



Promoting the Science of Ecology

Chaos in a Three-Species Food Chain

Author(s): Alan Hastings and Thomas Powell

Source: *Ecology*, Vol. 72, No. 3 (Jun., 1991), pp. 896-903

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1940591>

Accessed: 27/10/2010 08:19

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=esa>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

CHAOS IN A THREE-SPECIES FOOD CHAIN¹

ALAN HASTINGS

*Division of Environmental Studies and Institute for Theoretical Dynamics,
University of California, Davis, California 95616 USA*

THOMAS POWELL

Division of Environmental Studies, University of California, Davis, California 95616 USA

Abstract. A continuous time model of a food chain incorporating nonlinear functional (and numerical) responses exhibits chaotic dynamics in long-term behavior when biologically reasonable parameter values are chosen. The appearance of chaos in this model suggests that chaotic dynamics may be common in natural food webs.

Key words: *chaos; dynamics; food chain; food web; functional response; predation.*

INTRODUCTION

The classical ecological models of interacting populations typically have focussed on two species (e.g., May 1973, Hassell 1978). They have been applied to plant and animal systems in aquatic and terrestrial environments, and across many taxa (e.g., Roughgarden et al. 1989). However, it has long been recognized that the limited “caricature” of ecological systems by two interacting species can account for only a small number of the phenomena that are commonly exhibited in nature. This is particularly true in community studies where the essence of the behavior of a complex system may only be understood when the interactions among a large number of species are incorporated (Pimm 1982, Paine 1988).

One approach to the study of an ecological community begins with an important object: its food web. Theoretical studies of food webs must contend with the question of how to couple the large number of interacting species. One line of investigation assumes that the “building blocks” are species interacting in pairwise fashion (see the influential books of May 1973, Pimm 1982). Behavior of the entire community is then assumed to arise from the coupling of these strongly interacting pairs. The approach has the substantial virtue that it is tractable to theoretical analysis. Moreover, the considerable intuition that investigators have developed over decades with two-species models may be applied to community food web questions.

Note, however, that important behavior that may be critical to community function may arise only through the interaction of three or more species. Price et al. (1980) present a strong case that understanding of plant–insect interactions must be based on three-trophic-level schemes. In marine intertidal communities the influential studies of Paine (1966) demonstrated the importance of the strong coupling of higher trophic levels to lower ones in the food web. Similar results have emerged from experiments in freshwater

plankton communities (Carpenter and Kitchell 1984, Carpenter et al. 1987). Mathematical developments also suggest that community models involving only two species as the basic building blocks may miss important ecological behavior. For example, results that are much more complicated than those seen in two-species models appeared in early theoretical studies (Rosenzweig 1973, Wollkind 1976) of three-species, or three-trophic-level, models based on local stability analyses. These analyses considered only linear approximations to the nonlinear equations that ecologists conventionally assume apply to these more complex situations.

More importantly, two-species continuous time models have only two basic patterns: approach to an equilibrium or to a limit cycle (Segel 1984). In contrast, simple discrete time models of even a single species can exhibit chaotic behavior (e.g., May 1974, 1976). But research of the last 15 yr (e.g., Gilpin 1979, Guckenheimer and Holmes 1983, Schaffer 1985) demonstrates the very complex dynamics that can arise in model systems (in continuous time) with three or more species. The terms chaos, strange attractor, and fractal are becoming familiar to many, if not all, ecologists (Schaffer and Kot 1986a). The key feature of chaotic dynamics is the sensitive dependence on initial conditions. Even a very small change in initial conditions can lead to different results. Indeed, the divergence between results grows exponentially in time for virtually all pairs of starting conditions. Several of the early mathematical investigations of chaos were of ecological models (e.g., May 1974). An investigation by Gilpin (1979) showed that a system of one predator and two competing prey can exhibit chaotic behavior. Schaffer and collaborators (e.g., Schaffer and Kot 1985b) have been especially persuasive in their view that chaos may be a much more important phenomenon than ecologists had earlier believed. In particular, a number of simple ecological and epidemiological systems with seasonality in contact rates unequivocally demonstrate chaos (Schaffer and Kot 1986b). Schaffer and Kot (1985a) and Olsen et al. (1988) show that measles in

¹ Manuscript received 14 May 1990; accepted 20 August 1990; final version received 14 September 1990.

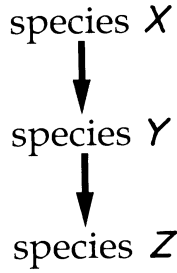


FIG. 1. The feeding relationships in the food chain. Arrows go from prey to predators.

New York, Baltimore, and Denmark may be a specific example of this behavior.

We investigate here perhaps the simplest three-species continuous time model, a three-level food chain. We demonstrate that, for biologically reasonable choices of parameters, chaotic dynamics result. These dynamics cannot arise in two-species models. We discuss the biologically significant implications that the presence of chaotic dynamics may have for more general food web models.

