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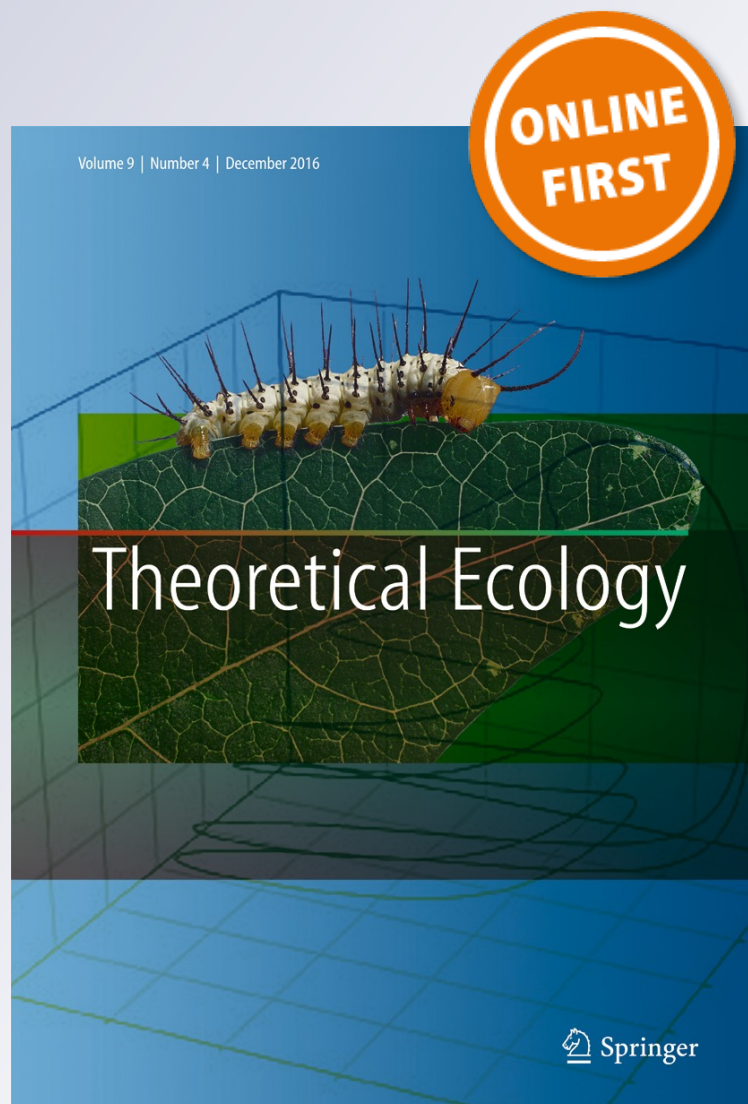
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Volume 9 | Number 4 | December 2016

Theoretical Ecology

Springer

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ORIGINAL PAPER

Chaotic attractor in two-prey one-predator system originates from interplay of limit cycles

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Abstract We investigate the appearance of chaos in a microbial 3-species model motivated by a potentially chaotic real world system (as characterized by positive Lyapunov exponents (Becks et al., Nature **435**, 2005). This is the first quantitative model that simulates characteristic population dynamics in the system. A striking feature of the experiment was three consecutive regimes of limit cycles, chaotic dynamics and a fixed point. Our model reproduces this pattern. Numerical simulations of the system reveal the presence of a chaotic attractor in the intermediate parameter window between two regimes of periodic coexistence (stable limit cycles). In particular, this intermediate structure can be explained by competition between the two distinct periodic dynamics. It provides the basis for stable coexistence of all three species: environmental perturbations may result in huge fluctuations in species abundances, however, the system at large tolerates those perturbations in the sense that the population abundances quickly fall back onto the chaotic attractor manifold and the system remains. This mechanism explains how chaos helps the system to persist and stabilize against migration. In discrete populations, fluctuations can push the system towards extinction of one or more species. The chaotic attractor protects the system and extinction times scale exponentially with system size in the same way as with limit cycles or in a stable situation.

