

UNIFORM PERSISTENCE IN REACTION-DIFFUSION PLANKTON MODELS

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ABSTRACT. In this paper, homogeneous Neumann problem for reaction-diffusion systems of plankton-nutrient models with instantaneous nutrient recycling is considered. By using the main theorem of Hale and Waltman [11], sufficient conditions for uniform persistence are derived.

1. Introduction. Reaction-diffusion equations have been extensively used to model ecological phenomena. For modeling of plankton dynamics, we refer to Leven and Segel [18], Mimura [20], Okubo [21], Wroblewski and Richman [24], Freedman and Ruan [7] and references cited therein.

In order to model the dynamics of plankton, Wroblewski and Richman [24] used a set of simplified reaction-diffusion equations which has properties characteristic of the pelagic marine ecosystem. They examined the response of the plankton dynamics to perturbations in the physical oceanographic environment caused by wind forcing. The model they constructed is consisted of three components, herbivorous zooplankton (Z), phytoplankton (P) and dissolved nutrients (N). They supposed that the nutrients are not limiting and neglected sinking losses of phytoplankton, vertical migration by zooplankton and vertical advection of Z , P and N by an organized flow. Hence the system of their model is closed.

An ecosystem is never totally closed to material fluxes from the outside, there are generally inputs of nutrients to the system, as well as losses from the system. In this paper, we consider an open system represented by a set of reaction-diffusion equations. Based on the model constructed by Wroblewski and Richman [24], we introduce a constant nutrient input rate and different constant washout rates to the system. We also use a general class of functions to describe nutrient uptake and functional response. The question of persistence is studied.

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Persistence is a fundamental problem in mathematical ecology. When a system of interacting species is persistent in a suitable sense, it means that all species survive in the long term. Recently, persistence in reaction-diffusion ecological systems has been studied by many authors, see Dunbar, Rybakowski and Schmitt [6], Hutson and Moran [14], Hale and Waltman [11], Hutson and Schmitt [15], Caristi, Rybakowski and Wessolek [4], Kuang [17], Hsu and Waltman [13], Cantrell, Cosner and Hutson [3] and the references cited therein.

In this paper, by using the main theorem of Hale and Waltman [11], we discuss uniform persistence of reaction-diffusion plankton models with instantaneous nutrient recycling under Neumann boundary conditions. Sufficient conditions are derived which are equivalent to those for the case without diffusion effect.

Let X be a complete metric space with metric d and suppose $T(t) : X \rightarrow X$, $t \geq 0$, is a C^0 -semigroup on X ; that is, $T(0) = I$, $T(t+s) = T(t)T(s)$ for $t, s \geq 0$ and $T(t)x$ is continuous in t and s . Suppose $X = X^0 \cup \partial X^0$, where ∂X^0 is the boundary of X^0 . The semigroup $T(t)$ is said to be *uniformly persistent* if there is an $\eta > 0$, such that for any $x \in X^0$, $\liminf_{t \rightarrow \infty} d(T(t)x, \partial X^0) \geq \eta$.

For other undefined terms we refer to the paper of Hale and Waltman [11].

2. The model. Let Ω be an open bounded set in R^3 with boundary $\partial\Omega$. $\partial/\partial n$ represents the outward normal derivative in $\partial\Omega$, and Δ is the Laplace operator, x is distance, t is time, $d_i > 0$ are diffusion coefficients, $i = 1, 2, 3$. We suppose that all parameters are positive and are interpreted as follows:

- a – maximal nutrient uptake rate for the phytoplankton
- c – maximal zooplankton ingestion rate
- N^0 – input concentration of the nutrient
- D – washout rate of the nutrient
- D_1 – washout rate of the phytoplankton
- D_2 – washout rate of the zooplankton
- γ – phytoplankton mortality rate
- ε – zooplankton death rate

- γ_1 – nutrient recycle rate after the death of the phytoplankton,
 $\gamma_1 \leq \gamma$
 ε_1 – nutrient recycle rate after the death of the zooplankton,
 $\varepsilon_1 \leq \varepsilon$
 δ – the fraction of zooplankton nutrient conversion, $0 < \delta \leq 1$