MODEL FORMULATION

Simple models for three-species food chains that incorporate a functional response in both of the consumer species have been studied previously (e.g., Rosenzweig 1973, Wollkind 1976). Following these efforts, we let X be the numbers of the species at the lowest level of the food chain, Y the numbers of the species that preys upon X , and Z the numbers of the species that preys upon Y . We use the letters X, Y, Z as both the names and variables. (We later introduce lower case letters as scaled measures of population size.) The food chain that this system models is illustrated diagrammatically in Fig. 1.

Incorporating "type II" saturating functional responses in both species (see Murdoch and Oaten 1975), the model takes the form:

$$\begin{aligned} dX/dT &= R_0 X(1 - X/K_0) - C_1 F_1(X)Y \\ dY/dT &= F_1(X)Y - F_2(Y)Z - D_1 Y \\ dZ/dT &= C_2 F_2(Y)Z - D_2 Z \end{aligned} \tag{1}$$

with

$$F_i(U) = A_i U / (B_i + U) \quad \text{for } i = 1, 2 \tag{2}$$

representing the functional response. Here T is time. The constant R_0 is the "intrinsic growth rate," and the constant K_0 is the "carrying capacity" of species X . The constants C_1^{-1} and C_2 are conversion rates of prey to predator for species Y and Z , respectively; D_1 and D_2 are constant death rates for species Y and Z , respectively. The constants A_i and B_i , for $i = 1, 2$ parametrize the saturating functional response; B_i is the prey population level where the predation rate per unit prey is half its maximum value.

The model we have just specified has 10 parameters,

which makes analysis difficult. To reduce the number of parameters and to determine which combinations of parameters control the behavior of the system, we nondimensionalize the system (see the discussion in Lin and Segel 1974 or Nisbet and Gurney 1982). We choose

$$\begin{aligned} x &= X/K_0, \\ y &= C_1 Y/K_0, \\ z &= C_1 Z/(C_2 K_0), \\ t &= R_0 T. \end{aligned} \tag{3}$$

Making these substitutions and simplifying yields the following system of equations, where the variables x, y, z are now scaled (nondimensional) measures of population size, and t is a new (nondimensional) time variable. We obtain:

$$\begin{aligned} dx/dt &= x(1 - x) - f_1(x)y \\ dy/dt &= f_1(x)y - f_2(y)z - d_1 y \\ dz/dt &= f_2(y)z - d_2 z \end{aligned} \tag{4}$$

with

$$f_i(u) = a_i u / (1 + b_i u). \tag{5}$$

The six nondimensional parameters in terms of the original parameters are listed in Table 1.

ANALYSIS AND RESULTS

The only choice for investigating the global dynamical behavior of the system (Eq. 4) is numerical integration. (A stability analysis and determination of Hopf bifurcations for this system is a relatively straightforward procedure but would not shed light on the global behavior we are interested in.) We employed a package developed by Hindmarsh (1980) that implements an algorithm due to Gear. Our choice of parameters was guided by two factors: first, we wanted to investigate biologically reasonable food chains, and second, we wanted to determine if chaotic dynamics were likely. Accordingly, we chose parameters for which the natural time scale of the interaction between Y and Z , i.e., at the higher trophic levels, was substantially longer than that between X and Y , that is, d_1 much larger than d_2 . Further, one of the ways to generate chaos is to "periodically force" nonlinear systems that

TABLE 1. Nondimensional parameters and values of the parameters used in the simulations.

Nondimensional parameters	Dimensional parameters	Parameter values used in the simulations
a_1	$(K_0 A_1)/(R_0 B_1)$	5.0
b_1	K_0/B_1	varied from 2.0 to 6.2
a_2	$(C_2 A_2 K_0)/(C_1 R_0 B_2)$	0.1
b_2	$K_0/(C_1 B_2)$	2.0
d_1	D_1/R_0	0.4
d_2	D_2/R_0	0.01

already exhibit limit cycle behavior. We chose parameter values that would lead to cycling in the pair of species X and Y , with Z absent, and also, with X constant, the pair Y and Z . The values of the parameters chosen using these guidelines are listed in Table 1. Since the parameter space is large, we concentrated our investigations on varying b_1 , holding the other parameters fixed. Earlier investigations (e.g., Murdoch and Oaten 1975) showed that the half saturation constant, which is proportional to b_1^{-1} , was a key parameter in determining stability in predator-prey models. As we demonstrate below in this section, for different values of b_1 , the system (Eq. 4) exhibited stability, limit cycle behavior, and chaos.