Keywords Bacteria · Deterministic chaos · Chaotic attractor · Chemostat system · Food web · Mean time to extinction · Predator prey system · Population dynamics

Introduction

Chaos can stabilize diversity in microbial communities. Numerical results (Huisman and Weissing 1999; Takeuchi and Adachi 1983) as well as experimental data (Costantino et al. 1997; Becks et al. 2005; Benincà et al. 2008) show that not only periodicity but also chaotic dynamics can sustain diversity. This paper investigates mechanisms giving rise to the formation of a chaotic attractor and its stabilizing properties in a two-prey one-predator model simulating the real world experiment of Becks et al. (2005).

Understanding and forecasting population dynamics and biodiversity are nowadays more important than ever for example to manage sustainable natural populations and fisheries considering changes like pollution, climate change or species migration etc. (Caswell et al. 2011; Sugihara et al. 2011; Shelton and Mangel 2011). In the 1920s, Lotka (1925) and Volterra (1928) formulated the first mathematical models for simple food webs. Since then theoretical modeling has led to important and often surprising contributions to the understanding of ecological dynamics (Turchin 2003). Studies predict that predators play an important role in maintaining species diversity: in the presence of a common predator more than one species can survive on a shared food source. In the absence of predation-pressure one species will suppress all others (Leibold 1996).

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Non-equilibrium dynamics can maintain diversity as well. In the 1930s, Gause elaborated on a concept formed in the 1830s and 1840s: the law of minimum. Experiments led him to the conclusion that two species competing for a mutual resource cannot coexist in a constant environment. One population will always outgrow the other until extinction (Sprengel 1831; von Liebig 1840; Gause 1934). This concept is limited to steady state conditions, though, and not universal. Systems with more competitors than resources can persist when nonlinear interactions generate cyclic behaviour (Koch 1974; Zicarelli 1975; Armstrong and McGehee 1976). In numerical simulations by Huisman and Weissing (1999), chaotic fluctuations allow diverse phytoplankton communities to thrive on a handful of resources.

Ecological dynamics show massive periodic and aperiodic fluctuations. This has been seen, e.g. in ciliate-bacteria interactions (Jost et al. 1973), flour beetle (*Tribolium castaneum*) dynamics (Costantino et al. 1997; Dennis et al. 1997) and rotifer–algae interactions (Fussmann et al. 2000). Different mechanisms may be responsible for such irregular features: demographic noise, i.e. the fluctuations caused by the discreteness of the replication steps at which population sizes change, may effectively randomize otherwise regular dynamics in small systems or induce periodicity (Traulsen et al. 2012; Gibson and Wilson 2013). Environmental fluctuations, i.e. fluctuations inferred through the inevitable coupling of realistic systems to a larger outside world, may also play an important role (Lorenz 1963; Laakso et al. 2003; Domis et al. 2007). A third source of fluctuations is intrinsically chaotic dynamics.

Nonlinearly coupled and interacting communities can show deterministic chaos for certain parameter values (May and Leonard 1975; Takeuchi and Adachi 1983; Hastings and Powell 1991; Vayenas and Pavlou 1999; Kooi and Boer 2003). The dynamics under such circumstances are deterministic in the sense that they are determined by deterministic (non-stochastic) differential equations. However, chaos manifests itself in that the slightest uncertainty in the system's initial condition will grow exponentially. As a consequence, the evolution of the system becomes unpredictable after a certain time interval, and population sizes fluctuate wildly even in very large populations. Nevertheless, the chaotic system may be stable in that population numbers evolve towards some 'attractor manifold', i.e. a lower dimensional complex structure embedded in the phase space of population sizes.

Perhaps counter-intuitively, the chaotic attractor acts as a very potent source of stability. Wild fluctuations in size notwithstanding, the populations are bound to the attractor and quickly (exponentially) fall back to it in the presence of external perturbations. In particular, they are protected against accidental extinction by fluctuations.

In this paper, we discuss and quantitatively model the conceptual mechanisms promoting chaotic multi-species coexistence in a two-prey one-predator model system motivated by the experiment Becks et al. (2005). Our system is governed by an important control parameter, an external dilution rate which acts as a paradigm for the abundance of basic resources consumable by the species. Both in the regime of low and high resource availability, the system builds up limit cycles controlling the population size. The two cycles at high and low dilution rate are topologically distinct, in a manner to be discussed below. The wide range of intermediate parameter strength is governed by a 'competition' between the two cycle regimes, and this will be shown to lead to the formation of a chaotic attractor interpolating between the limiting dynamics.

