0 *with* $\overline{\Omega}' \subseteq \Omega_0$, $v^*(\bar{h}, \varepsilon^2)$ *converges uniformly on* $\overline{\Omega}'$ *to the solution of* $[A\bar{h}/(1+B\bar{h}+Cw)] - D = 0$ *as* ε *tends to* 0; *i.e.,* $v^*(\bar{h}, \varepsilon^2)$ *converges uniformly on* $\overline{\Omega}'$ *to* $[(A-BD)\bar{h} - D]/CD$.

PROOF. Let $v_0 = [(A - BD)\bar{h} - D]/CD$ and set $z = v_0 - v^*(\bar{h}, \varepsilon^2)$. Then z satisfies

$$\text{(B.6)} \qquad \begin{aligned} -\varepsilon^2 \Delta z &= \frac{A\bar{h}(z - v_0)}{1 + B\bar{h} + Cv_0 - Cz} - D(z - v_0) \quad \text{in } \Omega \\ z &= v_0 \quad \text{on } \partial\Omega. \end{aligned}$$

We apply the aforementioned singular perturbation result (Lemma 4.6 in Cantrell and Cosner [1989]) to show that z tends to 0. It follows immediately that $v^*(\bar{h}, \varepsilon^2)$ tends to v_0. In order to apply the result, we must show that the right side of (B.6), which we denote by $k(z)$, satisfies

(i) $k(0) = 0$

(ii) $k'(0) < 0$

and

(iii) $K(w) = \int_0^w k(s)\, ds < 0$ if $w \in (0, v_0]$.

Requirement (i) is immediate from the definition of v_0. For (ii), note that

$$k'(z) = \frac{A\bar{h}(1 + B\bar{h})}{(1 + B\bar{h} + Cv_0 - Cz)^2} - D,$$

so that

$$k'(0) = \frac{A\bar{h}(1 + B\bar{h})}{(1 + B\bar{h} + Cv_0)^2} - D < \frac{A\bar{h}}{1 + B\bar{h} + Cv_0} - D = 0.$$

Finally, note that (iii) holds provided $k(z) < 0$ if $z \in (0, v_0)$. Since

$$k(z) = -(v_0 - z)\left(\frac{A\bar{h}}{1 + B\bar{h} + C(v_0 - z)} - D\right)$$

and

$$\frac{A\bar{h}}{1 + B\bar{h} + Cw} > D \quad \text{for } w \in (0, v_0),$$

$k(z) < 0$, when $z \in (0, v_0)$ as required. Consequently (iii) holds and we may apply Lemma 4.6 of Cantrell and Cosner [1989] to establish our claim.

We conclude with a lemma which establishes the relationship between the two eigenvalue problems which arise in our analysis.

Lemma B.4. *Let $\lambda_1^+(p(x))$ be the positive principal eigenvalue of*

$$\text{(B.7)} \qquad \begin{aligned} -\Delta\phi &= \lambda p(x)\phi \quad && \text{in } \Omega \\ \phi &= 0 && \text{on } \partial\Omega, \end{aligned}$$

and let $\sigma(d, p(x))$ denote the principal eigenvalue of

$$\text{(B.8)} \qquad \begin{aligned} d\Delta\psi + p(x)\psi &= \sigma\psi \quad && \text{in } \Omega \\ \psi &= 0 && \text{on } \partial\Omega. \end{aligned}$$

We have $\sigma_1(d, p(x)) > 0$ if and only if $\lambda_1^+(p(x)) < 1/d$ and $\sigma_1(d, p(x)) = 0$ if and only if $\lambda_1^+(p(x)) = 1/d$.

PROOF. The analogous result for the case of Neumann boundary conditions is proved in Senn [1983]. The proof extends to the Dirichlet case with only a few obvious modifications, see also Cantrell and Cosner [1991], page 1049. We immediately obtain the following.

Corollary B.5. *If $\sigma_1(\mu, [Ah(x)/(1+Bh(x))] - D) > 0$, then alternative* (i) *in Theorem* B.1 *holds. If $\sigma_1(\mu, [Ah(x)/(1+Bh(x))] - D) \leq 0$, then alternative* (ii) *in Theorem* B.1 *holds.*

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