Our initial investigations consisted of letting the system run for 10 000 time steps, and examining only the last 5000 time steps to eliminate transient behavior. We studied the behavior of the system by examining plots of each species against time, as well as a three-dimensional phase plot (eliminating the explicit dependence on the time variable) of all three species against each other. Dynamics that have the irregular behavior suggestive of chaos are illustrated in Fig. 2. Note that this irregular behavior, e.g., varying number of secondary maxima between primary maxima for species X and Y , is not the result of a transient, but represents the behavior on the attractor. (An attractor is the [possibly very complex] smallest set of points in three dimensions [the numbers of the three species] that is approached from nearby initial conditions.) The attractor in Fig. 2D resembles the surface of an upside-down teacup, although the solutions of the system (Eq. 4) do not lie on a surface.

The dynamics within the attractor are given roughly as follows. Starting in the "handle" of the "teacup," the system moves to the wide part of the teacup and then spirals along the teacup to the narrow end, entering the handle again. In terms of the species behavior, the top predator Z crashes, allowing wide swings in the population levels of X and Y . As Z increases in numbers, the swings in X and Y become damped, until Z causes the levels of Y to crash. This leads to a crash in Z , and an outbreak in X , starting the process again. The sequence of events, in terms of species numbers, always follows the same general pattern. What is unpredictable is the timing. One way to express this is that the time between crashes of species Z varies in an erratic fashion. Also, the number of peaks in species Y between major crashes varies, and the population size at the peaks varies. The sensitive dependence of future dynamics on the current state, the signature of chaos, is apparent from the fact that all the trajectories in the "handle" of the "teacup" are very close together.

Thus a small change in initial conditions may lead to different dynamic behavior. We have illustrated this behavior by comparing the trajectories generated by very slightly different initial conditions for the set of parameter values that led to the chaotic dynamics il-

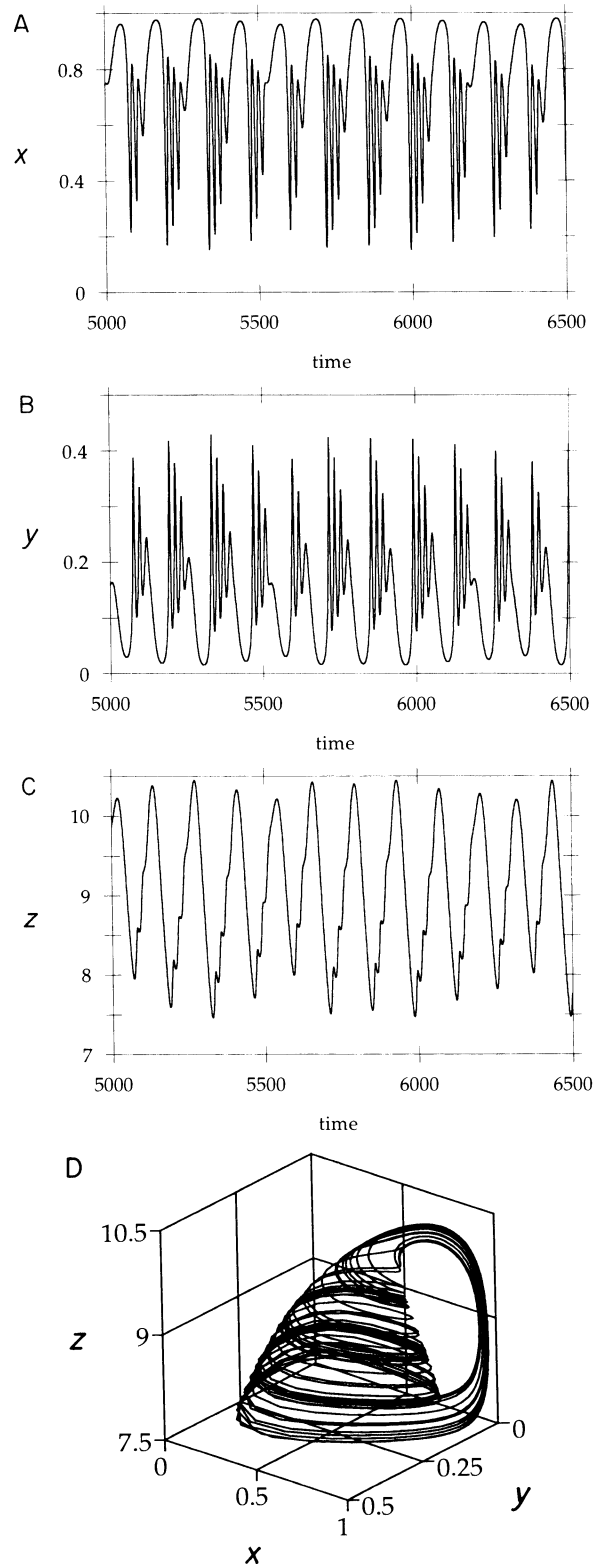


FIG. 2. Chaotic dynamics for the model system. Trajectories are plotted for the parameter values in Table 1, with $b_1 = 3.0$. Plots of x vs. time, y vs. time, and z vs. time are given in (A), (B), and (C), respectively. A three-dimensional phase plot is given in (D).

