Strange Periodic Attractors in a Prey-Predator System with Infected Prey[1]

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Strange periodic attractors with complicated, long-lasting transient dynamics are found in a prey-predator model with disease transmission in the prey. The model describes viral infection of a phytoplankton population and grazing by zooplankton. The analysis of the three-dimensional system of ordinary differential equations yields several semi-trivial stationary states, among them two saddle-foci, and the sudden (dis-)appearance of a continuum of degenerated nontrivial equilibria. Along this continuum line, the equilibria undergo a fold-Hopf (zero-pair) bifurcation (also called zip bifurcation). The continuum only exists in the bifurcation point of the saddle-foci. Especially interesting is the emergence of strange periodic attractors, stabilizing themselves after a repeated torus-like oscillation. This form of coexistence is related to persistent and permanent ecological communities and to bursting phenomena.

INTRODUCTION

Conceptual prey-predator models have been used often and successfully to model phytoplankton-zooplankton interactions and to elucidate mechanisms of spatio-temporal pattern formation such as patchiness

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and blooming (Segel and Jackson, 1972; Steele and Henderson, 1981; Scheffer, 1991; Malchow, 1993; Pascual, 1993). Little is known about marine viruses and their role in aquatic ecosystems and the species that they infect (Fuhrman, 1999). Suttle et al. (1990) have experimentally shown that viral disease can infect bacteria and phytoplankton in coastal water. There is some evidence that viral infection might acceler-ate the termination of phytoplankton blooms (Jacquet et al., 2002; Gastrich et al., 2004). However, despite the increasing number of reports, the role of viral infection in the phytoplankton population is still far from understood.

Mathematical models of the dynamics of virally infected phyto-plankton populations are rare as well. There is the already classical publication by Beltrami and Carroll (1994) and more recent work by Malchow et al. (2004, 2005). They observed oscillations and waves in a phytoplankton-zooplankton system with Holling-type II and III grazing under lysogenic viral infection and frequency-dependent transmission. The latter is also called proportionate mixing or stan-dard incidence (Nold, 1980; Hethcote, 2000; McCallum et al., 2001).

We investigate the local dynamics of phytoplankton with lytic infec-tion and frequency-dependent transmission as well as zooplankton with Holling-type II grazing. We show that coexistence in the form of a strange periodic attractor is possible even under nonstationary conditions. One section is devoted to the similarities with the concepts of permanence in ecological communities.

THE MODEL

Scheffer (1991) used the Rosenzweig-McArthur formulation (1963) for modeling the prey-predator dynamics of phytoplankton P and zoo-plankton Z. It reads for P, Z and time t in dimensionless quantities

$$\frac{dP}{dt} = rP(1-P) - \frac{aP}{1+bP}Z, \tag{1}$$

$$\frac{dZ}{dt} = \frac{aP}{1+bP}Z - m_3 Z. \tag{2}$$

There is logistic growth of the phytoplankton with intrinsic rate r and Holling-type II grazing with maximum rate a/b as well as natural mortality of zooplankton with rate m_3. The growth rate r is scaled as the ratio of local rate r_{loc} and a mean $\langle r \rangle$. The effects of nutrient sup-ply and planktivorous fish are neglected because we focus on the influ-ence of the viral infection of phytoplankton. The phytoplankton population P is split into a susceptible part S and an infected portion I.

Zooplankton Z grazes on both susceptible and infected phytoplankton. Then, the model system reads for symmetric inter- and intraspecific competition of susceptible and infected

$$\frac{dS}{dt} = r_1 S(1 - S - I) - \frac{aS}{1 + b(S + I)}Z - \lambda\frac{SI}{S + I}, \tag{3a}$$

$$\frac{dI}{dt} = r_2 I(1 - S - I) - \frac{aI}{1 + b(S + I)}Z + \lambda\frac{SI}{S + I} - m_2 I, \tag{3b}$$

$$\frac{dZ}{dt} = \frac{a(S + I)}{1 + b(S + I)}Z - m_3 Z. \tag{3c}$$

Frequency-dependent transmission rate λ as well as an additional disease-induced mortality of infected (virulence) with rate m_2 are assumed. The intrinsic growth rates of susceptible and infected are r_1 and r_2, respectively. In the case of lysogenic infection, it holds $0 \leq r_2 \leq r_1$, whereas in the case of lytic infection $r_2 \leq 0 \leq r_1$. Then, the first term on the righthand side of Eq. (3b) describes the losses due to natural mortality and competition.

