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PRACTICAL PERSISTENCE IN DIFFUSIVE FOOD CHAIN MODELS

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1. Introduction. Our aim in this article is to derive asymptotic upper and lower bounds on the components of solutions to a diffusive model for a three trophic level food chain. The particular food chain that we have chosen to examine embodies a general form of predator functional response to prey introduced by Beddington [1975] and DeAngelis, Goldstein and O'Neill [1975]. This form of functional response is of significance in large part because it can be derived from mechanistic considerations of mutual interference by foraging predators, as in Beddington [1975] or Ruxton, Gurney and De Roos [1992].

While there is a substantial body of work examining diffusive two species predator-prey models, particularly those in which the predation interaction is of Lotka-Volterra form, there have been to date few studies of diffusive three trophic level models. Moreover, the few such studies which have appeared, such as Feng [1994], have concentrated on Lotka-Volterra interactions. Consequently, we believe that an examination of a diffusive three trophic level model with realistic interactions between trophic levels is in order. We also believe that persistence theory techniques such as those we have been developing in Cantrell and Cosner [1996], for example, are well-suited to such an examination.

By appropriate rescalings, the class of models which we shall analyze

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can be reduced to the form:

$$
\begin{aligned}
\frac{\partial u}{\partial t} &= \mu_1 \Delta u + u(1-u) - \frac{A_1 uv}{1+B_1 u + C_1 v} \\
\frac{\partial v}{\partial t} &= \mu_2 \Delta v + \frac{A_1 uv}{1+B_1 u + C_1 v} - \frac{A_2 vw}{1+B_2 v + C_2 w} - D_{21} v \qquad (1.1) \\
\frac{\partial w}{\partial t} &= \mu_3 \Delta w + \frac{A_2 vw}{1+B_2 v + C_2 w} - D_{31} w, \quad \text{in } \Omega \times (0,\infty)
\end{aligned}
$$

with

$$u = v = w = 0 \quad \text{on } \partial\Omega \times (0,\infty).$$

Here Ω denotes the bounded spatial habitat shared by the species in question. The parameters in (1.1) are constants, with μ_1, μ_2, μ_3 diffusion rates and D_{21}, D_{31} predation death rates in the absence of prey. The parameters in the intertrophic level interactions, roughly speaking, represent maximal consumption rate of prey by predator (A_1 and A_2), the rate at which predators reach satiation as prey abundance increases (B_1 and B_2), and the extent of mutual interference between foraging predators (C_1 and C_2).

The general predator-prey structure of (1.1) does not generate a monotone flow in any reasonable solution space. However, the powerful notion of monotonicity can be employed effectively to provide asymptotic bounds on the components of solutions to (1.1) provided that, as in Cantrell and Cosner [1996], we examine the equations of (1.1) one at a time and compare them with solutions to boundary value problems for single parabolic equations. We begin by obtaining an asymptotic upper bound for the lowest trophic level, and then move up the food chain obtaining asymptotic upper bounds. Once we have asymptotic upper bounds on the components of a solution to (1.1), we repeat the process obtaining asymptotic lower bounds.

Finally, two additional observations are in order at this point. First, this kind of asymptotic analysis carries over to modelling contexts other than reaction-diffusion systems, as in Cosner [1996]. Second, this approach can be refined as in Cantrell and Cosner [to appear] to obtain bounds on entire trajectories. However, we shall not pursue either topic in this article.

2. Preliminaries. As noted in the preceding section, the asymptotic upper, respectively lower, bounds we obtain on the components of the solutions to (1.1) derive from viewing the components individually as lower, respectively upper, solutions to suitable single equation parabolic boundary value problems. In this context a single equation parabolic boundary value problem is "suitable" if it admits a globally attracting positive equilibrium. If such is the case, then the method of upper and lower solutions can be employed to obtain the desired asymptotic bounds on the components of the solutions to (1.1). The conditions for such "suitability" that we shall employ are given in the following result, which was established in Cantrell and Cosner [1989], see also Cantrell, Cosner and Hutson [1993], Hess [1977, 1991].