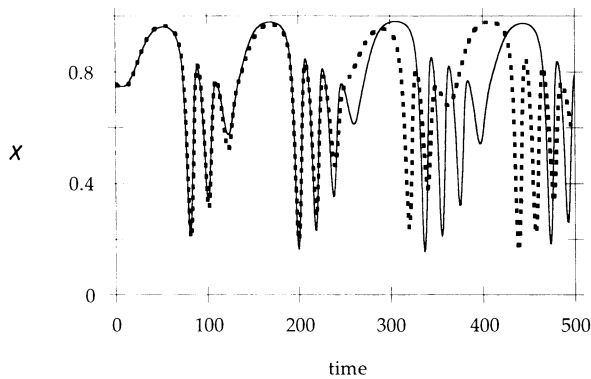


FIG. 3. Divergence of trajectories when the model system exhibits chaotic dynamics. Trajectories of species x are plotted for two different initial conditions (— and ····), differing only by 0.01 in x with y and z unchanged, for the parameter values in Table 1, with $b_1 = 3.0$.

illustrated previously in Fig. 2. One set of initial conditions is on the attractor, the other set differs from the first by changing x by 0.01. As shown in Fig. 3, the numbers of species X remain similar for the two initial conditions for a short time, but after two “crashes” of species Z the two different initial conditions lead to dynamics that are essentially uncorrelated (although, of course, restricted to the attractor). Note that in Fig. 3 the choice of $R_0 \approx 1/d$, a common value for reproductive rates of lower trophic level organisms, would imply that after ≈ 300 d (1 yr) the system would be indeterminate. Similarly, even a slight perturbation in species numbers, as would occur naturally, may lead to unpredictable results through time.

We then proceeded to a more systematic investigation of the dynamics, as a function of changes in b_1 , by constructing a bifurcation diagram. As noted in Glass and Mackey (1988), a compelling diagnostic test for chaos is the appearance in a bifurcation diagram of one of the typical routes to chaos. We found a sequence of period doublings as exhibited by one-dimensional difference equations such as the logistic model that has been extensively studied by May (1974) and May and Oster (1976). To construct a bifurcation diagram we integrated the system numerically using the parameter values in Table 1. Letting the system approach the attractor for each value of b_1 used, we then plotted successive maxima of z as a function of b_1 . We used values of b_1 between 2.0 and 3.2, changing b_1 in steps of 0.01, and values of b_1 from 3.2 to 6.2, changing b_1 in steps of 0.1. We did this both by starting with the smaller value of b_1 and increasing b_1 , and also by starting with the larger value of b_1 and decreasing b_1 . The bifurcation diagrams are plotted in Fig. 4. (Note that for clarity in our figures we have eliminated points due to apparent second branches for b_1 between 2.6 and 3.2 arising solely from the appearance of a second local maxima in the cyclic dynamics of species Z , as illustrated in Fig. 2C.) The values of b_1 (e.g., $b_1 = 2.3$) for

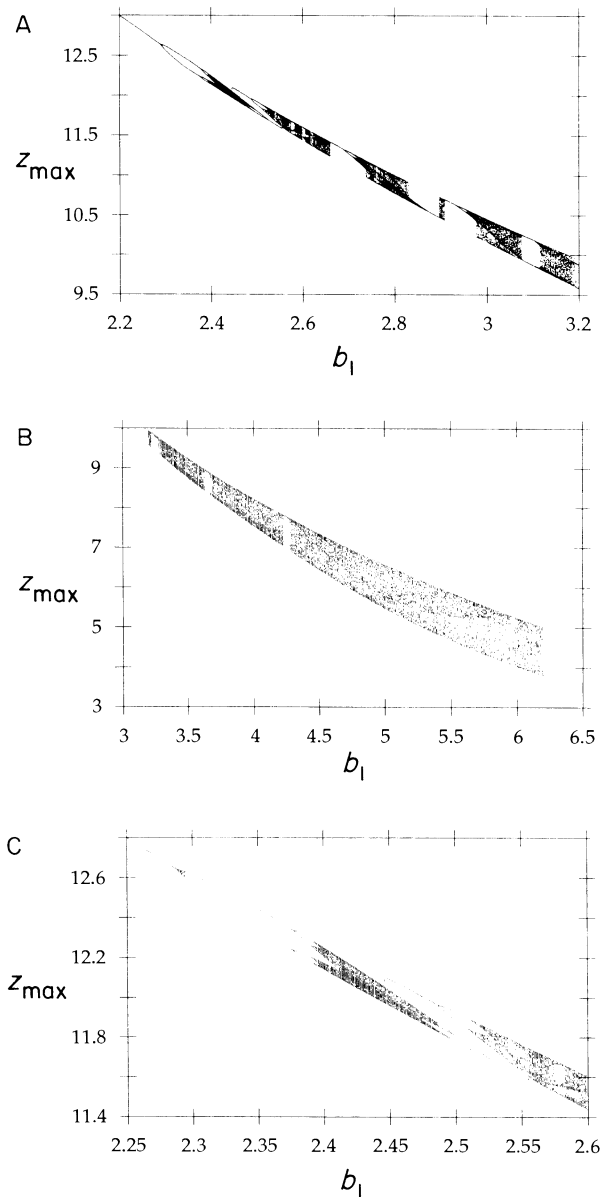


FIG. 4. Bifurcation diagram for the model system for the parameter values in Table 1. Plots are of the maximum value of z vs. b_1 . The procedure is described in the text (*Analysis and results*). In (A) values of b_1 from 2.2 to 3.2 are used, and in (B) values of b_1 from 3.2 to 6.2 are used. A detail of part (A) is given in part (C).