THE STATIONARY DYNAMICS

We now search for stationary and oscillatory solutions of the system (3a–3c). To do that, it is simplified through a convenient transformation, then by describing the dynamics of the total phytoplankton population $P = S + I$ and the prevalence $i = I/P$. The vector of population densities is $\mathbf{X} = \{P, i, Z\}$. The model equations read

$$\frac{dP}{dt} = [r_1(1 - i) + r_2 i](1 - P)P - \frac{aP}{1 + bP}Z - m_2 iP, \tag{4a}$$

$$\frac{di}{dt} = [(r_2 - r_1)(1 - P) + (\lambda - m_2)](1 - i)i, \tag{4b}$$

$$\frac{dZ}{dt} = \frac{aP}{1 + bP}Z - m_3 Z. \tag{4c}$$

System (4a–4c) possesses the following (semi-) trivial equilibria $E = \{P^S, i^S, Z^S\}$ with

$$\frac{dP}{dt}\bigg|_{\mathbf{X}=E} = \frac{di}{dt}\bigg|_{\mathbf{X}=E} = \frac{dZ}{dt}\bigg|_{\mathbf{X}=E} = 0:$$

1) $E_{00} = \{0, 0, 0\}$.
   The trivial state is always unstable.
2) $E_{01} = \{0, i_{01}^S, 0\}$ with $i_{01}^S = 1$.

This disease-induced extinction of the total prey population occurs for $r_2 < m_2 < \lambda + r_2 - r_1$.

3) $E_1 = \{P_1^S, 0, 0\}$ with $P_1^S = S = 1$.
   Only the susceptible prey species survive at their carrying capacity for $\lambda < m_2$ and $m_3 > a/(1+b)$.

4) $E_2 = \{P_2^S, i_2^S, 0\}$ with $P_2^S > 0, i_2^S > 0$.
   a) $E_{21} = \{P_{21}^S, i_{21}^S, 0\}$ with $P_{21}^S = I = 1 - m_2/r_2, i_{21}^S = 1$.
      Only the infected survive for $m_2 < r_2, m_2 < (r_2/r_1)\lambda$ and $aP_{21}^S/(1 + bP_{21}^S) < m_3$.
   b) $E_{22} = \{P_{22}^S, i_{22}^S, 0\}$ with

   $$P_{22}^S = 1 - \frac{\lambda - m_2}{r_1 - r_2}, \quad i_{22}^S = \frac{r_1}{\lambda}\frac{\lambda - m_2}{r_1 - r_2}.$$

   The stability ranges of this solution can easily be found by some computer algebra tool. However, the expressions are rather lengthy and omitted here.

5) $E_3 = \{P_3^S, 0, Z_3^S\}$ with

   $$P_3^S = \frac{m_3}{a - m_3 b}, \quad Z_3^S = \frac{r_1}{a}(1 + bP_3^S)(1 - P_3^S).$$

   The infected go extinct for too high virulence or too low transmission rate. The remaining textbook example of the *P-Z* prey-predator model is well studied. The solution can be a stable node or focus as well as, after a Hopf bifurcation, an unstable focus bound by a stable limit cycle.

   Nontrivial equilibria exist for a special parameter combination. In this case, there is a continuum of stationary states:

