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Nutrient-Plankton Models with Nutrient Recycling

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Abstract—In this paper, nutrient-phytoplankton-zooplankton interaction with general uptake functions in which nutrient recycling is either instantaneous or delayed is considered. To account for higher predation, zooplankton's death rate is modeled by a quadratic term instead of the usual linear function. Persistence conditions for each of the delayed and nondelayed models are derived. Numerical simulations with data from the existing literature are explored to compare the two models. It is demonstrated numerically that increasing zooplankton death rate can eliminate periodic solutions of the system in both the instantaneous and the delayed nutrient recycling models. However, the delayed nutrient recycling can actually stabilize the nutrient-plankton interaction. © 2005 Elsevier Ltd. All rights reserved.

Keywords—Instantaneous nutrient recycling, Delayed nutrient recycling, Uniform persistence.

NOMENCLATURE

N^0	constant input nutrient concentration	γ_1	phytoplankton recycling rate, $0 < \gamma_1 \leq \gamma$
D	nutrient input and washout rate	δ	zooplankton death rate
D_1	phytoplankton washout rate	c	zooplankton recycling rate, $0 < c \leq 1$
D_2	zooplankton washout rate	b	maximal zooplankton ingestion rate of phytoplankton
a	maximal nutrient uptake rate by phytoplankton	α	zooplankton conversion rate, $0 < \alpha \leq 1$
γ	phytoplankton death rate		

1. INTRODUCTION

Deterministic mathematical models of nutrient-plankton interaction with different complexity have been constructed and analyzed since the pioneering work of Riley *et al.* [1] in which a simple

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diffusion model was proposed. The majority of these latter models are formulated in terms of ordinary differential equations [2–15]. However, models of partial differential equations arise when spatial inhomogeneity of either nutrient or plankton distribution is incorporated [16–22].

The importance of nutrient recycling has been well documented [23] and extensively investigated for closed ecological systems. Nutrient recycling in many of these studies is usually assumed to be instantaneous. In other words, the time that is required to regenerate nutrient from dead plankton via bacterial decomposition is neglected in the model formulation. The consideration of delayed nutrient recycling dates back to Beretta *et al.* [24,25] in the early 1990s, where they modeled an open chemostat system with a single species of phytoplankton feeding upon a limiting nutrient and only past dead phytoplankton is partially recycled into the nutrient concentration. They examined the effect of delayed nutrient recycling upon the stability of the interior steady state. In a more recent study by Ruan [11], both the instantaneous and the delayed nutrient recycling were considered for an open nutrient-phytoplankton-zooplankton system. Ruan's numerical simulations demonstrated that the delayed nutrient recycling model exhibits more oscillations than the instantaneous nutrient recycling model [11].

Following the work of Lotka-Volterra, the death rate of an organism in most of the mathematical models is usually modeled by a linear functional, i.e., the per capita mortality rate of a biological population is a constant. The simplicity of this assumption makes the model mathematically tractable. The choice of zooplankton's mortality is biologically controversial and it has a significant impact on the dynamics of the resulting system. A quadratic term used to model zooplankton death rate was initiated by Edwards and Brindley [5]. They demonstrated numerically that the limiting cycle behavior for which a linear death rate was considered disappeared when a quadratic death rate for zooplankton was assumed.

The purpose of this study is to investigate nutrient-plankton interaction in an open ecological system with both the instantaneous and delayed nutrient recycling, where we use a quadratic term to model zooplankton mortality. Parameter values cited in the existing literature are numerically simulated to make our comparison. For each of these models, explicit conditions are derived for population persistence. Unlike other ecological models for which delays can destabilize the system, our numerical simulations presented here suggest that delayed nutrient recycling can actually stabilize the nutrient-plankton system. Moreover, the periodic solution of the system disappeared as we increase zooplankton's mortality rate, and this finding is the same as that of the result obtained by Edwards and Brindley [5].

The remaining manuscript is organized as follows. The nutrient-plankton model with instantaneous nutrient recycling is presented in the next section. Section 3 studies the model with delayed nutrient recycling. Numerical examples and simulations are given in Section 4. The final section provides a brief summary and discussion.

2. THE MODEL WITH INSTANTANEOUS NUTRIENT RECYCLING

Let $N(t)$, $P(t)$, and $Z(t)$ be the nutrient concentration, the phytoplankton population, and zooplankton population at time t , respectively. The two plankton levels are modeled in terms of nutrient content and therefore their units are nitrogen or nitrate per unit volume. We let γ and δZ denote the per capita death rate of phytoplankton and zooplankton, respectively. The quadratic mortality rate δZ^2 is used to model higher predation by invertebrate upon zooplankton. In a natural nutrient-plankton system, waters flowing into the system bring input of fluxes of nutrients and outflows also carry out nutrients [23]. We assume that the input nutrient concentration is a constant and is denoted by N^0 . The rate of the waters flowing in and out of the system is assumed to be a constant D . However, we use D_1 and D_2 for phytoplankton population and zooplankton population washout rate respectively, where D , D_1 , and D_2 may be different to account for other physical consideration such as sinking of phytoplankton.

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