The suggestion that chaotic attractors may emerge from the competition between parametrically separated limit cycles is one main result of the present paper. Fixed points and limit cycles for different parameter regimes are a generic feature of predator-prey systems and their interplay might suggest a generic mechanism promoting the transition to chaos.

Below, the predictions derived for our current specific model will be shown to be in good agreement with the experiment Becks et al. (2005) where population numbers in chemostat experiments could be tuned from stationary to periodic or chaotic and back depending on the applied dilution rate.

Another important outcome is the confirmation of the protecting properties of chaos. Although fluctuations strongly suppress population numbers the chaotic attractor actually protects them exponentially against extinction.

Methods

The system we consider models an aquatic well-mixed microbial community established in a chemostat. Prey populations compete with each other for nutrients but also via a common predator. In the experiments under consideration two bacterial strains live on soluble organic matter, while a bacterivorous ciliate feeds upon the two different bacterial strains. The competition is characterized by a trade-off: one bacterial strain is preferred by the predator but fast in growth. The other strain is less-preferred but slow-growing. At a rate D fresh nutrient solution flows into the chemostat vessel of constant volume. Via the overflow, a mixture of microbes and nutrients leaves the system and thereby dilutes the community inside the chemostat. By tuning this dilution rate/ turnover rate, we will test the behavioral range of the system (Fig. 1). The following differential equations describe the temporal behavior of the concentrations in the system. We assume growth according to Holling's type II or
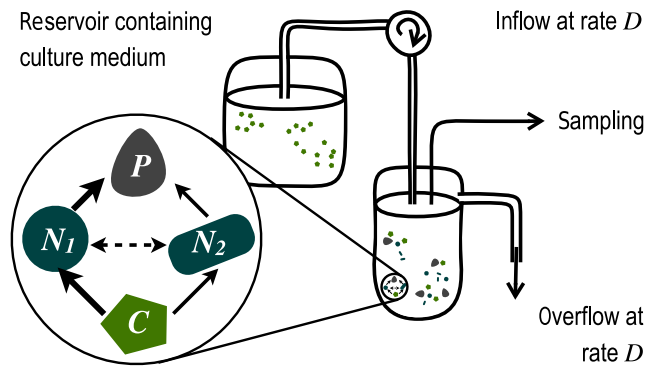
Fig. 1 The outline of the experimental setup. Inset the schematic structure of interactions in the the predator prey system. *Bold* (*thin*) *arrows* mark strong (weak) energy/biomass flow, indirect competition is shown as *dashed arrow*. P predator, C carbon source, N_1 prey 1, N_2 prey 2

Monod function (Monod 1949; Holling 1959). This is a well established choice in the context of bacterial and microbial growth (Levin et al. 1977; Bohannan and Lenski 1999).

$$\frac{dC}{dt} = (C_0 - C)D - \epsilon_1 N_1 \mu_1(C) - \epsilon_2 N_2 \mu_2(C)$$
$$\frac{dN_i}{dt} = N_i \mu_i(C) - P\phi_i(N_i) - DN_i \quad , i = 1, 2$$
$$\frac{dP}{dt} = \beta_1 P\phi_1(N_1) + \beta_2 P\phi_2(N_2) - DP \tag{1}$$

The concentration P of predators per unit volume grows at a per capita rate that depends on the prey populations; the concentration of prey N_i declines accordingly. The grazing rate of a predator on the bacteria i is denoted by $\phi_i(N_i)$. The ratio of new predators per ingested prey i is β_i (yield). In almost the same manner, the bacteria of type i multiply by a rate $\mu_i(C)$ while feeding with a rate $\epsilon_i \mu_i(C)$, where ϵ_i is the reciprocal yield of ingested biomass per new prey. The growth rate $\mu_i(C)$ of prey i saturates at $\hat{\mu}_i$ following Monod's equation (Monod 1949) with half saturation rate K_{si} just as the grazing rates $\phi_i(N_i)$:

$$\mu_i(C) = \frac{\hat{\mu}_i C}{K_{si} + C}$$
$$\phi_i(N_i) = \frac{\hat{\phi}_i N_i}{K_{Ni} + N_i} \tag{2}$$

For one specific microbial community and nutrient solution, the dilution rate is the only variable left. All other parameters define biological properties of species. These properties are chosen to model the species in experiments performed by Becks et al. (2005). The parameter values in Table 1 were determined experimentally by Lutz Becks and Mar Monsonis Nomdedeu for *Tetrahymena*, *Pedobacter* and *Brevundimonas/ Acinetobacter* (these bacteria act similar in the food web) (Nomdedeu 2010).

