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BIOLOGICAL CONDITIONS FOR CHAOS IN A THREE-SPECIES FOOD CHAIN

Kevin McCann¹ and Peter Yodzis¹

Although the discrete-time logistic model provided one of the very first examples of chaotic dynamics, and despite the fact that population models tend to be highly nonlinear, thus far chaos has played a surprisingly small role in ecology. Some investigators have found (in the context of insect population dynamics) that the parameters that produce chaos tend to be biologically unrealistic (Hassell et al. 1976); others have argued that evolution tends to favor nonchaotic dynamics (Berrymann and Millstein 1989). Indeed, the known examples of chaotic population systems tend to be extreme in one way or another.

Hastings and Powell (1991) have produced a new example of a chaotic population system, a simple three-species food chain with Type II functional responses. This is a particularly intriguing example because it can be viewed as an approximation—if admittedly a very crude one—to a whole ecological community, rather than some sort of subsystem. Moreover, the basic feature that generates the chaos—coupled oscillations—is just as likely to be present in more detailed whole-system models as in the simple food chain. But one still needs to ask whether there might be something extreme about the parameter values that produce chaos in this system. We show here that the parameter values used by Hastings and Powell are indeed rather improbable biologically, but we indicate biologically reasonable parameters that also produce chaos. Finally, we offer some generalities as to which biological conditions favor chaos in these food chains.

Yodzis and Innes (1992) have shown how to relate parameter values in just such models as employed by Hastings and Powell to the body sizes and metabolic characteristics of the animals involved. In the notation of Yodzis and Innes, Hastings and Powell's (1991) model reads

$$\frac{dR}{dt} = R(1 - R) - x_C y_C \frac{CR}{R + R_0},$$

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$$\frac{dC}{dt} = x_C C \left[-1 + y_C \frac{R}{R + R_0} \right] - x_P y_P \frac{PC}{C + C_0},$$

and

$$\frac{dP}{dt} = x_P P \left[-1 + y_P \frac{C}{C + C_0} \right].$$

This corresponds to a food chain in which a resource population with density R is eaten by a consumer with density C , which in turn is fed upon by a predator with density P . In addition, the predator consumes the entire biomass of each prey individual. Henceforth we will refer to the consumer C as the prey species. The parameter x_i is the mass-specific metabolic rate of species i , measured relative to the production-to-biomass ratio of the resource population, while y_i is a measure of ingestion rate per unit metabolic rate of species i . The point of parameterizing the equation in this way is that the parameters x_i scale allometrically with individual body size, while the metabolic types of the animals (endotherm, vertebrate ectotherm, or invertebrate ectotherm) constrain the plausible ranges of the parameters y_i (Yodzis and Innes 1992).

Specifically, y_i lies in the interval $(1, y_{i\max})$, where the value of $y_{i\max}$ (called the ecological scope by Yodzis and Innes) depends on the metabolic type of species i as follows: for an (endotherm, vertebrate ectotherm, invertebrate ectotherm) $y_{i\max}$ is (1.6, 3.9, 19.4, respectively). Furthermore, from expressions for x_i given by Yodzis and Innes (1992) it follows immediately that the ratio of predator to prey body mass is given by $m_P/m_C = (a_{TP}/a_{TC})^4 (x_C/x_P)^4$, where a_{Ti} is an allometric coefficient for metabolic rate appropriate to the metabolic type of species i . In units of $\text{kg} \cdot (\text{kg}^{-1} \cdot \text{yr}^{-1}) \cdot \text{kg}^{0.25}$, for a (vertebrate, invertebrate) ectotherm one finds $a_{Ti} = (2.3, 0.5)$.

The parameters chosen by Hastings and Powell (1991) are as follows: $(x_C, x_P, y_C, y_P) = (0.4, .01, 2.01\text{--}6.25, 5.)$. Since $y_P > 3.9$ we conclude that the predator can only be an invertebrate. The range of y_C values could include vertebrate ectotherms at the lower end (< 3.9); otherwise the prey must be an invertebrate as well. If the prey is a vertebrate ectotherm, then the mass ratio is $m_P/m_C = 5.7 \cdot 10^3$; if it is an invertebrate then $m_P/m_C = 2.6 \cdot 10^6$. A predator-to-prey mass ratio $5.7 \cdot 10^3$ makes no sense at all for an invertebrate feeding on a vertebrate ectotherm. If the prey is an invertebrate, the corresponding mass ratio $2.6 \cdot 10^6$ is, perhaps, thinkable, but rather extreme. Data surveys (Peters 1983, Cohen et al. 1993) suggest that "typical" predator-to-prey body mass ratios are in the range $10^1\text{--}10^3$.

