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CHAOS AND MICROBIAL SYSTEMS

Final Project Report

July 1989 - July 1992

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October 1992

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PREPARED FOR THE U.S. DEPARTMENT OF ENERGY

UNDER GRANT NUMBER DE-FG06-90ER61034

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§1. Brief Project Summary

The field of nonlinear dynamics has generated a variety of new techniques for identifying order in seemingly chaotic systems. These techniques have led to new insights for several ecological and epidemiological systems, most notably childhood disease epidemics.

To better test the efficacy and relevance of these new techniques to population biology, I proposed research with two components:

- (1) a mathematical analysis of some simple microbial models with chaotic dynamics; and
- (2) experimental (chemostat) population studies to evaluate the accuracy of these models.

I have pursued this research in close collaboration with colleagues in protozoology and microbiology.

On the theoretical side, I have completed a thorough analysis of the forced double-Monod model and of the phase-locking route to chaos that it exhibits. I have also analyzed a simpler pulsed system with mass action kinetics and a period-doubling route to chaos. This research also motivated detailed analyses of discrete-time predator-prey and dispersal models, and a fast new method for computing fractal dimension.

My colleagues and I have assembled a complete laboratory system to determine the appropriateness of the forced double-Monod model. We have tested assays for concentration and density and have performed a variety of diagnostic tests on this system. We have measured growth parameters for bacteria and for protozoa in chemostat. We are currently studying the interaction of these two populations under a variety of flow regimes.

This research with a glucose substrate is a natural springboard for additional studies on the effects of pulsing and of forcing on bioremediation and on indirect effects in simple microbial communities.

§2. Technical Information

Mathematical Investigations. Initially, our goal was to understand the qualitative properties of the forced double-Monod system. Towards this end, I undertook a detailed mathematical analysis of the equations using a variety of standard techniques from the field of nonlinear dynamics. At the same time, I began exhaustive numerical simulations of the forced double-Monod system using a Sun SparcStation. Briefly stated, the forced double-Monod system exhibits a phase-locking route to chaos with an increase in the amplitude or period of forcing. This research is reported in Kot et al. (1992).

The forced double-Monod systems was complex enough to prompt us to analyze a second, simpler, system. This involved a predator and prey with mass action functional response in a chemostat with periodically pulsed substrate. We derived an exact periodic solution with positive concentrations of substrate and prey for this system. In analyzing the stability of this solution, we derived an exact invasion threshold for the predator. Above this threshold, we observed periodic oscillations in substrate, prey and predator that gave way to chaos in a cascade of period doubling-bifurcations. These bifurcations occurred despite the presence of severe statistical constraints on the behavior of the dependent variables. In particular, we were able to determine the average substrate, bacterial, and protozoan concentrations for all periodic orbits, independent of the actual period. This work has been submitted as a manuscript (Funasaki and Kot, 1992) to *Theoretical Population Biology*. A preprint is included in section 5.

In addition to a better understanding of chemostat systems, there have been several spin-offs that have arisen in the course of this research. During the early stages of proposal writing, a student and I developed a rapid new method for computing a fractal dimension known as the correlation dimension. The method uses a spatial data structure, the kd-tree, to eliminate a large number of computationally time-consuming calculations. This algorithm was first used to compute the fractal dimensions of various strange attractors of the forced double-

Monod model in Bingham and Kot (1989).

This grant also supported detailed analyses of spatial statistical models (Gittleman and Kot, 1990), discrete-time predator-prey models (Neubert and Kot, 1992) and discrete-time dispersal models (Kot, 1992). Mike Neubert, a graduate student at the University of Washington, has an additional manuscript on pattern formation in predator-prey models in preparation that will acknowledge DE-FG06-90ER61034.

Experimental Investigations. During the last year of this grant, emphasis shifted to the experimental aspects of the proposal. The experimental work was done in close collaboration with Dr. Terry Schultz (Dept. of Animal Science & Veterinary Medicine, University of Tennessee), a protozoologist and toxicologist with over fifteen years of experience working with *Tetrahymena pyriformis*. We assembled a laboratory system, performed a variety of diagnostic tests, and measured the maximum growth rate and half-saturation constants of the heterotrophic prey (*Escherichia coli*) and holozoic predator (*Tetrahymena pyriformis*). The growth parameters were measured in continuous culture rather than in batch to more closely approximate conditions within the chemostat. These measurements are the basis of predictions about predator and prey coculture that are currently being tested by Dr. Schultz. We are holding these results in abeyance pending completion of the necessary controls, but plan to publish them upon completion of all appropriate experiments.

Manuscripts and Papers Acknowledging DOE Support

Published Papers

- Gittleman, J.L., and Kot, M. 1990. Adaptation: Statistics and a null model for estimating phylogenetic effects. *Systematic Zoology*, **39**, 227-241.
- Kot, M., Sayler, G.S., and Schultz, T.W. 1992. Complex dynamics in a model microbial system. *Bulletin of Mathematical Biology*, **54**, 619-648.
- Kot, M. 1992. Discrete-time travelling waves: Ecological examples. *Journal of Mathematical Biology*, **30**, 413-436.
- Neubert, M.G. and Kot, M. 1992. The subcritical collapse of predator populations in discrete-time predator-prey models. *Mathematical Biosciences*, **110**, 45-66.

Submitted Manuscripts

- Funasaki, E. and Kot, M. 1992. Invasion and chaos in a periodically pulsed mass-action chemostat. Submitted to *Theoretical Population Biology*.

*Preprint removed
+ cycled separately.*

Manuscripts In Preparation

- Neubert, M. 1992. Pattern formation in discrete-time population models.

Related Papers

- Bingham, S. and M. Kot. 1989. Multidimensional trees, range searching, and a correlation dimension algorithm of reduced complexity. *Physics Letters A*, **140**, 327-330.

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