Table 1 Model parameters determined by Lutz Becks and Nomdedeu (2010) and critical dilution values (numerical results up to four digits)

Concentration in nutrient medium [$\frac{\mu g\ Gluc}{ml}$]	
C_0	3
Reciprocal yields [$\frac{\mu g\ Gluc}{ind_i}$]	
ϵ_i	$2 \cdot 10^{-6}$
Predator yields [$\frac{ind_p}{ind_i}$]	
β	$2.5 \cdot 10^{-4}$
Maximal growth rates [h^{-1}]	
$\hat{\mu}_1$	0.15
$\hat{\mu}_2$	0.172
Maximal feeding rates [$\frac{ind_i}{ind_p \cdot h}$]	
$\hat{\phi}_1$	150
$\hat{\phi}_2$	450
Half saturation concentrations [$\frac{\mu g\ Gluc}{ml}$]	
K_{s1}	0.0274
K_{s2}	0.002
Half saturation concentrations [$10^3 \frac{ind_i}{ml}$]	
K_{N1}	422
K_{N2}	400
Critical dilution rates [h^{-1}]	
a	0.0267
b	0.0309
c	0.0544
d	0.0790

Results

Numerical integration of (1) shows that the population numbers perform dynamical patterns depending on the strength of dilution. They can be organized into a few general groups: stationary, periodic and chaotic dynamics. Without predator only one prey species will survive, the other will quickly go extinct while in the presence of a predator two species coexist. More interestingly, all three species can coexist. The dilution values corresponding to qualitative changes

Fig. 2 Real parts of the eigenvalues of the Jacobian of the linearized system for all fixed points of coexistence with varying dilution. Negative real parts correspond to stable directions, dark bars indicate regimes of stable fixed points. *Green*: X^{+0+}, *blue*: X^{0++}, *purple*: the two 3-species fixed points $X_{1,2}^{+++}$. Critical values a – d refer to Table 1
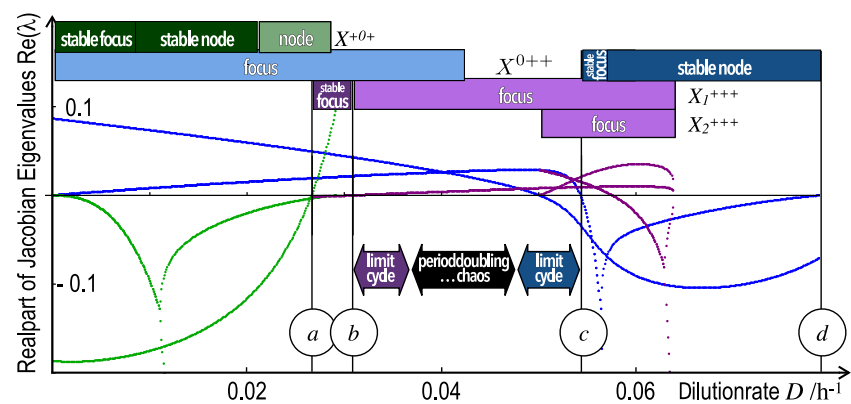
in the dynamics are summarized in Table 1. The regimes of different dynamics can be described in several ways. Before analysing the dynamical patterns via bifurcation diagram, we note that an alternative way to encode system information is in terms of its fixed point structure (Fig. 2).