THEOREM 2.1. *Suppose that* $f : \overline{\Omega} \times \mathbf{R} \to \mathbf{R}$ *is* C^1. *Consider the parabolic boundary value problem*

$$\begin{aligned} u_t &= \mu \Delta u + u f(x,u) \quad \text{in } \Omega \times (0,\infty) \\ u &= 0 \quad \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{2.1}$$

and the related linear elliptic eigenvalue problem

$$\begin{aligned} \mu \Delta z + f(x,0) z &= \sigma z \quad \text{in } \Omega \\ z &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.2}$$

Assume, in addition,

(i) $(\partial f/\partial u)(x,u) \leq 0$ *for* $x \in \overline{\Omega}$ *and* $u \geq 0$.

(ii) *There is a* $K > 0$ *so that* $f(x,u) \leq 0$ *for* $x \in \overline{\Omega}$ *and* $u \geq K$.

Let σ_1 *denote the unique real value for which* (2.2) *admits a solution* z *with* $z > 0$ *in* Ω. *Then*

(a) *If* $\sigma_1 > 0$, (2.1) *admits an equilibrium solution* $u^*(x)$ *with* $u^*(x) > 0$ *for* $x \in \Omega$. *Moreover, any solution* $u(x,t)$ *of* (2.1) *with* $u(x,0) > 0$ *has the property that* $\|u(\cdot,t) - u^*(\cdot)\|_{C^{1+\alpha}(\overline{\Omega})}$ *tends to 0 as* $t \to \infty$.

(b) *If* $\sigma_1 \leq 0$, *any solution* $u(x,t)$ *of* (2.1) *with* $u(x,0) \geq 0$ *is such that* $\|u(\cdot,t)\|_{C^{1+\alpha}(\overline{\Omega})}$ *tends to 0 as* $t \to \infty$.

REMARK. Alternative (b) of Theorem 2.1 always obtains if $f(x,0) \leq 0$ on $\overline{\Omega}$. If, however, $f(x_0,0) > 0$ for some $x_0 \in \Omega$, either alternative is possible and, moreover, which alternative obtains depends upon the related eigenvalue problem

$$(2.3) \qquad \begin{aligned} -\Delta w &= \lambda f(x,0) w \quad \text{in } \Omega \\ w &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

In this situation, (2.3) admits a unique positive principal eigenvalue $\lambda_1(f(x,0))$, i.e., a value $\lambda_1(f(x,0)) > 0$ for which (2.3) admits a solution w with $w(x) > 0$ in Ω. It is shown in Cantrell, Cosner and Hutson [1993] that if $f(x_0, 0) > 0$ for some $x_0 \in \Omega$, then $\sigma_1 > 0$ if and only if $\mu < [\lambda_1(f(x,0))]^{-1}$.

Once a suitable parabolic boundary value problem for a single equation is identified, the desired asymptotic upper or lower bounds arise via a comparison based on the following well-known result:

THEOREM 2.2. *Suppose* $f : \overline{\Omega} \times \mathbf{R} \to \mathbf{R}$ *is* C^1 *and that* $\bar{u}, \underline{u} : \overline{\Omega} \times [0,T] \to \mathbf{R}$ *are* C^2 *with*

$$\begin{aligned} &\bar{u}_t \geq \mu \Delta \bar{u} + \bar{u} f(x, \bar{u}) \quad \text{on } \Omega \times (0,T] \\ &\bar{u} \geq 0 \quad \text{on } \partial\Omega \times (0,T] \end{aligned}$$

and

$$\begin{aligned} &\underline{u}_t \leq \mu \Delta \underline{u} + \underline{u} f(x, \underline{u}) \quad \text{on } \Omega \times (0,T] \\ &\underline{u} \leq 0 \quad \text{on } \partial\Omega \times (0,T]. \end{aligned}$$

Then $\underline{u}(x,0) \leq \bar{u}(x,0)$ *for* $x \in \overline{\Omega}$ *implies* $\underline{u}(x,t) \leq \bar{u}(x,t)$ *for* $x \in \overline{\Omega}$ *and* $t \in (0,T]$. *Moreover, either* $\underline{u}(x,t) \equiv \bar{u}(x,t)$ *for* $x \in \overline{\Omega}$ *and* $t \in (0,T]$ *or* $\underline{u}(x,t) < \bar{u}(x,t)$ *for* $x \in \Omega$ *and* $t \in (0,T]$.