6) $E_{Z_4^S(i)} = \{P_4^S, i, Z_4^S(P_4^S, i)\}$ with $P_4^S > 0, 0 < i < 1, Z_4^S(P_4^S, i) > 0$.
   From Eq. (4b) and (4c) one finds the expressions

   $$P_{41}^S = 1 - \frac{\lambda - m_2}{r_1 - r_2} \text{ and} \tag{5a}$$

   $$P_{42}^S = \frac{m_3}{a - m_3 b}, \tag{5b}$$

   which define two parallel planes independent of i and Z in $(P - i - Z)$ phase space. These planes are orthogonal to the $(P - Z)$ and parallel to the $(i - Z)$ plane. Both must coincide; that is, the system parameters must obey the relationship

   $$1 - \frac{\lambda - m_2}{r_1 - r_2} = \frac{m_3}{a - m_3 b} = P_4^S. \tag{6}$$

From Eq. (4a), one obtains the plane

$$Z = Z(P,i) = \frac{1+bP}{a}\left\{r_1(1-P) + [(r_2 - r_1)(1-P) - m_2]i\right\} \qquad (7)$$

Then, all points $E_{Z_4^S(i)}$ lying on the straight intersection line of planes (6) and (7), which is given by

$$Z_4^S(P_4^S,i) = Z(P_4^S,i) \text{ with } P_4^S \text{ as in (6)} , \qquad (8)$$

independent of i for $0 < i < 1$ are stationary states. This line of stationary states is a heteroclinic connection between the semitrivial equilibria E_2 and E_3.

For $m_3 < a(b-1)/(b(b+1))$, the $P - Z$ subsystem has an unstable focus bound by a stable limit cycle. In the stationary case (6), numerical analysis shows that all equilibria $E_{Z_4^S(i)}$ on line (8), including E_2 and E_3, are degenerated, say their third eigenvalue is zero. The upper part of line (8) consists of degenerated unstable foci. A fold-Hopf (zero-pair)
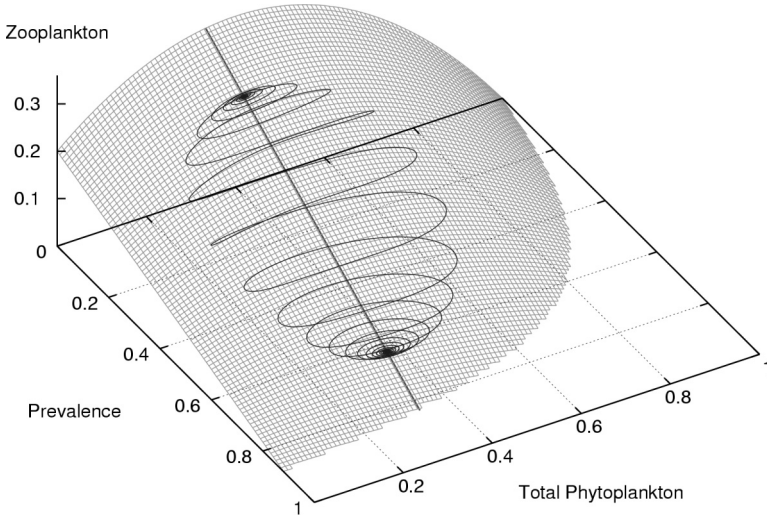

FIGURE 1 Stationary dynamics of system (4a–4c) with coexistence of all three populations. The trajectory starts at the upper unstable part of the line of stationary points, passes the fold-Hopf bifurcation point, and finally relaxes on the neutrally stable lower part. Parameters: $r_1 = 1$, $r_2 = 0$, $a = b = 5$, $\lambda = 4/5$ from Eq. (6), $m_2 = 2/15$, $m_3 = 5/8$. Initial conditions: $P_0 = 0.335$, $i_0 = 1/5$, Z_0 from Eq. (8). The straight line is the continuum of equilibria $E_{Z_4^S(i)}$, lying on the shaded plane (7).

bifurcation point (Kuznetsov, 1995; Nicolis, 1995) separates the foci from the lower part closer to the $(P - i)$ plane with degenerated stable foci. A corresponding numerical simulation, starting on the unstable upper branch, is shown in Figure 1. This kind of bifurcation has also been called a *zip bifurcation* (Farkas, 1984), because a singular curve folds into periodic solutions when a parameter is varied (when the prevalence decreases).

The closer the initial condition to the $(P - Z)$ plane, the longer is the journey through phase space. The location of the final stationary state on the line strongly depends on the initial conditions. Hence, the final positions are only neutrally stable. This remains true in the case that the intersection point of (8) in the $P - Z$ subsystem is a stable focus or stable node, and the line (8) becomes a continuum of stable solutions. The latter case is not presented here.