Fixed points of the differential equations (1), i.e. configurations (C, N_1, N_2, P) where $d_t C = d_t N_i = d_t P = 0$, can be found numerically. Depending on the parameter values of the system different fixed points are realized and shown in Fig. 3. We denote the different multiple-species fixed points as

– X^{+0+}: predator feeds only on prey 1
– X^{0++}: predator feeds only on prey 2
– $X_{1,2}^{+++}$: the two different 3-species equilibria

To investigate the stability properties of these stationary configurations, we determine the eigenvalues of the Jacobian of the linearized system. Eigenvalues with non-zero imaginary parts correspond to a spiral point (or focus), three real eigenvalues imply nodes. If all three eigenvalues possess negative real parts the focus or node respectively is stable while positive real parts correspond to unstable directions.
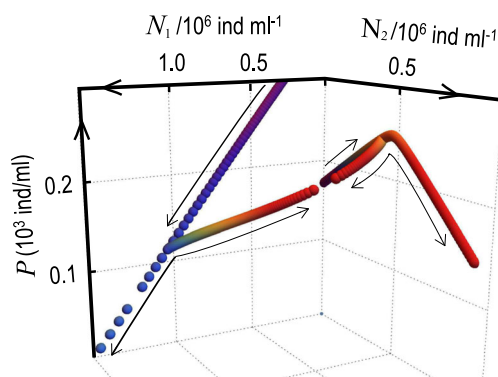
We here restrict ourselves to a discussion of the fixed points relevant to the attractor formation (Fig. 2):

– $D < a$: stable 2-species coexistence X^{+0+}
– $D = a$: stable 3-species equilibrium X_1^{+++} emerges from X^{+0+} (Fig. 3) and X^{+0+} looses stability.
– $D = b$: the 3-species equilibrium X_1^{+++} becomes a saddle, i.e. looses stability
– $c \leq D \leq d$: stable 2-species coexistence X^{0++}
– $D > d$: no stable fixed point

In the parameter window without stable fixed points $b < D < d$ the population numbers oscillate periodically or chaotically. Two foci are of particular interest to the formation of the chaotic attractor: at the lower end of the window ($D = b$) a 3-species focus X_1^{+++} looses stability; at the other end ($D = c$) a 2-species focus X^{0++} becomes stable.

Simulating the dynamics numerically, we learn that the foci evolve into limit cycles (of 3 or 2 species respectively) when entering the window of fixed-point instability from the respective ends. In-between, the influences overlap and enable dynamical 3-species coexistence (Fig. 4). Starting at $D = b$ with increasing dilution cycles of higher order develop via period doubling until no periodicity occurs anymore and a chaotic attractor determines the dynamics. A trajectory starting in the proximity of the central saddle focus X_1^{+++} circles inwards in the corresponding stable plane. Near X^{+++}, the trajectory leaves that plane to orbit around X^{0++} until it enters again the region of influence of X_1^{+++}. Figure 4 shows a plot of the ensuing dynamical patterns in phase space: For small dilution rates, a 3-species limit cycle around an unstable fixed point governs the dynamics. For strong dilution rates the trajectories follow a 2-species limit cycle. In the intermediate regime, a chaotic attractor appears interpolating between those dynamics. This attractor resembles a two-dimensional ribbon folded in three-dimensional phase space. (Strictly speaking, the mathematical dimensionality of chaotic attractor manifolds is fractal, it takes non-integer values. But this will not be a point of much
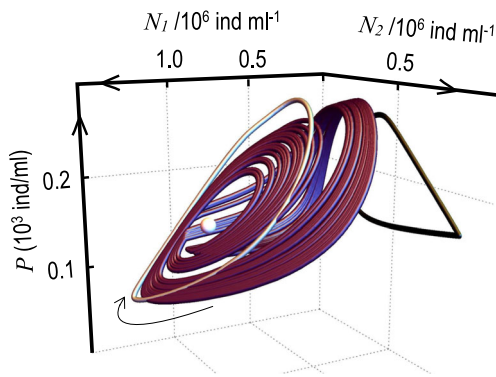

Fig. 3 Fixed points migrating through the phase space of population numbers with growing dilution. Dilution rate D is color-coded from weak dilution (*purple*, $D = 0.001 \ h^{-1}$) to strong dilution (*red*, $D = 0.07 \ h^{-1}$)

Fig. 4 Trajectories in phase space for three exemplary dilution rates and the central saddle X_1^{+++} demonstrating the origin of the attractor manifold. X^{0++} is hidden behind the chaotic attractor. *Left*: stable 3-species limit cycles at $D = 0.035$ h^{-1}; centre: chaotic attractor at intermediate dilution rates at $D = 0.045$ h^{-1}; *right*: stable 2-species limit cycles at $D = 0.05$ h^{-1};

concern to our present discussion.) Visual inspection suggests the attractor to have the topology of the well known Rössler attractor (Rössler 1976). However, we have not been able to identify the Rössler differential equations as a limiting case of our model equations and therefore cannot say with certainty that the identification holds. Attractors of this topology have been shown to exist in other mathematical three dimensional predator-prey models by Gilpin (1979).