The model we consider consisting of zooplankton (Z), phytoplankton (P) and nutrient (N) and involving instantaneous nutrient recycling is given by the following set of reaction-diffusion equations:

$$\begin{aligned}
 (2.1) \quad & \frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aPu(N) \\
 & \quad + (1 - \delta)cZw(P) + \gamma_1 P + \varepsilon_1 Z \\
 & \frac{\partial P}{\partial t} = d_2 \Delta P + aPu(N) - cZw(P) - (\gamma + D_1)P \\
 & \frac{\partial Z}{\partial t} = d_3 \Delta Z + Z[\delta cw(P) - (\varepsilon + D_2)]
 \end{aligned}$$

with initial value conditions

$$(2.2) \quad \begin{aligned}
 N(x, 0) &= N_0(x), & P(x, 0) &= P_0(x), \\
 Z(x, 0) &= Z_0(x), & x &\in \Omega
 \end{aligned}$$

and the Neumann boundary value conditions

$$(2.3) \quad \left(\frac{\partial N}{\partial n}, \frac{\partial P}{\partial n}, \frac{\partial Z}{\partial n} \right) = (0, 0, 0) \quad \text{on } \partial\Omega \times R^+.$$

The homogeneous Neumann boundary value conditions (2.3) can be interpreted as a “no flux” condition, i.e., there is no migration of any of the populations across the boundary of habitat.

The function $u(N)$ describes the nutrient uptake rate of phytoplankton and satisfies the following general hypotheses (Hale and Somolinos [10]).

- (i) The function is nonnegative, increasing and vanishes when there is no nutrient.
- (ii) There is a saturation effect when the nutrient is very abundant.

That is, we assume that $u(N)$ is a continuous function defined on $[0, \infty)$ and satisfies

$$(2.4) \quad u(0) = 0, \quad \frac{du}{dN} > 0 \quad \text{and} \quad \lim_{N \rightarrow \infty} u(N) = 1.$$

In particular, this kind of function includes the Michaelis-Menten function (Wroblewski and Richman [24])

$$u(N) = \frac{N}{k + N},$$

where k is the half-saturation constant or Michaelis-Menten constant.

$w(P)$ represents the response function describing herbivore grazing. It is also assumed that $w(P)$ is continuous on $[0, \infty)$ and satisfies

$$w(0) = 0, \quad \frac{dw}{dP} > 0.$$

Usually, Ivlev's functional response formulation [16]

$$w(P) = 1 - e^{-\lambda P}$$

is used to describe the zooplankton grazing, where λ is the rate at which saturation is achieved with increasing phytoplankton levels (per unit concentration). Alternatively, Mayzaud and Poulet formulation [19]

$$w(P) = \lambda P(1 - e^{-\lambda P})$$

is also used to describe the food-acclimatized herbivore grazing (Wroblewski and Richman [24]).

We assume that only a fraction of the dead phytoplankton, γ_1 , $\gamma_1 \leq \gamma$, is recycled into dissolved nutrient. The zooplankton dynamics includes growth as assimilated ingested ration and a loss rate of ε due to high level predation, physiological death, etc. Also, we assume that only a fraction, ε_1 , $\varepsilon_1 \leq \varepsilon$, of the dead zooplankton is recycled into dissolved nutrient.

During consumption, only a fraction of the biomass removed from the resources compartment, δ , $\delta \leq 1$, is assumed to be assimilated by the consumer, the remainder goes directly to the dissolved nutrient.

Besides the loss related to consumption, a second phytoplankton loss term, $-\gamma P$, represents loss due to extracellular release and senescent cell autolysis and sinking.

D , D_1 and D_2 are washout rates (or removal rates, diffusive rates) of biotic components from the system resulting from washout, diffusion, harvesting, burial in deep sediments, soluble metabolic loss or cell sinking, for example. Those processes in general do not take place at the same time, so we suppose that D , D_1 and D_2 are different.

For the plankton-nutrient models neglecting diffusion, we refer to Ruan [22]. The existence of solutions of the Neumann problem (2.1)–(2.3) can be discussed similarly as in Freedman and Ruan [7].

3. Uniform Persistence. Let $X^0 = \{(N, P, Z) \in C^1(\overline{\Omega}, R_+^3) \mid N > 0, P > 0, Z > 0\}$. ∂X^0 consists of the states with at least one component zero. Clearly X^0 is open, and X^0 and ∂X^0 are invariant. Define

$$H_1 = \{(N, P, Z) \in C^1(\overline{\Omega}, R_+^3) \mid P = Z = 0\},$$

$$H_{12} = \{(N, P, Z) \in C^1(\overline{\Omega}, R_+^3) \mid Z = 0\}.$$

We say an equilibrium E of (2.1)–(2.3) is hyperbolic if it, as an equilibrium of the corresponding ordinary differential equation, is hyperbolic (Freedman and So [8]).