Our first conclusion, then, is that the example of food chain chaos provided by Hastings and Powell is bio-

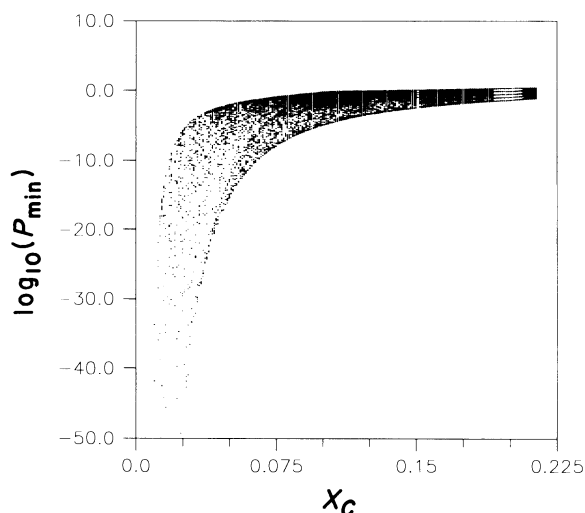


FIG. 1. For a range of values of the parameter x_C , a set of local minima taken on by the predator density P in solutions of the system of equations discussed in the text. Plausible predator-to-prey body mass ratios range from about $x_C = 0.018$ ($m_P/m_C = 10$) to about $x_C = 0.056$ ($m_P/m_C = 10^3$). The other parameters are held constant at: $y_C = 2.01$, $x_P = 0.01$, $y_P = 5.0$, $R_0 = 0.161$, $C_0 = 0.5$. C = consumer (prey species) density; R = resource population density.

logically extreme. This raises the question of whether there are also chaotic solutions for biologically plausible parameter values.

If we change x_C while keeping all other parameters at the Hastings–Powell values we see immediately that we need to refine our question. Fig. 1 plots the set of local minima taken on by the density P , starting after a very long time so that one is very near the attractor, for values of x_C less than the Hastings–Powell value of 0.4, hence for smaller predator-to-prey mass ratios than theirs. There is complex dynamics all the way down to $x_C = 0.02$ (indicated by phase space plots as well as the “thick” nature of the attractor as viewed in Fig. 1), but at approximately $x_C = 0.06$ the attractor begins to move very quickly (with respect to further changes in x_C) toward the R – C plane. (Note that the minimum values of P are plotted in Fig. 1 on a log scale.) For x_C less than approximately 0.06, values of the density P on the attractor become so very small that the predator population would be unlikely to persist. This corresponds to an invertebrate-to-invertebrate mass ratio of $1.3 \cdot 10^3$ —just on the very threshold of plausibility. So, by reducing x_C to get a mass ratio $< 10^3$ we can get chaos, but not chaos that is likely to persist. What we seek are chaotic solutions in which all three densities remain bounded away from zero by some “healthy” amount. We will call this *persistent chaos*.

We can achieve persistent chaos by increasing x_P from the value 0.01 used by Hastings and Powell (Fig.

2). We obtain chaotic solutions that are nicely bounded away from zero for x_P in the range 0.065–0.095, corresponding to mass ratios in the range $1.4 \cdot 10^3$ – $3.1 \cdot 10^2$.

Our second conclusion, then, is that there do exist biologically plausible parameter values such that the food chain system possesses chaotic solutions, nicely bounded away from zero.

However, this biologically plausible chaos occurs near the transition to chaos at $x_P = 0.095$ (Fig. 2). It is a rather mild chaos (Fig. 3), in which the “handle” of Hastings and Powell’s “teacup” (Hastings and Powell 1991:898) is only just beginning to separate (Figs. 4 and 5). Reducing either y_C or y_P below the maximum plausible value 1.6 for endotherms, while keeping all other parameters at the Hastings–Powell values, does not permit chaos. This much creates an impression that persistent chaos, while present in the biologically plausible region in parameter space, is not very common there.