3. Main results. We may employ the ideas of the previous section to obtain asymptotic upper and lower bounds on the components u, v and w of (1.1). We begin with an asymptotic upper bound on u. Since

$$u_t = \mu_1 \Delta u + u(1-u) - \frac{A_1 uv}{1 + B_1 u + C_1 v}$$

on $\Omega \times (0,\infty)$ with $u = 0$ on $\partial\Omega$, u is a lower solution for the parabolic boundary-value problem

$$(3.1) \qquad \begin{aligned} y_t &= \mu_1 \Delta y + y(1-y) \quad \text{in } \Omega \times (0,\infty) \\ y &= 0 \quad \text{on } \partial\Omega \times (0,\infty). \end{aligned}$$

Note that (3.1) is of the form (2.1) with $f(x,y) = 1 - y$, so that the conditions of Theorem 2.1 are met. Consequently, provided $\mu_1 < 1/\lambda_1(1)$, (3.1) admits a globally attracting positive equilibrium solution y^*, which by the maximum principle (Protter & Weinberger [1967]) is ≤ 1 on $\overline{\Omega}$. Let $(u(x,t), v(x,t), w(x,t))$ be a solution to (1.1) with $u(x,0) \not\equiv 0$ on $\overline{\Omega}$. Let $\overline{y}$ denote the solution to (3.1) with $\overline{y}(x,0) \equiv u(x,0)$. Let $\varepsilon > 0$ be given. Theorem 2.1 implies there is a $\overline{t}_\varepsilon > 0$ so that if $t > \overline{t}_\varepsilon$, $\|\overline{y}(\cdot,t) - y^*(\cdot)\|_{C^{1+\alpha}(\overline{\Omega})} < \varepsilon$. It follows that if $t > \overline{t}_\varepsilon$, $|\overline{y}(x,t) - y^*(x)| < \varepsilon$ for $x \in \overline{\Omega}$ so that $\overline{y}(x,t) < y^*(x) + \varepsilon \leq 1 + \varepsilon$. Theorem 2.2 now applies (with $\overline{y}$ playing the role of upper solution) to give

$$u(x,t) \leq \overline{y}(x,t) < 1 + \varepsilon$$

for $x \in \overline{\Omega}$ and $t > \overline{t}_\varepsilon$.

Let $(u(x,t), v(x,t), w(x,t))$ be as above. We now use the above estimate on u to obtain an asymptotic upper bound on v. Since

$$v_t = \mu_2 \Delta v + \frac{A_1 uv}{1 + B_1 u + C_1 v} - \frac{A_2 vw}{1 + B_2 v + C_2 w} - D_{21} v$$

on $\Omega \times (0,\infty)$, v is a lower solution for the parabolic problem

$$y_t = \mu_2 \Delta y + \frac{A_1(1+\varepsilon)y}{1 + B_1(1+\varepsilon) + C_1 y} - D_{21} y \tag{3.2}$$

on $\Omega \times (\overline{t}_\varepsilon, \infty)$ with $y = 0$ on $\partial\Omega \times (\overline{t}_\varepsilon, \infty)$. That such is the case follows from the estimate $u(x,t) < 1 + \varepsilon$ for $t > \overline{t}_\varepsilon$ and the fact that $A_1 uv/(1 + B_1 u + Cv)$ is increasing in u. Note that (3.2) is of the form (2.1) with