The growth rate of infected r_2 has simply been set to zero. This choice describes cell lysis of infected phytoplankton cells and nonsymmetric competition of infected and susceptible; the infected still have an impact on the growth of susceptible by shading and need for space, but not vice versa. Furthermore, m_2 stands for an effective mortality (virulence plus natural mortality) of the infected.

STRANGE PERIODIC ATTRACTORS

The strong parameter relationship (6) is surely not realistic. The probability to meet such a setting in a natural system is almost zero. Therefore, nonstationary situations will be simulated now, with parameter settings when the planes (5a) and (5b) do not coincide and the intersection lines with the plane of Eq. (7) are no longer stationary.

At first, virulence is increased. Numerical bifurcation and stability analysis show that in this case E_2 is a saddle-focus with a stable two-dimensional manifold and an unstable one-dimensional manifold. In the $(P - Z)$ plane, E_3 is also a saddle-focus, but with an unstable two-dimensional manifold and a stable one-dimensional manifold. In Figure 2, the trajectory starts in the upper corner and approaches the lower end point of the right-hand line (5a) in the $(P - i)$ plane which is the semi-trivial stationary state E_2. This is the mentioned saddle-focus with stable oscillation but unstable in direction of Z. Therefore, the trajectory is shot along the heteroclinic connection to the $(P - Z)$ plane and gets into the sphere of influence of the end point of the left-hand line (5b). This is also a semi-trivial saddle-focus, namely E_3 with unstable oscillation and stable in Z direction. Hence, the trajectory bounces back, spirals down the lines and "tube-rides" up again and again. On the way up, it is "reinjected" (Nicolis, 1995)
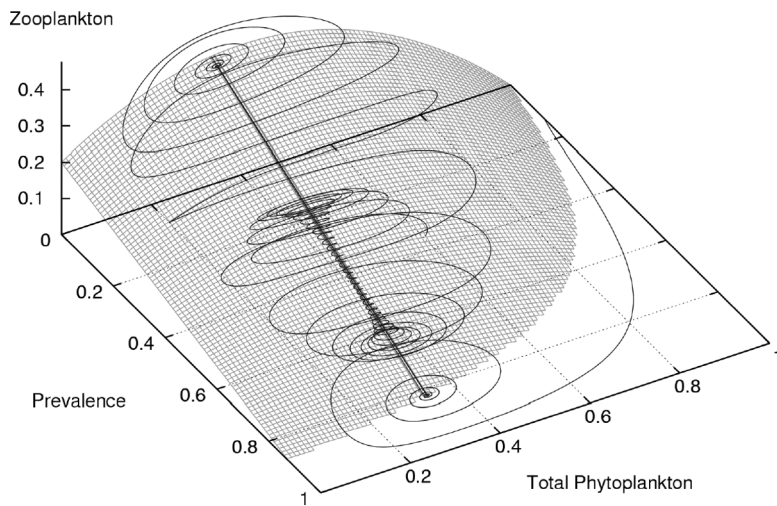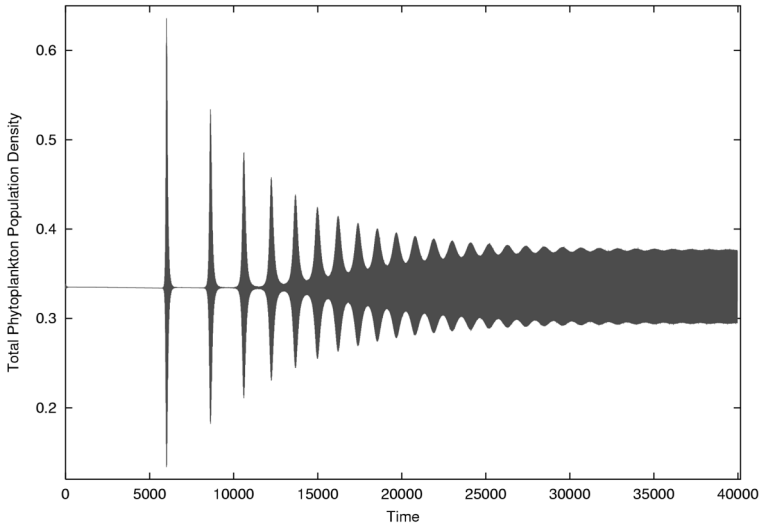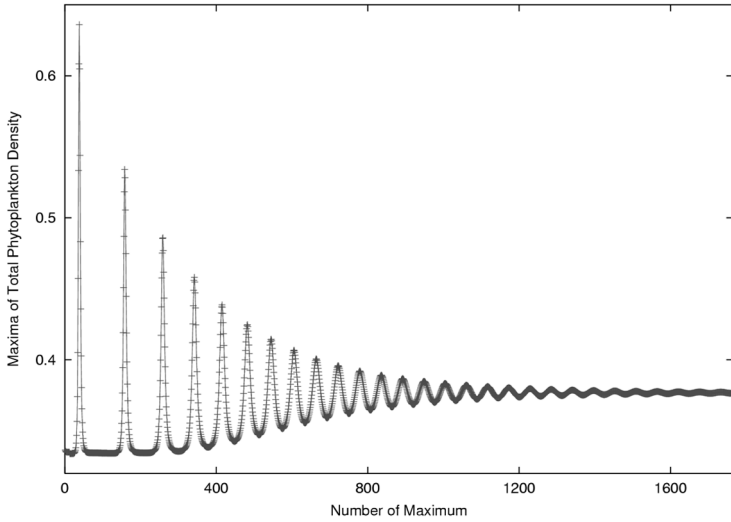
(a) $t = 0$–3000
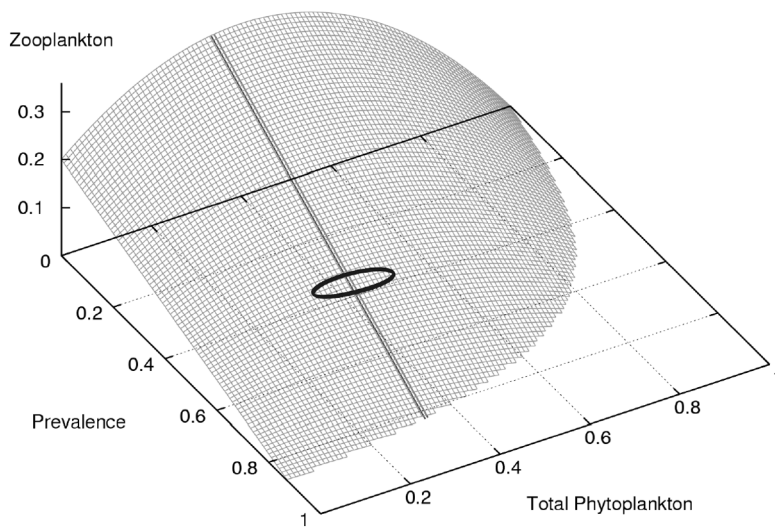
(b) t= 9000–10000