Up to this point we have said nothing about the parameters R_0 , C_0 . They are the half saturation densities for the consumer and predator functional responses, measured in the units of resource carrying capacity (which has been scaled to unity in our form of the equations). Decreasing these parameters is equivalent to increasing the resource carrying capacity. We have done a full mathematical analysis of the bifurcation structure of solutions to this system of equations, to be published elsewhere, that suggests that, for

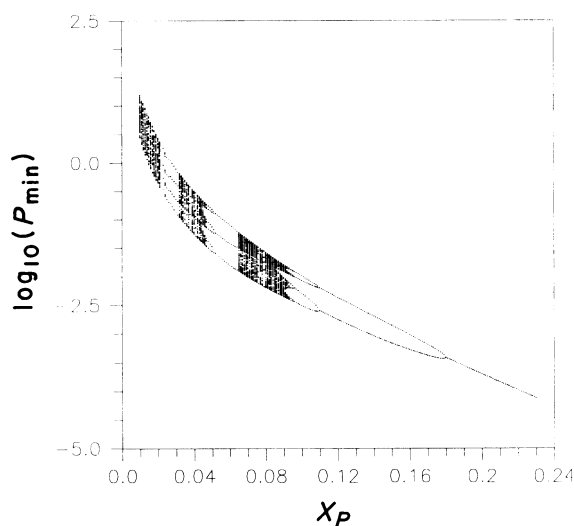


FIG. 2. For a range of values of the parameter x_P , the set of local minima taken on by the predator density P in solutions of the system of equations discussed in the text. Plausible predator-to-prey body mass ratios range from about $x_P = 0.071$ ($m_P/m_C = 10$) to about $x_P = 0.225$ ($m_P/m_C = 10^3$). The other parameters are held constant at: $y_C = 2.01$, $x_C = 0.4$, $y_P = 5.0$, $R_0 = 0.161$, and $C_0 = 0.5$.

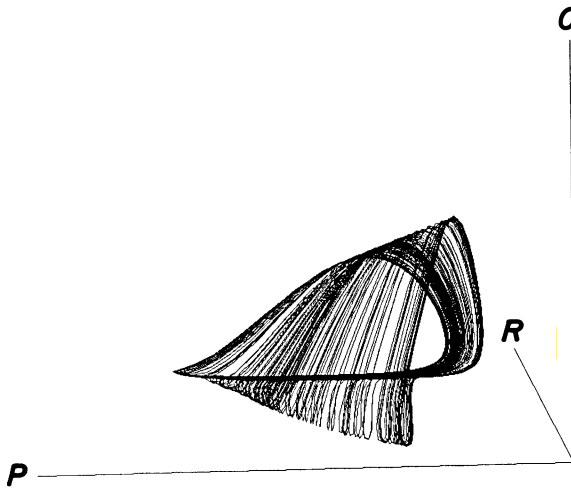


FIG. 3. Chaotic attractor for $x = 0.08$, other parameters as in Fig. 2. Displayed is the trajectory in phase space after integrating for a very long time to avoid transient behavior.

a very broad range of the other parameters, one can almost always obtain chaotic dynamics by decreasing one or both of the half saturation densities R_0 and C_0 (or, equivalently, by increasing the resource carrying capacity). Indeed, one of the sources of chaos in these systems is the coupling of incommensurate oscillations, a common phenomenon in many other contexts (for instance, Guckenheimer and Holmes 1983:71–72). But the constituent predator–prey oscillations themselves require large carrying capacities (Rosenzweig 1972).

Our third conclusion, then, is that the primary biological condition for chaos is a productive environment—in the sense either of large turnover of the resource (which translates into small x_i [Yodzis and Innes 1992]) or of large standing crop (carrying capacity) of the resource. Thus, the most likely systems for food chain chaos are enriched systems, or those in naturally very productive environments.

However, in many cases this will not be persistent chaos. Then we have a “paradox of enrichment” (Rosenzweig 1972) for food chains. Unfortunately, the formal bifurcation analysis, while lending insight into the occurrence of chaos, cannot easily be used to find persistent chaos. However, the underlying source of this chaos suggests a reduction of the persistence question of the three-species system to a simpler problem. Numerical experiments suggest very strongly that chaos arises in these systems from the coupling of oscillations (of the consumer–resource and predator–prey subsystems) with incommensurate frequencies. Boundedness of the chaotic attractor appears to be strongly associated with boundedness of the oscillations of each of these subsystems.

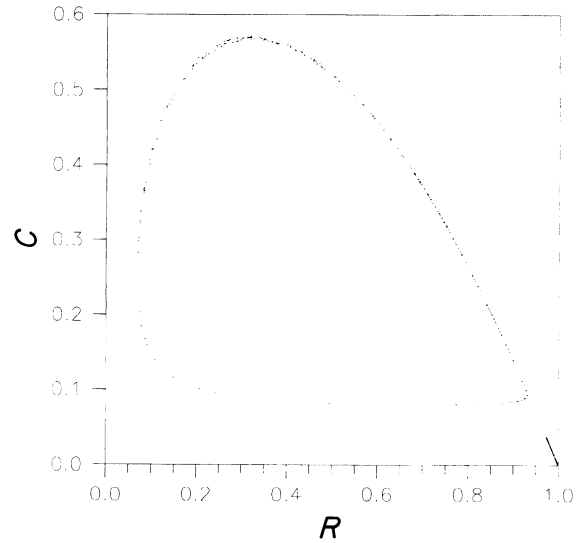


FIG. 4. Poincaré section for the attractor of Hastings and Powell. Displayed are the points at which the trajectory crosses the plane $P = 0.4$. Notice the “handle” of the “teacup” in the lower right hand corner.