$$f(x,y) = \frac{A_1(1+\varepsilon)}{1 + B_1(1+\varepsilon) + C_1 y} - D_{21},$$

so that the conditions (i) and (ii) of Theorem 2.1 are met. Consequently, all solutions to (3.2) with $y(x, \overline{t}_\varepsilon) > 0$ converge to a unique positive equilibrium y_ε^{**} provided $\overline{\sigma}_{2,\varepsilon}$ is positive when the eigenvalue problem

$$\begin{aligned} \mu_2 \Delta \phi + \phi \left(\frac{A_1(1+\varepsilon)}{1 + B_1(1+\varepsilon)} - D_{21} \right) &= \overline{\sigma}_{2,\varepsilon} \phi \quad \text{in } \Omega \\ \phi &= 0 \quad \text{on } \partial\Omega \end{aligned} \tag{3.3}$$

admits an eigenfunction ϕ which is positive on Ω. Such will be the case for all $\varepsilon > 0$ sufficiently small if

$$\frac{A_1/(1+B_1) - D_{21} - \bar{\sigma}_{2,0}}{\mu_2} = \lambda_1(1)$$

implies $\bar{\sigma}_{2,0} > 0$. *A priori*, this requires $A_1/(1+B_1) > D_{21}$. In such a case, $\bar{\sigma}_{2,0} > 0$ is equivalent to

$$\mu_2 < \left(\frac{A_1}{1+B_1} - D_{21}\right)\Big/\lambda_1(1). \tag{3.4}$$

Let us assume (3.4) and denote the resulting positive equilibrium to

$$\begin{aligned} \rho_t &= \mu_2 \Delta \rho + \left(\frac{A_1}{1+B_1+C_1\rho} - D_{21}\right)\rho \quad \text{in } \Omega \times (0,\infty) \\ \rho &= 0 \quad \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{3.5}$$

by y_0^{**}. The maximum principle guarantees that $y_0^{**}(x) \leq \bar{\rho}$, where $\bar{\rho}$ is the root of

$$\frac{A_1}{1+B_1+C_1\rho} - D_{21} = 0,$$

namely,

$$\bar{\rho} = \frac{(A_1 - B_1 D_{21}) - D_{21}}{D_{21} C_1}.$$

That $\varepsilon \to y_\varepsilon^{**}$ is a continuous mapping from $[0,\infty)$ into $C^{1+\alpha}(\overline{\Omega})$ can be argued as in the proof of Theorem 2.2 of Cantrell and Cosner [1989]. Hence, if $\eta > 0$ is given,

$$y_\varepsilon^{**}(x) < \left(1 + \frac{\eta}{2}\right)\left[\frac{(A_1 - B_1 D_{21}) - D_{21}}{D_{21} C_1}\right]$$

for $\varepsilon \in (0,\eta)$ and sufficiently small. Suppose that $\eta > 0$ is so given, and choose an appropriate $\varepsilon = \varepsilon(\eta)$. An application of Theorem 2.2 now guarantees that there is a time $\bar{\bar{t}}_{\varepsilon(\eta)} > \bar{t}_{\varepsilon(\eta)}$ so that

$$v(x,t) < (1+\eta)\left[\frac{(A_1 - B_1 D_{21}) - D_{21}}{D_{21} C_1}\right]$$

for $x \in \overline{\Omega}$ and $t > \bar{\bar{t}}_{\varepsilon(\eta)}$. As a consequence, if $A_1 > (1 + B_1)D_{21}$ and (3.4) obtains, there is a $\bar{t}_\eta > 0$ so that

$$\begin{aligned} &u(x,t) < 1+\eta \\ &v(x,t) < (1+\eta)\left(\frac{(A_1 - B_1D_{21}) - D_{21}}{D_{21}C_1}\right) \end{aligned} \tag{3.6}$$

for $x \in \overline{\Omega}$ and $t > \bar{t}_\eta$.