which there are a small number of values of z_{\max} in the diagram represent limit cycle behavior, while the values of b_1 (e.g., $b_1 = 3.0$) for which the values of z_{\max} form approximately an interval represent chaos. We see evidence in Fig. 4A and in more detail in Fig. 4C for period doubling leading to chaos, both as b_1 is increased, and as it is decreased. This is observed when: b_1 is increased from 2.3 to 2.4, b_1 is decreased from 2.55 to 2.45, b_1 increased from 2.437 to 2.55, and b_1 is increased from 2.93 to 2.96.

Also, from Fig. 4C we can deduce that for some values of b_1 there are two separate attractors, one chaotic and one which is a limit cycle. This occurs both for b_1 lying between 2.45 and 2.48 and between 2.53 and 2.56. Thus, the presence of chaotic dynamics may depend on the initial conditions, with some initial conditions leading to a limit cycle, and some leading to chaos.

Most striking, we see that the asymptotic behavior of the system is extremely sensitive to the value of b_1 . Over ecological time scales, a population level parameter like b_1 , a component of the predation rate per unit prey, which, in fact, is a composite of various individual responses, would certainly be expected to vary, perhaps significantly. From Fig. 4, it is easy to see that even small variations in b_1 may cause a shift from limit cycles to chaos or vice versa.

Although we do not present the results here, we have also examined the behavior of this system for other values of the parameter b_2 . We found chaos for values of b_2 other than the one ($b_2 = 2.0$) we used in the majority of our work; moreover, chaos appears more likely for larger values of b_2 , similar to the dependence on b_1 .

We further examined the behavior of the system for some selected values of b_1 by constructing a Poincaré map (Fig. 5). For our system, we chose a Poincaré section corresponding to a plane with z constant, in the "handle" of the teacup, where the trajectories pass through the plane from above. Thus, the Poincaré section is a set of x and y values. Moreover, for our system, as exhibited in the Fig. 5, the set of points on the Poincaré section is nearly one dimensional, i.e., it is very close to a line. Thus, we can approximate the dynamics of the Poincaré map by considering only one variable. We therefore considered $x(n+1)$ as a function of $x(n)$, where $x(n)$ is the value of x at the n th intersection of the trajectory with the Poincaré section. (Note that we could just as easily have used the y variable.)

We illustrate in Fig. 5 these Poincaré maps for two different values of b_1 (3.0 and 6.0) for which the bifurcation diagram suggested that the behavior would be chaotic. Note that the slope of the function relating $x(n+1)$ to $x(n)$ in these Poincaré maps is large in magnitude, another diagnostic feature of chaos. Recall that the quadratic map and the discrete time logistic function are single humped functions (e.g., May 1976, Guckenheimer and Holmes 1983), which lead to chaotic behavior if the functions are steep enough, i.e., if the absolute value of the slope of the function is large enough on average. However, the behavior is more complex in our food chain because there is more than a single hump in the Poincaré map. The presence of a multimodal Poincaré map indicates a variety of interesting dynamical properties for the differential equations (see, e.g., May 1979, Skjolding et al. 1983), which we will not explore further here.

ECOLOGICAL IMPLICATIONS

We have shown that chaos is possible for a simple, biologically reasonable, continuous-time, food chain model. The specific saturating forms for the consumption of prey by predators (i.e., "Type II" functional and numerical responses) are the most commonly chosen representations. Type II functional responses have been extensively used in ecological models since their introduction by Holling (1959). Since that time, applications include (but are not limited to): arthropod models (Murdoch and Oaten 1975, Hassell 1978) and models of phytoplankton competing for nutrients (Taylor and Williams 1975, Waltman et al. 1980, Smouse 1981, Tilman 1982, Powell and Richerson 1985). Further, these forms were used in the early mechanistic models of marine food chains (Steele 1974) and still form the basis for such applications (Frost 1987). Note that Table 1 and Fig. 2 show that the chaotic regime includes the region where b_1x and b_2y are not far from unity. This is precisely the region of greatest biological interest. If b_1x (and b_2y) are much greater than unity, then the saturating Type II forms are close to constant, and the predator saturation effect (i.e., predator grazing is saturated by more than ample prey) is eliminated. Conversely, when b_1x is small compared to one, then the Type II forms are nearly linear, and no saturation effect is seen. It is precisely the regions where "the biology" becomes important, i.e., when b_1x is ≈ 1 and predators begin to saturate, that the nonlinearities in $f_1(x)$ and $f_2(y)$ in Eq. 5 generate chaos.