FIGURE 2 Nonstationary dynamics of system (4a–4c) with coexistence of all three populations. Parameters: $m_2 = 7/50$, all others as in Fig. 1. Inital condition: $P_0 = 1.01$, $i_0 = 0.1$, $Z_0 = 0.001$.

(a) Total Phytoplankton Density


(b) Unfolded next-maximum map

FIGURE 3 Nonstationary dynamics of system (4a–4c) with coexistence of all three populations. Parameters: $m_2 = 27/200$, all others as in Fig. 1. Inital condition: $P_0 = 1/3$, $i_0 = 0.825$, $Z_0 = 0.0015$.

and tunnels through the two formed funnels. This is illustrated in Figure 2a. It resembles the movement on a torus, where the center hole of

the torus is shrinked to a thin tube. However, the precessing trajectory gets "phase-locked" and finally, for long times, approaches a periodic attractor (Langford, 1983: 233). This is shown in Figure 2b. The oscillation takes place in a plane which is orthogonal to the $(i - Z)$ plane.
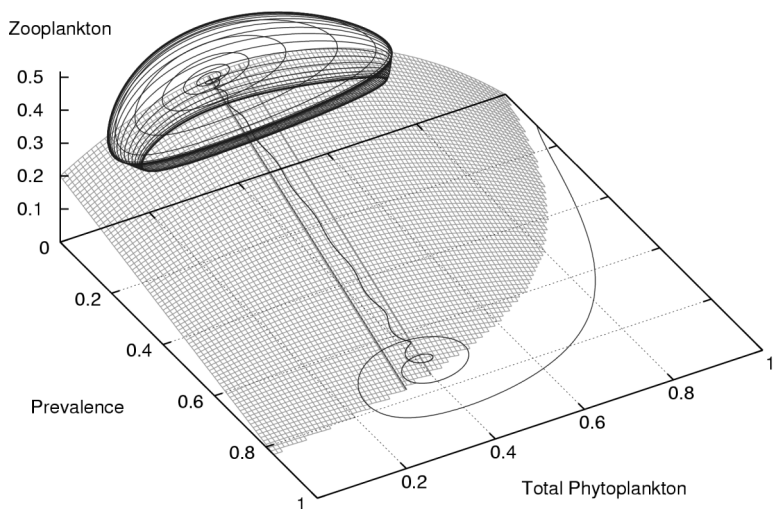
(a) $m_2 = 1/5$, coexistence of all three populations
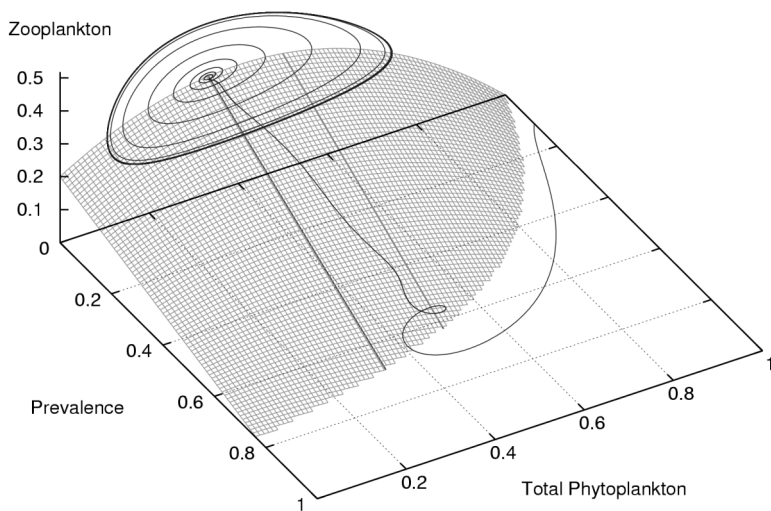
(b) $m_2 = 3/10$, extinction of infected

FIGURE 4 Dynamics of system (4a–4c). Parameters as in Fig. 1 except for m_2. Inital condition: $P_0 = 1.01$, $i_0 = 0.1$, $Z_0 = 0.001$.

The attractor surrounds the two intersection points of the two lines of nonstationary points and the plane of oscillation.

Because of the long-lasting, peculiar approach toward the asymptotic oscillations, we call the attractor a *strange periodic attractor*. Clearly, the attractor is not chaotic (sometimes called strange). In order to highlight the exciting transient dynamics, which actually occurs during a rather long time, we label it as "strangely periodic."

For further illustration, the temporal development of the total prey density and its unfolded next-maximum map are given in Figure 3. The latter resembles a damped oscillation.

The location of the asymptotic periodic attractor is independent of the initial conditions as in the case of a limit cycle. For further increasing values of m_2, the behavior of the system becomes simpler. The distinct funnel formation disappears, and the periodic attractor stabilizes faster and faster. For too high virulence, the infected go extinct and the system oscillates in the $P - Z$ subsystem. This is illustrated in Figure 4.

