Dynamics of a Food Web Model of an Aquatic Ecosystem

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The paper presents a model of an aquatic ecosystem with four species (bacteria, algae, zooplankton and fish) and with three different dead pools (detritus and accessible nutrients in the water column, and nutrients bound to the sediment). The structure of the model is that of a food web with the bacterial population representing the microbial loop. No distinction is made between different nutrients, and all uptake rates are expressed in terms of modified Monod kinetics. Though the model does not explicitly account for shifting abilities of the various species, the modified Monod kinetics enable predators with more than one prey (i.e., zooplankton and fish) to adjust their foraging habits in accordance with the conditions in the system. Simulations of the model show a variety of different solutions, ranging from simple oscillations with the annual periodicity of the external forcing to higher order chaos.

1 Introduction

The growing pressure of human activities on the environment makes it increasingly important for us to understand the behaviour of complex ecological systems. During the last decade it has become common to base political and technical decisions related to the management and/or protection of aquatic ecosystems on the predictions of mathematical models [10]. Such applications often focus on specific results (e.g., the consequences of a particular action), and considerable effort is usually made to develop as realistic a representation of the system as possible. In most cases, this leads to highly disaggregated models which contain many different variables and require large
amounts of data. There is a clear tendency for these investigations to be of a nature that favors well controlled, stable outcomes.

On the other hand, originating with the works of Lotka [19] and Volterra [36] in the 1920's, environmental science also makes use of mathematical modeling to improve our understanding of the basic dynamical phenomena that can occur in systems with several interacting species. Ecological systems are thermodynamically open systems which owe their complexity in structure, the many interacting species, and their evolutionary potential to the continuous throughput of resources and energy. This throughput also provides the potential for complicated temporal behaviours as well as for the development of spatial patterns and biological turbulence [21]. Until the mid 1970's progress in this field was relatively slow. However, catalyzed among other things by significant breakthroughs in nonlinear science [8, 18, 30] the development started to accelerate, and from the beginning of the 1980's, the interest in chaotic phenomena in ecological systems has become very strong. In fact, several of the earliest works on chaos involved population dynamics models [22, 23, 24].

Gilpin [9] was presumably the first to find chaos in a continuous time model with Lotka-Volterra kinetics. He considered a three-species system with one predator and two preys. Since then many different ecological models have been investigated with respect to their nonlinear dynamical behaviours [12, 28, 32]. There has also been some success in showing the existence of chaos in experimental data for various epidemiological systems, particularly for childhood diseases [32, 33], where the available time series are relatively long and complete. These studies seem to show that whereas for children pox, the basic pattern is an annual cycle, for measles and rubella chaotic fluctuations are superimposed onto the yearly cycle. This is particularly the case for large first world cities. For small isolated communities, the epidemic has more of a stochastic character.

By virtue of the positive feedback associated with reproduction, because of the bilinear (or, more generally, nonlinear) predation terms, and because of maturation and other delays, ecological systems possess all the attributes required for instabilities and nonlinear dynamic phenomena to arise [1]. However, all of the above studies have been concerned with systems with a few interacting species, and the question naturally arises what happens when more realistic details and additional species are introduced in the models.

In principle, higher dimensional systems could show even more complicated behaviour. The general conception, however, appears to be that raising the dimension of an ecological system by introducing more and more species will add to its stability [5, 20]. Most of the reported examples of oscillatory predator — prey dynamics seem to come from small, isolated ecosystems or from regions with cold climates and relatively few species. With more species around, a predator can substitute a more abundant prey for a less abundant one, thus introducing a negative feedback control