Note that $E_0 = (N^0, 0, 0)$ is always a spatially homogeneous steady state of the problem (2.1)–(2.3). E_0 is globally asymptotically stable with respect to H_1 and is hyperbolic (Ruan [22]).

By Theorem 2.1 of Kuang [17], we have the following result.

Theorem 3.1. *Solutions of problem (2.1)–(2.3) exist for $t \geq 0$ and are continuous, classical and bounded in $C^1(\overline{\Omega} \times R_+, R_+^3)$. Furthermore, there is a positive constant K such that*

$$\lim_{t \rightarrow \infty} [N(x, t) + P(x, t) + Z(x, t)] < K.$$

This result indicates that eventually all nonnegative solutions of (2.1)–(2.3) will enter a compact set in R_+^3 , which is essential for the uniform persistence of system (2.1).

Consider the subsystem

$$(3.1) \quad \begin{aligned} \frac{\partial N}{\partial t} &= d_1 \Delta N + D(N^0 - N) - aPu(N) + \gamma_1 P \\ \frac{\partial P}{\partial t} &= d_2 \Delta P + aPu(N) - (\gamma + D_1)P \end{aligned}$$

and the boundary values

$$(3.2) \quad \left(\frac{\partial N}{\partial n}, \frac{\partial P}{\partial n} \right) = (0, 0) \quad \text{on } \partial\Omega_1 \times \mathbb{R}_+,$$

where Ω_1 is a bounded and connected domain in \mathbb{R}^2 . By a result of De Mottoni and Rothe [5], problem (3.1)–(3.2) possesses a positive steady state if the corresponding ODE has a positive steady state. So by the analysis of Ruan [22], if the following inequalities

$$(3.3) \quad a > \gamma + D_1$$

and

$$(3.4) \quad N^0 > u^{-1} \left(\frac{\gamma + D_1}{a} \right)$$

hold, then the problem (3.1)–(3.2) has a positive steady state, say (N_1, P_1) . Hence $E_1 = (N_1, P_1, 0)$ is a spatially homogeneous steady state solution of problem (2.1)–(2.3).

Theorem 3.2. E_1 is globally asymptotically stable with respect to H_{12} .

Proof. Define a Liapunov function as follows:

$$\begin{aligned} V(N, P, t) &= \int_{\Omega_1} \left[\int_{N_1}^N \frac{u(\xi) - u(N_1)}{u(\xi)} d\xi \right. \\ &\quad \left. + \frac{au(N_1) - \gamma_1}{au(N_1)} \int_{P_1}^P \frac{\eta - P_1}{\eta} d\eta \right] dx \\ &= \int_{\Omega_1} [V_1(N) + V_2(P)] dx. \end{aligned}$$

The derivative of V along any positive solutions of (3.1)–(3.2) has the form

$$\begin{aligned} \frac{dV}{dt} &= \int_{\Omega_1} \left(\frac{dV_1}{dN} \cdot \frac{dN}{dt} + \frac{dV_2}{dP} \cdot \frac{dP}{dt} \right) dx \\ &= \int_{\Omega_1} \left(\frac{dV_1}{dN} d_1 \Delta N + \frac{dV_2}{dP} d_2 \Delta P \right) dx \\ &\quad + \int_{\Omega_1} \left\{ \frac{u(N) - u(N_1)}{u(N)} [D(N^0 - N) - aPu(N) + \gamma_1 P] \right. \\ &\quad \left. + \frac{au(N_1) - \gamma_1}{au(N_1)} (P - P_1) [au(N) - (\gamma + D_1)] \right\} dx. \end{aligned}$$