Our model suggests that chaotic behavior may be much more common in natural systems with interacting producers and consumers (predators and prey) than Hassell et al. (1976) predicted on the basis of one-species discrete time models. It is our interpretation that chaos ultimately arises in this food chain model because of the tendency for predator-prey systems to oscillate. One predator-prey subsystem, for concreteness say X and Y , oscillates at one frequency, while another, Y and Z , oscillates at a different frequency; the frequencies are determined by the model parameters. In particular, the interaction at the higher trophic levels has a longer natural period because the average lifetime of the top predators is longer than the average lifetime of the consumers at the lower trophic levels. (Our simulations reflect this.) The two systems are (nonlinearly) coupled through species Y because the predator in one is the prey in the other. We conjecture that when the period of one oscillation is not some multiple of the other frequency (i.e., the frequencies are incommensurate) chaos arises, in a manner similar to the occurrence of chaos in periodically forced oscillations. Food webs depict a complex net of (nonlinearly) coupled producer-consumer interactions; accordingly, one should not be surprised to find many subsystems within a food web going through the oscillations that are a common feature of all predator-

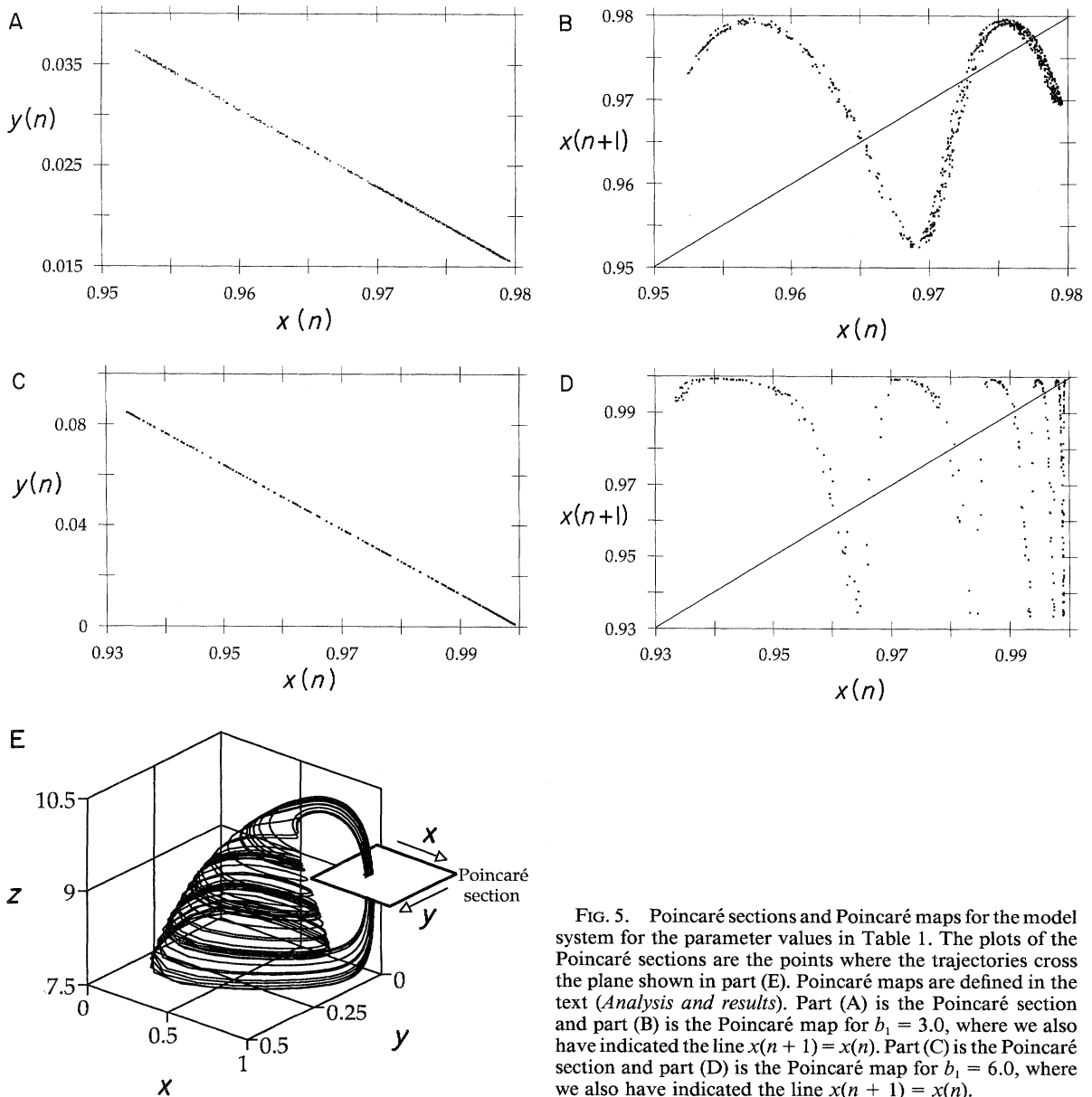


FIG. 5. Poincaré sections and Poincaré maps for the model system for the parameter values in Table 1. The plots of the Poincaré sections are the points where the trajectories cross the plane shown in part (E). Poincaré maps are defined in the text (*Analysis and results*). Part (A) is the Poincaré section and part (B) is the Poincaré map for $b_1 = 3.0$, where we also have indicated the line $x(n + 1) = x(n)$. Part (C) is the Poincaré section and part (D) is the Poincaré map for $b_1 = 6.0$, where we also have indicated the line $x(n + 1) = x(n)$.

prey systems. It seems unlikely that the frequencies of all the linked subsystems will be commensurate. Accordingly, one expects that at least some, perhaps most, of the linked predator-prey subsystems may be simultaneously undergoing chaotic oscillations.

It is instructive to compare this view with the three-species study (a predator consuming two competing prey) of Gilpin (1979), in which chaotic behavior was identified. Typically, one does not associate oscillations with competition models based on results from two-species Lotka-Volterra competition (e.g., May 1973). However, once three or more species are allowed, oscillations can occur (May and Leonard 1975, Powell and Richerson 1985). We conjecture that food webs containing a number of competing species can

also “go chaotic” in the same way as our consumer-producer food chain does.

Consequences for food web models