Bifurcation diagram Figure 5 substantiates the range of dynamical behavior. In a bifurcation diagram, all extremal values of the long-term dynamics of one quantity (presently nutrient concentration C) are plotted with respect to the bifurcation parameter (here the dilution rate D); a line represents a shifting fixed point; two lines mean that the population number is oscillating between those two extrema; four indicate periodic dynamics with two maxima and two minima et cetera. The diagram clearly shows different regimes and transitions between them. For weak and strong dilution,
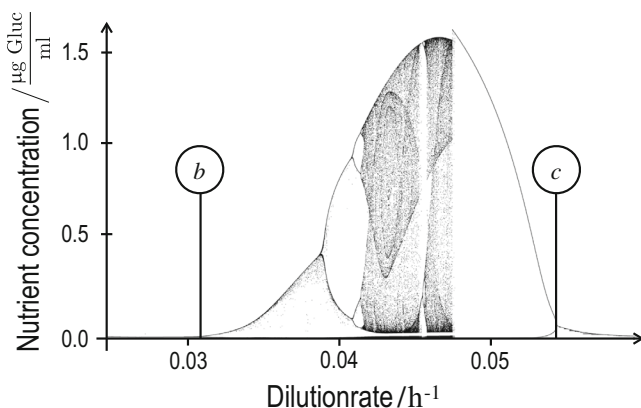
the system is in equilibrium (one point). A Hopf bifurcation at $D = b$ leads to chaotic dynamics via consecutive period doublings: a stable cycle (two points) and cycles of higher order (more points) arise. This oscillating or chaotic regime ends with the 2-species focus turning stable for $D > c$. When dilution exceeds $D = d$ this node grows unstable as well and all species are washed out.

In finite systems, fluctuations due to the discreteness of population numbers — demographic noise — drive populations into extinction that deterministically would survive. These events will occur at random at a certain rate or probability. Stochasticity was taken into account in numerical Monte-Carlo simulations of the model following the established Gillespie Algorithm (Gillespie 1976, 1977). In each iteration step, the rates or probabilities a_μ of the birth and death processes $\mu = 1, \ldots 6$ of all three species and the total rate for 'any event' $a_0 = \sum a_\mu$ were calculated. The time τ until the next occurrence of an event was calculated from the Poisson-distribution $P_1(\tau) = a_0 \exp(-a_0\tau)$. A birth or death process μ was generated according to the probability densities a_μ/a_0 such that events follow the probability density

$$P(\tau, \mu) = a_\mu \exp(-a_0\tau). \tag{3}$$

This was done for a set of dilution rates that allow 3-species coexistence and system sizes starting at 0.5 ml to exclude extreme finite size effects and ranging up to 1.45 ml. For each dilution rate, the system started from an initial state on the deterministic attractor with concentrations of the order 100 predatory organisms, and 10^6 and 10^5 bacteria respectively. Population numbers evolved until one of the species went extinct or a maximum time of 20,000 days was reached and the mean time to extinction was calculated. Simulations without extinction events where excluded from the calculation of mean extinction times. Where mean time to extinction here refers to the extinction of the food web, i.e. to the extinction of either one of the species. Figure 6
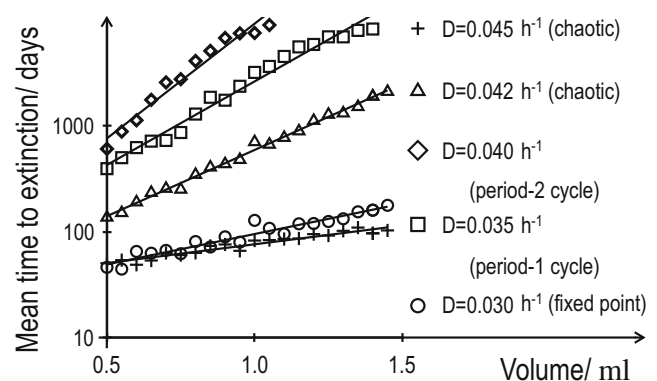