The estimates (3.6) can now be used to obtain an asymptotic upper bound on w. Since

$$w_t = \mu_3 \Delta w + \frac{A_2 v w}{1 + B_2 v + C_2 w} - D_{31} w$$

on $\Omega \times (0, \infty)$ with $w = 0$ on $\partial\Omega \times (0, \infty)$, (3.6) implies that w is a lower solution for

$$\begin{aligned} y_t = \mu_3 \Delta y + &\frac{A_2(1+\eta)\left[\frac{((A_1 - B_1 D_{21}) - D_{21})}{(D_{21}C_1)}\right] y}{1 + B_2(1+\eta)\left[\frac{((A_1 - B_1 D_{21}) - D_{21})}{(D_{21}C_1)}\right] + C_2 y} - D_{31} y \\ &\text{in } \Omega \times (\bar{t}_\eta, \infty) \\ &y = 0 \quad \text{on } \partial\Omega \times (\bar{t}_\eta, \infty). \end{aligned} \tag{3.7}$$

The model problem (3.7) has the property that all solutions corresponding to nonnegative, nontrivial initial data converge over time to a unique positive equilibrium y_η^{***} so long as $\bar{\sigma}_{3,\eta}$ is positive when

$$\begin{aligned} \mu_3 \Delta \phi + \left(\frac{(1+\eta)A_2[(A_1 - B_1 D_{21}) - D_{21}]}{D_{21}C_1 + (1+\eta)B_2[(A_1 - B_1 D_{21}) - D_{21}]} - D_{31}\right)\phi &= \bar{\sigma}_{3,\eta}\phi \\ \text{in } \Omega \\ \phi = 0 \quad \text{on } \partial\Omega \end{aligned} \tag{3.8}$$

admits an eigenfunction $\phi > 0$. In (3.8), ϕ can be taken as ϕ_1, the positive eigenfunction corresponding to $\lambda_1(1)$. Consequently,

$$\bar{\sigma}_{3,\eta} = \frac{(1+\eta)A_2[(A_1 - B_1 D_{21}) - D_{21}]}{D_{21}C_1 + (1+\eta)B_2[(A_1 - B_1 D_{21}) - D_{21}]} - D_{31} - \mu_3 \lambda_1(1).$$

The eigenvalue $\bar{\sigma}_{3,\eta}$ will be positive for all $\eta > 0$ sufficiently small if $\bar{\sigma}_{3,0}$ is positive. *A priori*, this requires $[A_2 - B_2D_{31}][(A_1 - B_1D_{21}) - D_{21}] - D_{31}D_{21}C_1 > 0$, and in such a case, $\bar{\sigma}_{3,0} > 0$ is equivalent to

$$\mu_3 < \left\{ \frac{A_2[(A_1 - B_1D_{21}) - D_{21}]}{D_{21}C_1 + B_2[(A_1 - B_1D_{21}) - D_{21}]} - D_{31} \right\} \Big/ \lambda_1(1). \tag{3.9}$$

The maximum principle guarantees that $y_0^{***} \leq \bar{\rho}$ where $\bar{\rho}$ is the root of

$$\frac{A_2[(A_1 - B_1D_{21}) - D_{21}]}{D_{21}C_1 + B_2[(A_1 - B_1D_{21}) - D_{21}] + C_2D_{21}C_1\rho} - D_{31} = 0,$$

namely,

$$\bar{\rho} = \frac{[A_2 - B_2D_{31}][(A_1 - B_1D_{21}) - D_{21}] - D_{31}D_{21}C_1}{D_{31}C_2D_{21}C_1}.$$

Arguing as before, we may establish the following result.