By using the boundary value conditions (3.2) and Lagrange-Green identity, we have

$$\begin{aligned} \int_{\Omega_1} \left(\frac{dV_1}{dN} d_1 \Delta N + \frac{dV_2}{dP} d_2 \Delta P \right) dx \\ = - \int_{\Omega_1} \left(\frac{d^2 V_1}{dN^2} \cdot |\nabla N|^2 + \frac{d^2 V_2}{dP^2} \cdot |\nabla P|^2 \right) dx, \end{aligned}$$

where

$$\begin{aligned} |\nabla N|^2 &= \left(\frac{\partial N}{\partial x_1} \right)^2 + \left(\frac{\partial N}{\partial x_2} \right)^2 + \left(\frac{\partial N}{\partial x_3} \right)^2, \\ |\nabla P|^2 &= \left(\frac{\partial P}{\partial x_1} \right)^2 + \left(\frac{\partial P}{\partial x_2} \right)^2 + \left(\frac{\partial P}{\partial x_3} \right)^2. \end{aligned}$$

Since

$$\frac{d^2 V_1}{dN^2} = \frac{u(N_1)}{(u(N))^2} > 0, \quad \frac{d^2 V_2}{dP^2} = \frac{P_1}{P^2} > 0,$$

we have

$$\begin{aligned} \frac{dV}{dt} \leq - \int_{\Omega_1} \left\{ \frac{D(N^0 - N) + \gamma_1 P}{u(N)u(N_1)} [u(N) - u(N_1)]^2 \right. \\ \left. + \frac{D}{u(N)} (N - N_1) [u(N) - u(N_1)] \right\} dx. \end{aligned}$$

Since $\gamma_1 \leq \gamma$, by (3.4) and the maximum principle, $N < N^0$ for sufficiently large $t > 0$, which implies that the first term in the integrand

is negative. The second term is negative because $u(N)$ is an increasing function. Thus, $dV/dt \leq 0$ and $dV/dt = 0$ if and only if $N = N_1$. Hence

$$\left\{ (N, P) : \frac{dV(N, P, t)}{dt} = 0 \right\} \subset \{ (N, P) : N = N_1, \nabla P = 0 \}.$$

Let \mathcal{A} be the largest invariant set in the set $\{(N, P) : dV/dt = 0\}$. Then $(N, P) \in \mathcal{A}$ implies $(N, P) = (N_1, P_2)$, where P_2 is a constant. Hence

$$0 = \frac{dN_1}{dt} = d_1 \Delta N_1 + D(N^0 - N_1) - aP_2 u(N_1) + \gamma_1 P_2,$$

that is, $P_2 = P_1$. By the invariance principle (Alikakos [1] or Henry [12]), we see that for initial values $(N_0(x), P_0(x)) \geq 0$, the solutions of (3.1)–(3.2) satisfy

$$(N(x, t), P(x, t)) \rightarrow (N_1, P_1) \quad \text{as } t \rightarrow \infty \quad \text{in } L_1 \text{ norm,}$$

which is equivalent to

$$\lim_{t \rightarrow \infty} (N(x, t), P(x, t)) = (N_1, P_1) \quad \text{uniformly on } \overline{\Omega}_1.$$

This completes the proof. \square

Theorem 3.3. *If the inequalities (3.3), (3.4) and*

$$(3.5) \quad w(P_1) > \frac{\varepsilon + D_2}{\delta c}$$

hold, then system (2.1) with (2.2) and (2.3) is uniformly persistent.

Proof. Since there are two boundary equilibria E_0 and E_1 , the omega limit set of the boundary ∂X^0 consists of exactly E_0 and E_1 . Let $M = \{M_1, M_2\} = \{E_0, E_1\}$ be a covering of the omega limit set as defined in Hale and Waltman [11]. In order to prove uniform persistence by using the main theorem of Hale and Waltman [11], we need to show that

- (i) this covering is isolated,

- (ii) $W^s(E_n) \cap X^0 = \emptyset$ for $n = 0, 1$, and
- (iii) this covering is acyclic.

Since E_0 and E_1 are globally asymptotically stable with respect to H_1 and H_{12} , respectively, there are no cycles on the boundary, (iii) is proved.

To prove E_0 is isolated and $W^s(E_0) \cap X^0 = \emptyset$, we suppose that every neighborhood of E_0 contains a full orbit. If such an orbit lies in the N -axis in a small neighborhood of E_0 , since E_0 is globally asymptotically stable with respect to H_1 and is hyperbolic, by Theorem 2.2 of Dunbar, Rybakowski and Schmitt [6] or Theorem 4.1 of Butler and Waltman [2], the alpha limit set of E_0 is nonempty and disjoint from E_0 , but this contradicts the stability of E_0 . If the orbit lies in the $N - P$ plane, by condition (3.4) and the second equation of system (3.1), we know E_0 is locally unstable relative to $P > 0$. Since E_1 is globally asymptotically stable with respect to H_{12} , for any point of X^0 sufficiently close to E_0 , the component P must increase along the orbit near E_0 and eventually exits the orbit, hence the point cannot approach E_0 along $W^s(E_0)$. Therefore, E_0 is isolated and $W^s(E_0) \cap X^0 = \emptyset$.