What are the implications of our results for food web models? First, our conclusions question the conventional wisdom that chaos must be rare in nature. Whenever consumers and producers are undergoing oscillations, chaotic oscillations, as we have described here, may be a strong possibility for realistic parameter values. Second, chaotic behavior, as Fig. 2 shows, need not lead to an erratic and unpatterned trajectory in time that one might infer from the usual (not mathematical) connotation of the word “chaos.” Rather, the term “regular oscillations” better describes the curves

of x , y , and z vs. t as seen in Fig. 2. As emphasized by Schaffer, detecting chaos in natural populations may be very difficult. Third, the time scales under consideration are very important. Over short time scales, say a few oscillation periods, the behavior is fairly regular. However, over many periods of oscillation the effects of sensitivity to initial conditions and unpredictability become much more important.

If a generalization from a food web model depends critically upon behavior after a long time, then the role of chaos may be much more crucial. For example, when a model formulation suggests that chaotic behavior is a strong possibility, then one might be skeptical about conclusions drawn from linear stability analyses around equilibria. This includes conclusions drawn on the basis of "return time" arguments (Pimm 1982, 1984), since "return times" are the inverses of eigenvalues of Jacobian matrices evaluated at equilibria. Moreover, the existence of chaotic behavior may depend very delicately on the exact form that terms in equations take. For example, we have not included any feedback effects of recycling through activities of the predators upon the prey. We have not examined solutions to our model suitably modified to account for these considerations. We do not know with certainty that chaotic behavior will be found.

For what ecological questions is chaotic behavior important? The answer depends on the number of species, the kinds of interactions, and the time scale. Results of our and earlier investigations certainly suggest that much more complex behavior will be seen in models of simple three-species food chains than in any two-species models. Nonetheless, a great many important results can be obtained on the basis of behavior in the nonchaotic region of parameter space. Moreover, it is much easier to develop intuition from the simpler two-species models. The geometry of strange attractors in three dimensions is exceedingly complicated (Guckenheimer and Holmes 1983). The addition of more species that "inhabit" a food web can only make analysis of models more challenging.

ACKNOWLEDGMENTS

We profited from comments by S. Vail and C. L. Hom on earlier drafts. We are particularly indebted to W. Schaffer who pointed out an error in our earlier interpretation, and suggested the use of the bifurcation diagram and the Poincaré map. We appreciate his encouragement and enthusiasm. We appreciate the reviews of M. Kot and an anonymous referee. A. Hastings was supported by grant DE-FG03-89ER60886/A000 from the Ecological Research Division, Office of Health and Environmental Research, United States Department of Energy. This support does not constitute an endorsement of the views expressed here. T. Powell thanks NSF for support to project SUPER (NSF OCE 86-13749).