THEOREM 3.1. *Let (u, v, w) be a componentwise nonnegative solution to (1.1). Assume that $[A_1 - B_1D_{21}] - D_{21} > 0$ and that $[A_2 - B_2D_{31}][(A_1 - B_1D_{21}) - D_{21}] - D_{31}D_{21}C_1 > 0$. Then if*

$$\mu_1 < 1/\lambda_1(1)$$
$$\mu_2 < \left[\frac{A_1}{1 + B_1} - D_{21}\right] \Big/ \lambda_1(1),$$
$$\mu_3 < \left[\left(\frac{A_2[(A_1 - B_1D_{21}) - D_{21}]}{D_{21}C_1 + B_2[(A_1 - B_1D_{21}) - D_{21}]}\right) - D_{31}\right] \Big/ \lambda_1(1),$$

and $\gamma > 0$ is given, there is a $\bar{t}_\gamma > 0$ so that

$$u(x,t) < 1 + \gamma$$
$$v(x,t) < (1 + \gamma)\left[\frac{(A_1 - B_1D_{21}) - D_{21}}{D_{21}C_1}\right]$$
$$w(x,t) < (1 + \gamma)\left[\frac{(A_2 - B_2D_{31})[(A_1 - B_1D_{21}) - D_{21}] - D_{31}D_{21}C_1}{D_{31}C_2D_{21}C_1}\right]$$

for $x \in \overline{\Omega}$ and $t \in (\bar{t}_\gamma, \infty)$.

We now turn to asymptotic lower bounds. Once again, let $(u(x,t), v(x,t), w(x,t))$ be a componentwise nonnegative solution to (1.1) with $u(x,0) \not\equiv 0$. Since

$$u_t = \mu_1 \Delta u + u(1-u) - \frac{A_1 uv}{1 + B_1 u + C_1 v}$$

in $\Omega \times (0,\infty)$ with $u = 0$ on $\partial\Omega \times (0,\infty)$, and since $A_1 uv/(1+B_1 u + C_1 v)$ increases in v with $A_1 uv/(1 + B_1 u + C_1 v) \leq A_1 u/C_1$ for all $v \geq 0$, we must have that u is an upper solution for the parabolic boundary-value problem

$$\begin{aligned} z_t &= \mu_1 \Delta z + z\left(1 - \frac{A_1}{C_1} - z\right) \quad \text{in } \Omega \times (0,\infty) \\ z &= 0 \quad \text{on } \partial\Omega \times (0,\infty). \end{aligned} \tag{3.10}$$

In this case (3.10) is of the form (2.1) with $f(x,z) = 1 - A_1/C_1 - z$, and the conditions of Theorem 2.1 are met. Consequently, all solutions to (3.10) with $z(x,0) \overset{>}{\not\equiv} 0$ converge to a unique positive equilibrium ψ_* provided $\underline{\sigma}_1$ is positive when the eigenvalue problem

$$\begin{aligned} \mu_1 \Delta \phi + \phi\left(1 - \frac{A_1}{C_1}\right) &= \underline{\sigma}_1 \phi \quad \text{in } \Omega \\ \phi &= 0 \quad \text{on } \partial\Omega \end{aligned} \tag{3.11}$$

admits an eigenfunction which is positive on Ω. Such will be the case provided

$$\frac{1 - A_1/C_1 - \underline{\sigma}_1}{\mu_1} = \lambda_1(1)$$

implies that $\underline{\sigma}_1$ is positive. *A priori*, such requires $1 - A_1/C_1 > 0$ and, in that case, $\underline{\sigma}_1 > 0$ is equivalent to

$$\mu_1 < \left[1 - \frac{A_1}{C_1}\right] \Big/ \lambda_1(1). \tag{3.12}$$

Now (3.12) is equivalent to $(1 - A_1/C_1)/\mu_1 > \lambda_1(1)$. It follows from Theorem 2.1 that, for $\alpha > \lambda_1(1)$, the parabolic boundary value problem

$$\begin{aligned} \theta_t &= \Delta\theta + (\alpha - \theta)\theta \quad \text{in } \Omega \times (0,\infty) \\ \theta &= 0 \quad \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{3.13}$$

admits a unique globally attracting positive equilibrium solution. This equilibrium is frequently denoted θ_α in the literature (see Cantrell and Cosner [1987], Cosner and Lazer [1984], Eilbeck, Furter and López-Gómez [1994], for example) and a simple rescaling argument shows that

$$\psi_* = \mu_1 \theta_{((1-A_1/C_1)/\mu_1)}.$$

An upper-lower solution argument now gives that, for $\varepsilon > 0$, there is a $\underline{t}_\varepsilon > 0$ so that

$$u(x,t) \geq (1-\varepsilon)\mu_1 \theta_{((1-A_1/C_1)/\mu_1)}(x) \tag{3.14}$$

for $x \in \overline{\Omega}$ and $t \geq \underline{t}_\varepsilon$.