By assumption (3.5), we know that E_1 is locally unstable relative to $Z > 0$. Similarly we can prove that E_1 is isolated and $W^s(E_1) \cap X^0 = \emptyset$. This completes the proof. \square

Remark. If the coefficients are spatially varying or the Neumann boundary value conditions are replaced by the Dirichlet boundary value conditions, uniform persistence conditions could be obtained in terms of eigenfunctions and eigenvalues of linearized problems (see Cantrell, Cosner and Hutson [3]). For the above Neumann boundary value problem, since the equilibria are spatially constants, the eigenfunctions of linearized problem are constants and the eigenvalues are simply the numerical values of the zero order coefficients.

Theorem 3.3 demonstrates that if the maximal nutrient uptake rate of phytoplankton is greater than its loss rate ($a > \gamma + D_1$), there are sufficient nutrients ($N^0 > u^{-1}((\gamma + D_1)/a)$) and near the boundary equilibrium $E_1 = (N_1, P_1, 0)$ the growth rate of zooplankton is greater than its loss rate ($\delta cw(P_1) > \varepsilon + D_2$), then all three interacting components survive in the long term. Note also that the uniform persistence conditions (3.3), (3.4) and (3.5) are equivalent to uniform

persistence in the ODE models (Ruan [22]).

Consider the functional response functions used by Wroblewski and Richman [24]. If $u(N)$ is the Michaelis-Menten function and $w(P)$ is the Ivlev function, i.e.,

$$u(N) = \frac{N}{k + N}, \quad w(P) = 1 - e^{-\lambda P},$$

then the spatially homogeneous boundary equilibrium E_1 takes the form

$$\left(\frac{(\gamma + D_1)k}{a - (\gamma + D_1)}, \frac{D(N^0 - ((\gamma + D_1)k)/(a - (\gamma + D_1)))}{\gamma + D_1 - \gamma_1}, 0 \right).$$

Now condition (3.4) has the form

$$(3.6) \quad N^0 > \frac{(\gamma + D_1)k}{a - (\gamma + D_1)}$$

and condition (3.5) becomes

$$(3.7) \quad \exp \left[- \frac{\lambda D(N^0 - ((\gamma + D_1)k)/(a - (\gamma + D_1)))}{\gamma + D_1 - \gamma_1} \right] < \frac{\delta c - (\varepsilon + D_2)}{\delta c}.$$

If $w(P)$ is the Mayzaud and Poulet function, i.e.

$$w(P) = \lambda P(1 - e^{-\lambda P}),$$

then condition (3.5) has the form

$$(3.8) \quad \exp \left[- \frac{\lambda D(N^0 - ((\gamma + D_1)k)/(a - (\gamma + D_1)))}{\gamma + D_1 - \gamma_1} \right] < 1 - \frac{\varepsilon + D_2}{\lambda \delta c D(N^0 - ((\gamma + D_1)k)/(a - (\gamma + D_1)))}.$$

The above analysis is summarized as the following result.

Theorem 3.4. *Let $u(N)$ be the Michaelis-Menten function and $w(P)$ the Ivlev (or Mayzaud and Poulet) function. If (3.3), (3.6) and (3.7)*

(or (3.8)) hold, then system (2.1) with (2.2) and (2.3) is uniformly persistent.

4. Discussion. It is well known that if diffusive rates are large enough, then a reaction-diffusion system has very similar qualitative properties as those possessed by its reaction system (Hale [9]). This is also true for the property of persistence in Volterra-Lotka models (Dunbar, Rybakowski and Schmitt [4] and Kuang [17]). Our analysis is again consistent with this observation. The conditions we obtained in this paper for the reaction-diffusion systems are equivalent to uniform persistence for the case without diffusion effect (Ruan [22]).

We supposed that nutrient recycling is an instantaneous process. It will be of great interest to consider the models both with delayed nutrient recycling (see Ruan [23]) and with diffusion effect. We leave this for future consideration.

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