is this similar to b_1/b_2 variation? they encompass the carrying capacity i think

We conjecture that persistent chaos tends to be associated with relatively bounded oscillations both of the consumer–resource pair (C, R) and of the predator–prey pair (P, C). The boundedness of two-species oscillations has been addressed by Yodzis and Innes (1992), who conclude that the conditions favoring bounded oscillations are (a) larger values of the param-

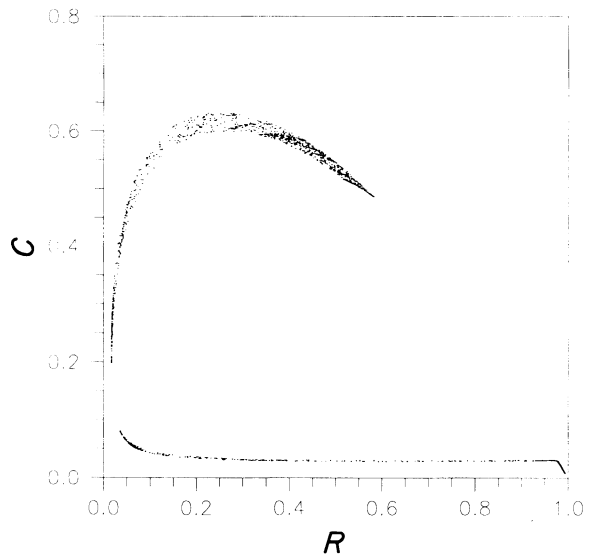


FIG. 5. Poincaré section for the attractor shown in Fig. 3. Though not evident in Fig. 3, a hint of the “handle” of a “teacup” can be seen in the lower right hand corner.

eters y_i , from which it follows that invertebrates would be more likely than vertebrate ectotherms, which would be more likely than endotherms, to be involved in food chain chaos; and (b) certain ranges of values of the mass ratios m_p/m_c and m_c/m_R , which affect the growth of oscillation magnitude in ways that are simple but fairly lengthy to describe explicitly (but see Yodzis and Innes [1992] for a complete discussion).

Chaos in food chains (and, surely, in other whole-system models as well) ought to be quite common when the resource productivity is sufficiently high. The obvious question, how high is sufficiently high, is particularly difficult to answer in this context, for the appropriate measure of resource carrying capacity is relative to the half saturation density of consumers in the system. There are few data available on this point, but one would expect a great deal of variation among taxa. Functional responses under field conditions, while difficult to measure, are vital for theoretical understanding.

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PATCH SIZE EFFECTS ON MARSH PLANT SECONDARY SUCCESSION MECHANISMS

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The response of communities to natural disturbance has historically been of interest to ecologists (Clements 1916) and has recently received renewed attention (Pickett and White 1985). Natural disturbances are ubiquitous in nature and the frequency, intensity, and spatial scale of disturbance can greatly affect the species composition, diversity, and organization of communities. In densely packed environments such as salt marshes, old fields, and rocky intertidal and subtidal habitats where 100% of available substrate is often

occupied, disturbance releases valuable resources (space, light, nutrients), allowing expansion by clonal species and the opportunity for recruitment by fugitive species (Bazzaz 1979, Sousa 1984, Connell and Keough 1985, Bertness et al. 1992). Successional mechanisms may be influenced by competition, predation, and environmental conditions (Connell and Slatyer 1977). Moreover, the Clementsian facilitation model of succession has recently been revived by experimental studies. These studies suggest that facilitation is associated with physically stressful environments that must be modified by pioneer species before competitive dominants are able to colonize (Wood and del Moral 1987, Bertness 1991, Bertness and Shumway 1993).

New England salt marshes are physically stressful communities inhabited by a small number of stress-tolerant halophytes. These communities are subject to annual disturbance by the tidal deposition of plant debris. If this debris (wrack) remains in place it can smother underlying vegetation and create bare patches ranging from fractions of a square metre to 50 m² in size (Bertness and Ellison 1987). Solar evaporation of tidal water on the surface of bare patches drives a salinization process that renders bare patches highly stressful to plant growth (Bertness et al. 1992). Patches are initially colonized by *Salicornia europaea* and *Distichlis*

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