For virulences below the stationary value given in Figure 1, E_2 becomes a stable and E_3 an unstable focus, respectively. Numerical simulations yield that zooplankton dies out and the dynamics relaxes to E_2 in the $P - i$ subsystem, cf. Figure 5.
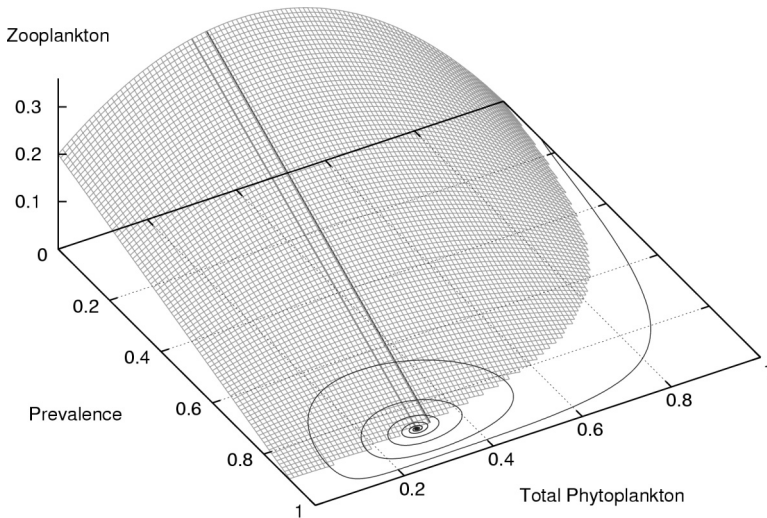

FIGURE 5 Dynamics of system (4a–4c). Parameters: $m_2 = 0.1$, all others as in Fig. 1. Inital condition: $P_0 = 1.01$, $i_0 = 0.1$, $Z_0 = 0.001$.

In summary, this means that E_2 has undergone a bifurcation from an unstable saddle-focus to a stable focus. At this bifurcation point, the continuum of degenerated nontrivial equilibria $E_{Z_4^S(i)}$ appeared simultaneously. A zero-pair Hopf bifurcation took place along this continuum line.

NON-EQUILIBRIUM COEXISTENCE AND PERMANENCE

The strange periodic attractor is biologically interesting, because it allows for coexistence with all three species positive in a substantial parameter range. This makes the model much more realistic, because the special condition (6) unlikely holds exactly in reality. The nontrivial oscillations in the interior of the first octant are remarkable, because no nontrivial stationary state exists. So where does the attractor come from? What are the mechanisms behind the distinct joint tube-ridings (funnel formation) and back-twirlings of the strange periodic attractor?

The second question is left as an open problem for future work. Here, we want to discuss the first question from the point of view of persistence theory and permanence. These concepts have attracted much interest in the ecological literature and are still a growing field. Their roots can be traced back to the "principle of competitive exclusion" that states, roughly speaking, that two or more consumer species cannot coexist on a single resource (Gause, 1934; Hardin, 1960) or the famous "paradox of the plankton" (Hutchinson, 1961). Ayala (1969) provided an experimental invalidation of the competitive exclusion principle, and later theoretical work showed that it is restricted to assumptions such as a linear per head growth rate of the resource and interactions of Lotka-Volterra-type (Armstrong and McGehee (1980) and references therein).

One example leading to coexistence is the model by McGehee and Armstrong (1977), in which two predators y_1 and y_2 share a common prey x:

$$\frac{dx}{dt} = Rx\left(1 - \frac{x}{K}\right) - Mxy_1 - \frac{Ax}{1 + Bx}y_2, \tag{9a}$$

$$\frac{dy_1}{dt} = Exy_1 - D_1y_1, \tag{9b}$$

$$\frac{dy_2}{dt} = \frac{Cx}{1 + Bx}y_2 - D_2y_2. \tag{9c}$$

There is logistic growth of the prey species with intrinsic growth rate R and carrying capacity K. Predation of species y_1 is of

Lotka-Volterra-type with coefficient M and conversion efficiency E/M. Predation of species y_2 is of Holling-type II with half-saturation constant B, maximum predation rate A/B and conversion efficiency C/A. Both predators y_1 and y_2 are subject to natural mortalities D_1 and D_2, respectively (in chemostat models, the mortality would correspond to the dilution rate). There are some surprising similarities to our $P-i-Z$ model (4a–4c), if one would relate the total phytoplankton density to the resource, the prevalence to the first predator and the zooplankton to the second predator. The consumers in both models interact only by the consumption of the common limiting resource. Next, the equation for zooplankton as a Holling-type II grazer is just the same.

