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Deterministic approach to the study of the interaction predator–prey in a chemostat with predator mutual interference. Implications for the paradox of enrichment

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ABSTRACT

Our understanding of predator–prey systems has progressed in recent decades mainly due to the ability to test models in chemostats. This study aimed to develop a deterministic model using differential equations to reproduce the dynamics of the interaction of a predator and a prey in a two stage chemostat focusing in the proposed previous prey dependent model of Fussmann et al. (2000) [Fussmann, G.F., Ellner, S.P., Shertzer, K.W., Hairston Jr., N.G., 2000. Crossing the Hopf bifurcation in a live predator–prey system. Science 290, 1358–1360]. The main problem with that model, but parameterized with the values obtained in this study (particularly the concentration of nutrient), was that the temporal trajectory of both the prey and the predator showed very high peaks that eventually led to the extinction of predator in all cases. In the same way the experimental time series obtained in this study does not exhibit the behavior predicted by the model of Fussman et al. On the contrary, as prey density increases, the system actually becomes more stable. Finally, the model that best explained the behavior of the predator and prey in the chemostat, at medium to high dilution rates, was the ratio dependent (algae–nitrogen) model with mutual interference measured in the chemostat (rotifer–alga) and that incorporated the age structure of the predator. Qualitative analysis of the dynamic behavior enabled evaluation of coexistence at equilibrium, coexistence on limit cycles, extinction of the predator or extinction of both populations.

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1. Introduction

Biologists use mathematical models to understand and predict nature. For most biological processes, though, the exact analytical form of the functions that describe them is unknown (Wood and Thomas, 1999; Fussmann and Blasius, 2005; Jensen and Ginzburg, 2005; Roy and Chattopadhyay, 2007). This fact is true for one of the most important ecosystem processes, the predator–prey interaction, which determines the flow of energy and matter along a food chain. To understand the dynamics of this interaction, it is essential to obtain in depth knowledge of the mechanisms that regulate the growth of populations. In most field and laboratory studies, however, the growth of organisms is in a state of transition where the abundance, fertility, sex, age structure and other important properties of populations are time dependent variables, which is why the mathematical models of populations that grow by transition phases are, in most cases, extremely complex. In contrast, growth in a steady state ensures that the physiological state of the organisms and all variables of population growth remain constant over time. Thus, quantitative analysis and steady state models are simpler, greatly reducing the ambiguity in the interpretation of the biological response to environmental variables. The two methods that are known to maintain the populations in steady state are continuous culture and exponentially sustained growth in closed culture. For Walz (1993a) factors that regulate the growth of the species in simple experimental systems must be clearly defined before systems with many species can be understood. Recently, progress in understanding predator–prey systems has been accelerated by combining modeling with experimental testing (Boraas, 1983; Rothhaup, 1985; Boraas et al., 1998; McNair et al., 1998; Fussmann et al., 2000; Yoshida et al., 2003). This testing primarily has been conducted in chemostats (Monod, 1950; Novick and Szilard, 1950; Contois, 1959; Jannasch, 1974; Lampert, 1976; Cabrera F, 2008) where food is continuously supplied to the target population and where population growth is determined by the rate at which the limiting resource is provided to the container culture. Essentially, the chemostat provides a constant environment to the organisms where the specific growth rate can be controlled by making the dilution rate, D (flow rate F/volume of culture V) controls the population density (the dependent variable). Media containing new nutrients are added at a constant rate while simultaneously

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the same amount of suspension, including organisms, is removed. During the modeling process, the most important processes of the resource that can limit population growth are taken into account through mathematical formulations and by incorporating empirical estimates of parameter values into the model.

Making comparisons of experimental results reveal the limitations of a model, and it suggests places where the mathematical formulation can be refined. This approach is the best method for revealing the fundamental mechanisms that govern the population growth of both unicellular and metazoan organisms (Smith and Walkman, 1995; McNair et al., 1998; Kooi and Kooijman, 1999; Jessup et al., 2005).

A decade ago, Fussmann et al. (2000), proposed a non-linear model of four differential equations to reproduce the endogenous oscillatory dynamic behavior of a nitrogen limited predator–prey system in a single chemostat. The mathematical model is prey dependent, where the relationship between the growth rates of the prey and the predator with their respective resources is assumed as Monod type, similar to the model of Canale (1970), but demographically structured. At high concentrations of nitrogen the system is extinguished after extreme oscillations.

This study aimed to build a deterministic model of differential equations, focusing in the proposed previous prey dependent model of Fussmann et al. (2000), and that to a first approximation, reproduces the dynamic interaction of a predator and its prey, in a two stage chemostat, at medium to high dilution rates, in the range when μ_{max} is reached and where the small variations in the dilution rate greatly affect the values of prey and predator density allowing a better visualization of the effect of their interaction, taking both the transition phase and the stationary phase of population growth into account.