We now use the estimate (3.14) to obtain an asymptotic lower bound on v. Since

$$v_t = \mu_2 \Delta v + \frac{A_1 uv}{1 + B_1 u + C_1 v} - \frac{A_2 vw}{1 + B_2 v + C_2 w} - D_{21} v$$

on $\Omega \times (0, \infty)$ and $A_2 vw/(1 + B_2 v + C_2 w)$ is increasing in w, v is an upper solution for the parabolic problem

$$z_t = \mu_2 \Delta z + \frac{A_1(1-\varepsilon)\psi_* z}{1 + B_1(1-\varepsilon)\psi_* + C_1 z} - \frac{A_2}{C_2} z - D_{21} z \tag{3.15}$$

on $\Omega \times (\underline{t}_\varepsilon, \infty)$ with $z = 0$ on $\partial\Omega \times (\underline{t}_\varepsilon, \infty)$. Since (3.15) is of the form (2.1) with

$$f(x,z) = \frac{A_1(1-\varepsilon)\psi_*(x)}{1 + B_1(1-\varepsilon)\psi_*(x) + C_1 z} - \frac{A_2}{C_2} - D_{21},$$

conditions (i) and (ii) of Theorem 2.1 are met. Consequently, all solutions to (3.15) with $z(x, \underline{t}_\varepsilon) \underset{\not\equiv}{>} 0$ converge to a unique positive equilibrium ψ_{**}^ε provided $\underline{\sigma}_{2,\varepsilon}$ is positive when the eigenvalue problem

$$\begin{aligned} \mu_2 \Delta \phi + \phi \left(\frac{A_1(1-\varepsilon)\psi_*(x)}{1 + B_1(1-\varepsilon)\psi_*(x)} - \frac{A_2}{C_2} - D_{21} \right) &= \underline{\sigma}_{2,\varepsilon} \phi \quad \text{in } \Omega \\ \phi &= 0 \quad \text{on } \partial\Omega \end{aligned} \tag{3.16}$$

admits an eigenfunction which is positive on Ω. For such to be the case requires *a priori* that there is an $x_0 \in \Omega$ so that

$$\frac{A_1(1-\varepsilon)\psi_*(x_0)}{1+B_1(1-\varepsilon)\psi_*(x_0)} > \frac{A_2}{C_2} + D_{21}$$

and in such a case, that

$$\mu_2 < \left[\lambda_1\left(\frac{A_1(1-\varepsilon)\psi_*}{1+B_1(1-\varepsilon)\psi_*} - \frac{A_2}{C_2} - D_{21}\right)\right]^{-1}.$$

Hence, provided

$$\frac{A_1\psi_*(x_0)}{1+B_1\psi_*(x_0)} > \frac{A_2}{C_2} + D_{21} \tag{3.17}$$

and

$$\mu_2 < \left[\lambda_1\left(\frac{A_1\psi_*}{1+B_1\psi_*} - \frac{A_2}{C_2} - D_{21}\right)\right]^{-1}, \tag{3.18}$$

we may argue that, given $\eta > 0$, there is a $\underline{t}_\eta > 0$ so that

$$\begin{aligned} u(x,t) &\geq (1-\eta)\psi_*(x) \\ v(x,t) &\geq (1-\eta)\psi_{**}^0(x) \end{aligned} \tag{3.19}$$

for $x \in \overline{\Omega}$ and $t \in [t_\eta, \infty)$.