Fig. 5 Bifurcation diagram for the nutrient concentration with varying dilution rate. Critical values $a-c$ refer to Table 1

Fig. 6 Logarithmic plot of the mean time to first extinction for dilution rates $D = 0.03$h^{-1}, 0.035 h^{-1}, 0.04h^{-1}, 0.042 h^{-1} and 0.045h^{-1}
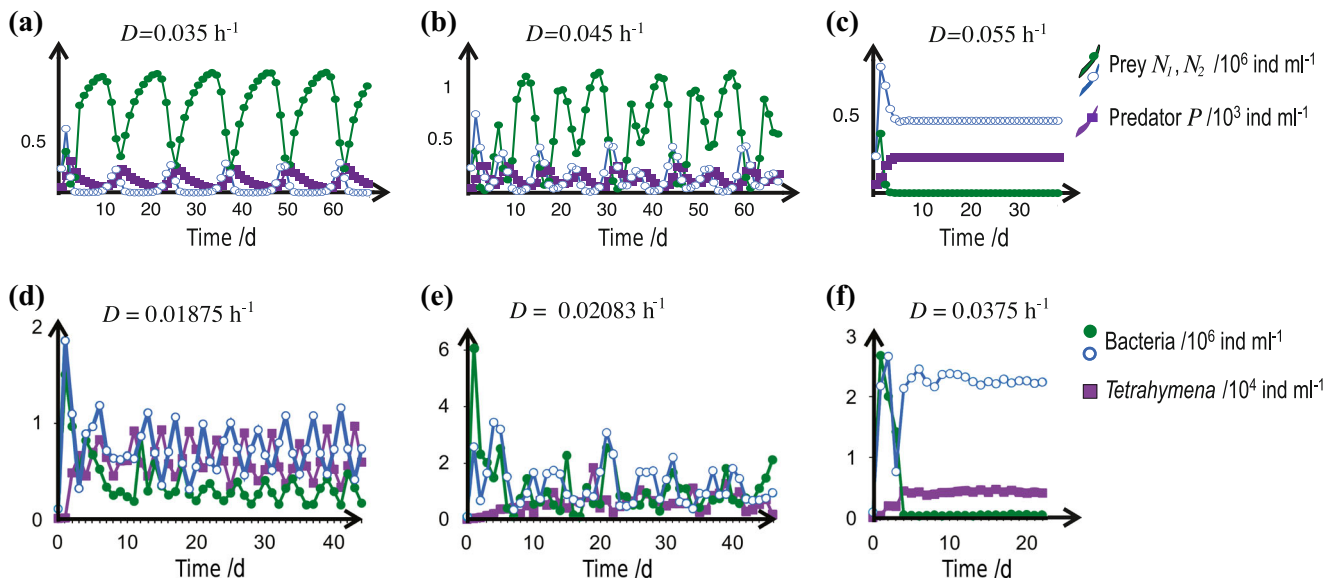
Fig. 7 a–c Time series data from numerical simulations. **a** stable limit cycles at $D = 0.035$ h^{-1}; **b** chaotic attractor at intermediate dilution rates, as an example $D = 0.045$h^{-1}; **c** fixed point at $D = 0.055$ h^{-1}; **d–f** Time-series data from Becks et al. (2005). *Open circles*, abundances of *Pedobacter* (preferred prey); *filled circles*, abundances of *Brevundimonas* (less-preferred prey); *squares*, numbers of *Tetrahymena* (predator); **d** $D = 0.01875$h^{-1}, **e** $D = 0.02083$h^{-1}, **f** $D = 0.0375$h^{-1}

shows that the mean time to extinction scales exponentially with population size. As expected the chaotic attractor indeed protects populations exponentially as well as limit cycles and fixed points do.