2. Materials and methods

Experiments were performed using the rotifer predator *Brachionus rotundiformis* (lorica length: 72.5–235 μm; lorica width: 52.5–162.5 μm, $n = 386$) isolated from a temporary saline lake in the coastal area of Lake Maracaibo and where the maximum density values obtained, during the day, were between 7 to 25 ind/ml, in the pelagic zone. The prey used was the alga *Chlorella sorokiniana* (biovolume: 19.7 μm^3; $n = 124$), which was also isolated from bodies of water in the area, characteristic of mesoeutrophic to hypereutrophic environments (Reynolds et al., 2002; Mora et al., 2004; Vera et al., 2004; Moronta et al., 2006; Fanés, 2008) where nitrogen reaches levels of 3–24 mg N/L according to the trophic state index (TSI) of Carlson (1977). The experiments (see also Cabrera F, 2008) were conducted in a two stage chemostat (based on Boraas, 1983) that was built in the laboratory and placed within an environmental cabinet, which allowed to keep the environment relatively stable (6% salinity, 25 °C and 2000 lux). The culture vessel of the algae (1) had a capacity of 500 ml while the culture vessel of the rotifers (2) had a capacity of 250 ml. The culture vessel of the algae can be considered a separate culture from the algae that were harvested to feed the rotifers. *Chlorella* densities of 12×10^6, 2.5×10^6, 1.5×10^6, 1×10^6, 0.6×10^6 and 0.4×10^6 cells/ml were used. *Chlorella* was limited by nitrogen (NO_3 = 1.47–5.88 mM/L)[1] and was cultivated in the medium developed by Rodríguez-López et al. (1980). Richardson et al. (1969) whom were working specifically with the growth of *C. sorokiniana* in chemostat found similar results stating that 5 mM NO_3 is limiting for *C. sorokiniana* in continuous culture conditions. Eyster (1978) also working in continuous culture conditions, determined that the minimum, optimum and maximum concentration of *N* to *C. sorokiniana* is 1×10^3 μM, 1–5×10^4 μM and 2×10^5 μM, respectively. In relation to the regeneration of N by the rotifer, Hino et al. (1997) using ^{15}N as a tracer, found that *B. rotundiformis* requires only 20 min for the passage of food (*Nannochloropsis*) through the digestive tract, where 77% of N ingested is ejected back into the medium. Of the remaining N, 23% is assimilated and 5% is excreted in the following 2–5 h. This result indicates that, depending on the dilution rate, the concentration of *N* in the rotifer chemostat can be greater than the supplied medium.

The inoculum of *Brachionus* (300 ind/ml) was introduced into the culture vessel of 250 ml at the start of each experiment. As *B. rotundiformis* requires vitamin B12, this supplement was supplied directly into the rotifer culture vessel (5 μg/L). Daily counts, both of the algae in both culture vessels and of the rotifers, were made in duplicate. To count the algae a Neubauer chamber was used, whereas to count the rotifers a Sedgwick-Rafter chamber was used. To control the algal density in the rotifer culture vessel and establish the desired concentrations of algae, dilution rates (δ = 0.89; 1; 1.01; 1.02; 1.03; 1.09 $days^{-1}$) were synchronized with population growth rates using a peristaltic pump with multiple pathways.

The experiments lasted approximately two weeks until rotifer growth stabilized. Wall growth of the algae was removed daily and the mixing was complete.

Once steady state in the chemostat has been reached, samples can be removed as often as desired (Cabrera F, 2008). Population growth rates in the transition phase were calculated using a linear regression of ln (population size) (Graham and Wilcox, 2000). The growth rates at steady state were estimated by calculating the dilution rates in culture vessel 2. The steady state is the relatively flat area of the population curve after the initial transition state. To statistically check for stationarity in such areas, an analysis of autocorrelation functions for the time series of population curves were conducted, even when sample sizes were not recommended for this type of analysis. Also the coefficient of variation (CV = standard deviation/mean [%]) of the same areas of the curves were analyzed, which is a methodology used by some authors to determine the degree of stability of the stationary phase (Boraas, 1983; Fussmann et al., 2000; Cabrera F, 2008). The ingestion rates at steady state were estimated in culture vessel 2 according to Boraas (1983). The rest of the parameters required to model the system along with their values are shown in Table A1 of the appendix. To estimate the parameters, the non-linear quasi-Newton regression method was used. The simulation routines were written in *C*. For the numerical integration of systems of differential equations, a 5th control order with an adaptive step size Runge-Kutta method was used (Press et al., 1992).

[1] Previously, experiments (in closed cultures) were carried out, to determine the growth curve of the microalgae as a function of the concentration of NO_3 in order to estimate the limiting concentration. These experiments used 7 concentrations of NO_3 (1.47, 2.94, 5.88, 11.75, 23.5, 47 and 94 mM) obtained from successive dilutions of stock solution having a concentration of 187.86 mM NO_3. For each concentration, 150 ml of culture medium placed in 200 ml containers with 1 ml of *Chlorella* culture were used. The treatments were performed in triplicate for a total of 21 containers with an initial inoculum that ranged from 0.51×10^6 to 0.68×10^6 cell/ml of *Chlorella*. The containers were placed in an environmental cabinet under controlled temperature (25 °C) and light (2000 lux). The experiment lasted 17 days; daily counts were made in an optical microscope with 10× magnification using a Neubauer chamber for cell density. Finally, the [NO_3] = 5.88 mM (3250 μmol/L N) in the culture vessel of the algae and [NO_3] = 1.47 mM (813 μmol/L N) + N regeneration by *Brachionus* in the culture vessel of the rotifer (the mixing chamber diluted the culture vessel of the algae four-fold). In the experiment, to obtain 12×10^6 cell/ml of *C. sorokiniana* was necessary to increase the concentration of NO_3 to 23.5 mM in the chemostat culture vessel 1 to reach 5.88 mM NO_3 (3250 μmol/L N) in the chemostat culture vessel 2. To convert moles of *N* to numbers of organisms, the following relationships were used: 1 μmol/L N *Chlorella* is approximately 12.5×10^3 to 22×10^3 cell/ml and 1 μmol/L N *Brachionus* is approximately 3–6 ind/L.

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