Finally, the estimates (3.19) can be used to obtain an asymptotic lower bound on w. Since

$$w_t = \mu_3 \Delta w + \frac{A_2 v w}{1+B_2 v + C_2 w} - D_{21} w$$

on $\Omega \times (0,\infty)$ with $w = 0$ on $\partial\Omega \times (0,\infty)$, (3.19) implies that w is an upper solution for
(3.20)

$$\begin{aligned} z_t = \mu_3 \Delta z + z\left(\frac{A_2(1-\eta)\psi_{**}^0}{1+B_2(1-\eta)\psi_{**}^0 + C_2 z} - D_{31}\right) \quad &\text{in } \Omega \times (\underline{t}_\eta, \infty) \\ z = 0 \quad \text{on } \partial\Omega \times (\underline{t}_\eta, \infty).& \end{aligned}$$

The model problem (3.20) has the property that all solutions corresponding to nonnegative, nontrivial initial data coverage over time to a unique positive equilibrium ψ^{η}_{***} so long as $\underline{\sigma}_{3,\eta}$ is positive when

$$\mu_3 \Delta\phi + \left(\frac{A_2(1-\eta)\psi^0_{**}}{1+B_2(1-\eta)\psi^0_{**}} - D_{31}\right)\phi = \underline{\sigma}_{3,\eta}\phi \quad \text{in } \Omega \tag{3.21}$$
$$\phi = 0 \quad \text{on } \partial\Omega$$

admits an eigenfunction $\phi > 0$. For such to be the case requires *a priori* that there is an $x_1 \in \Omega$ so that

$$\frac{A_2(1-\eta)\psi^0_{**}(x_1)}{1+B_2(1-\eta)\psi^0_{**}(x_1)} > D_{31}$$

and in such a case, that

$$\mu_3 < \left[\lambda_1\left(\frac{A_2(1-\eta)\psi^0_{**}}{1+B_2(1-\eta)\psi^0_{**}} - D_{31}\right)\right]^{-1}.$$

These requirements are met, provided

$$\frac{A_2\psi^0_{**}(x_1)}{1+B_2\psi^0_{**}(x_1)} > D_{31} \tag{3.22}$$

and

$$\mu_3 < \left[\lambda_1\left(\frac{A_2\psi^0_{**}}{1+B_2\psi^0_{**}} - D_{31}\right)\right]^{-1}. \tag{3.23}$$

Arguing as before, we may now establish the following result.

THEOREM 3.2. *Let (u, v, w) be a componentwise nonnegative solution to (1.1). Assume that $1 - A_1/C_1 > 0$, and that (3.12), (3.17), (3.18), (3.22) and (3.23) hold. Then if $\gamma > 0$ is given, there is a $\underline{t}_\gamma > 0$ so that*

$$u(x,t) \geq (1-\gamma)\psi_*(x)$$
$$v(x,t) \geq (1-\gamma)\psi^0_{**}(x)$$
$$w(x,t) \geq (1-\gamma)\psi^0_{***}(x)$$

for $x \in \overline{\Omega}$ *and* $t \in (\underline{t}_\gamma, \infty)$.

REMARKS. (i) The lower bounds we have obtained above may appear to the reader as somewhat implicit. More explicit and computable lower bounds can sometimes be obtained by further application of the method of upper and lower solutions. Such analysis is carried out for a logistic equation in Cosner and Lazer [1984] and for a Lotka-Volterra predator-prey system in Cantrell and Cosner [1996, pages 260–261].

(ii) It is reasonably straightforward to give biological interpretations of the conditions we impose to obtain asymptotic lower bounds. For instance, consider (3.12) and (3.17). These conditions are met if $A_1 \ll C_1$, $A_2 \ll C_2$ and $D_{21} \ll 1$. These relationships mean that predator mutual interference (as measured by the C_is) is large compared with foraging efficiency (as measured by A_i's) and also that death rates are relatively low. Certainly, further interpretation and analysis of these conditions is possible and desirable, but we shall not pursue such at this point due to the spatial constraints of this volume.

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