The prevalence could be interpreted as consumer on P with Lotka-Volterra-type interaction in (9a). However, things are much more delicate (what might explain the strangeness of the periodic attractor), because there is an additional term $(1 - i)$ in (4b), and for $r_2 = 0$ the phytoplankton population is affected by a reduced intrinsic growth rate due to i. What happens in system (9a-9c) is that either there is a line of nontrivial stationary states for a specific parameter combination (Eq. (7.2) in McGehee and Armstrong (1977)) or that there is a periodic attractor even in the nonequilibrium case. Both effects are similar to the results presented here, except the complicated approach to the periodic attractor.

Koch (1974) numerically observed what appeared to be periodic oscillations in a model similar to (9a–9c) but with the second predator being a Holling-type II grazer as well (Hsu et al., 1978). Later work showed that the stable periodic orbit bifurcates from the subsystems on the boundaries and reported more and more precise parameter ranges for this kind of coexistence (Butler and Waltman, 1981; Smith, 1981; Keener, 1983; Farkas, 1984; Muratori and Rinaldi, 1989; Rinaldi and Muratori, 1992; Liu et al., 2003). What is of interest here is that some common features have been described: (i) the segment line of equilibria, (ii) the emergence of relaxation oscillations in the positive octant and (iii) their collapse into the subsystem of the boundary, cf. Figure 4b.

Schreiber (2004) constructs another model with a periodic attractor or a continuum line of equilibria, depending on the parameter values. The system models "apparent competition" (Holt, 1977) in which two prey species share a common enemy. In his example, both predation terms are of Holling-type II and the prey species exhibit logistic growth. Because there is no nontrivial equilibrium, the system is not permanent. But because the periodic orbit attracts Lebesgue almost every (but not every) initial condition, he introduces the term "almost

sure permanence," following Jansen and Sigmund (1988), "almost permanence". Due to the obvious similarities, we would guess that our model is almost surely permanent as well, but leave its proof for a more detailed study.

CONCLUSION

A conceptual biomass-based model of phytoplankton-zooplankton prey-predator dynamics has been investigated for temporal pattern formation in a deterministic environment. It has been assumed that the phytoplankton is partly virally infected. Holling-type II zooplankton grazing has been considered and simulations have been performed for the case of lytic infection.

The dynamics of the system are surprisingly complex. Especially interesting is the coexistence of all populations on a strange periodic attractor that stabilizes itself under nonstationary parameter settings as well as the interplay of two saddle-foci that are connected by a heteroclinic orbit. This form of coexistence is of considerable interest in theoretical ecology, and we have related our results to similar work and the concepts of persistence theory and permanence in ecological communities. The found analogies might help in finding a rigorous explanation for the strange periodic attractor.

Moreover, the transient dynamics when approaching the attractor resembles the bursting electrical activities that can be observed in some cell types (Keener and Sneyd, 1998, chapter 6). The communication by firing and transmitting action potentials can become quite complex, involving brief bursts of oscillations interspersed with quiescent periods. Various bifurcation scenarios have been identified that can explain the observed dynamics (Izhikevich, 2000). A similar behavior can also be found in the oscillations of the total phytoplankton population in Figure 3a. Especially at the beginning, nearly constant phytoplankton densities alternate with strongly increasing but likewise rapidly decreasing oscillations. This corresponds to the repeated "tube-riding" and back-twirling on the strange periodic attractor.

Recent work by Abrams et al. (2003) has revealed that in the McGehee and Armstrong model (1977) more complex dynamics such as chaos are possible. This raises the question whether similar effects can be observed in system (4a–4c) with the additional terms as well.

Future studies will also have to consider the transitions from lysogeny to lysis and backwards within a system of population, for example, induced by external noise (Hilker et al., 2006). Thus, one might get a repeated transient approach to the strange periodic attractor if the lytic cycle would be in a corresponding parameter range.

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