Chemostat experiments performed by Becks et al. (2005) realized the model presented above in a laboratory setting. With experimentally determined parameter values the data indeed agrees qualitatively with the sequence of dynamical patterns of Fig. 7d–f: at weak dilution, the three species show periodic behavior as with a limit cycle, increasing the dilution leads to strongly fluctuating aperiodic dynamics in all three species and at even stronger dilution the fast-growing preferred prey and the predator coexist in stable equilibrium. In the model, the slow-growing strain goes extinct for strong dilution. In the experiment, population abundances do not vanish completely but drop by a factor of 50. A reason for this deviation might be that small areas in the chemostat do not mix well — thereby protecting some bacteria from being washed out by dilution. Predator populations are smaller in the model but the order of magnitude of bacteria abundances and of time match the experimental results.

Discussion

We have investigated the formation of chaos and its stabilizing features against intrinsic stochasticity in a quantitive simulation of a real world experiment. Our model successively shows the transition from limit cycles to chaos to stable populations that experiments observed. A robust result is that a chaotic attractor emerges from the interplay of competing limit cycles and, fluctuations notwithstanding, stabilizes the system against demographic noise.

Population sizes in small ecological networks can show strong fluctuations even if stochastic effects and/or exterior causes are ruled out by high population numbers and constant environmental conditions, respectively (Becks et al. 2005; Benincà et al. 2008). Under such conditions, deterministic chaotic dynamics remain as the dominant source of fluctuations. In contrast to the theoretical attention to the occurrence of chaotic dynamics in biological systems, convincing empirical evidence of chaos in real ecosystems is rare. Since it is nearly impossible in experimental studies to obtain data sets large enough to carry out convincing statistical treatment, the development of mathematical models describing the behavior of experimental studies serves as an alternative to analyse the potential occurrence of chaotic dynamics in real world systems. There is only one ecological system, where a model was able to reproduce the experimental data in detail qualifying them as chaotic dynamics (Costantino et al. 1997).

We here studied a predator-prey system that is minimal in the sense that a chaotic attractor manifold is generated out of the interplay of only three species. The system addressed has been realized in experiment (Becks et al. 2005), and in our numerical analysis, parameters were chosen to describe

the bacterial species *Pedobacter*, *Brevundimonas* and the ciliate *Tetrahymena* involved in that work. Numerical simulations reproduce the succession of population dynamics in the experiment with bacterial abundances and time scales of the correct order of magnitude. As previous studies suggest (Takeuchi and Adachi 1983; Klebanoff and Hastings 1994; Vayenas and Pavlou 1999; Gakkhar and Naji 2005; Křivan and Eisner 2006), the system shows periodic and chaotic coexistence. An attractor evolves that topologically resembles Gilpin's classification of Vance's simpler two-prey one-predator model (Vance 1978; Gilpin 1979). Via a mechanism that is arguably universal chaos arises due to the parameter-controlled competition of two limit cycles governing the regime of extremely high and low net resource availability.

On general grounds, one expects chaos to act as a source of fluctuations and of stability against extinction at the same time. Large fluctuations are a hallmark of chaotic dynamics, and stability follows if a chaotic attractor manifold sitting in the bulk of population number phase space prevents population numbers from escaping to the boundaries of extinction. The beneficial character of chaos was demonstrated in the sense that the chaotic attractor makes the system less prone to extinction by demographic noise. For several dilution rates, the system shows 3-species coexistence with different dynamical patterns; fixed points, simple limit cycles and more complex or chaotic dynamics. In all of these cases, the mean time to extinction scales exponentially with the system size. Quantitative results for the exponents show comparable persistence in the chaotic regime as for fixed points and limit cycles.

An important observation of the present study is that chaos appears to present itself as an emergent feature when distinct limit cycles get 'tuned' into each other upon variation of a parameter. Limit cycles are an abundant motif in dynamical equations or at least in few-variable sub-sectors of these equations. For example, in the solution of a complex equation, a limit cycle may be transiently realized in the behavior of few of its variables. Upon changing parametric conditions, the patterns of such cycles change, and the present work demonstrates how this may be accompanied by the onset of chaos. Perhaps, then, chaos is a transient phenomenon more frequently realized than one may naively think, and this would entail consequences for both the strength of fluctuations and the stability of food web dynamics. Further work will be required to address these questions in generality.

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