LITERATURE CITED

- Carpenter, S. R., and J. F. Kitchell. 1984. Plankton community structure and limnetic primary production. *American Naturalist* **124**:159–172.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cocharan, J. J. Elser, D. M. Lodge, D. Kretchmer, and X. He. 1987. Regulation of lake primary productivity by food-web structure. *Ecology* **68**:1873–1876.
- Frost, B. W. 1987. Grazing control of phytoplankton stock in the open subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid *Neocalanus* spp. *Marine Ecology Progress Series* **39**:49–68.
- Gilpin, M. E. 1979. Spiral chaos in a predator-prey model. *American Naturalist* **107**:306–308.
- Glass, L., and M. M. Mackey. 1988. From clocks to chaos. Princeton University Press, Princeton, New Jersey, USA.
- Guckenheimer, J., and P. Holmes. 1983. Nonlinear oscillations, dynamical systems and bifurcations of vector fields. Springer-Verlag, New York, New York, USA.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey, USA.
- Hassell, M. P., J. H. Lawton, and R. M. May. 1976. Patterns of dynamical behaviour in single-species populations. *Journal of Animal Ecology* **45**:471–486.
- Hindmarsh, A. C. 1980. LSODE and LSODI, two new initial value ordinary differential equation solvers. *ACM-SIGNUM Newsletter* **15**:10–11.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* **91**:385–398.
- Lin, C. C., and L. Segel. 1974. Mathematics applied to deterministic problems in the natural sciences. MacMillan, New York, New York, USA.
- May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.
- . 1974. Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. *Science* **186**:645–647.
- . 1976. Simple mathematical models with very complicated dynamics. *Nature* **261**:459–467.
- . 1979. Bifurcations and dynamic complexity in ecological systems. *Annals of the New York Academy of Sciences* **316**:517–529.
- May, R. M., and W. J. Leonard. 1975. Nonlinear aspects of competition between three species. *SIAM Journal on Applied Mathematics* **29**:243–253.
- May, R. M., and G. F. Oster. 1976. Bifurcation and dynamic complexity in simple ecological models. *American Naturalist* **110**:573–599.
- Murdoch, W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* **9**:1–125.
- Nisbet, R. M., and W. S. C. Gurney. 1982. Modelling fluctuating populations. John Wiley & Sons, New York, New York, USA.
- Olsen, L. F., G. L. Truty, and W. M. Schaffer. 1988. Oscillations and chaos in epidemics: a non-linear dynamic study of six childhood diseases in Copenhagen, Denmark. *Theoretical Population Biology* **33**:344–370.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- . 1988. Food webs: road maps of interaction or grist for theoretical development? *Ecology* **69**:1648–1654.
- Pimm, S. L. 1982. Food webs. Chapman and Hall, New York, New York, USA.
- . 1984. Food chains and return times. Pages 397–412 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities*. Princeton University Press, Princeton, New Jersey, USA.
- Powell, T., and P. J. Richerson. 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton systems: a theoretical model. *American Naturalist* **125**:431–464.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPherson, J. N.

- Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* **11**:41–65.
- Rosenzweig, M. L. 1973. Exploitation in three trophic levels. *American Naturalist* **107**:275–294.
- Roughgarden, J., R. M. May, and S. A. Levin. 1989. *Perspectives in ecological theory*. Princeton University Press, Princeton, New Jersey, USA.
- Schaffer, W. M. 1985. Order and chaos in ecological systems. *Ecology* **66**:93–106.
- Schaffer, W. M., and M. Kot. 1985a. Nearly one dimensional dynamics in an epidemic. *Journal of Theoretical Biology* **112**:403–427.
- Schaffer, W. M., and M. Kot. 1985b. Do strange attractors govern ecological systems? *BioScience* **35**:342–350.
- Schaffer, W. M., and M. Kot. 1986a. Chaos in ecological systems: the coals that Newcastle forgot. *Trends in Ecology and Evolution* **1**:58–63.
- Schaffer, W. M., and M. Kot. 1986b. Differential systems in ecology and epidemiology. Pages 158–178 in A. V. Holden, editor. *Chaos: an introduction*. University of Manchester Press, Manchester, England.
- Segel, L. 1984. *Modelling dynamic phenomena in molecular and cellular biology*. Cambridge University Press, Cambridge, England.
- Skjolding, H., B. Branner-Jorgenson, P. L. Christiansen, and H. E. Jensen. 1983. Bifurcations in discrete dynamical systems with cubic maps. *SIAM Journal on Applied Mathematics* **43**:520–534.
- Smouse, P. E. 1981. Mathematical models for continuous culture growth dynamics of mixed populations subsisting on a heterogeneous resource base. II. Predation and trophic structure. *Theoretical Population Biology* **20**:127–149.
- Steele, J. H. 1974. *The structure of marine ecosystems*. Harvard University Press, Cambridge, Massachusetts, USA.
- Taylor, P. A., and P. J. L. Williams. 1975. Theoretical studies on the coexistence of competing species under continuous flow conditions. *Canadian Journal of Microbiology* **21**:90–98.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.
- Waltman, P., S. P. Hubbell, and S. Hsu. 1980. Pages 107–152 in T. A. Burton, editor. *Modelling and differential equations in biology*. Marcel Dekker, New York, New York, USA.
- Wollkind, D. J. 1976. Exploitation in three trophic levels: an extension allowing intraspecific carnivore interaction. *American Naturalist* **110**:431–447.