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Multiple attractors and resonance in periodically forced population models

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Abstract

Oscillating discrete autonomous dynamical systems admit multiple oscillatory solutions in the advent of periodic forcing. The multiple cycles are out of phase, and some of their averages may resonate with the forcing amplitude while others attenuate. In application to population biology, populations with stable inherent oscillations in constant habitats are predicted to develop multiple attracting oscillatory final states in the presence of habitat periodicity. The average total population size may resonate or attenuate with the amplitude of the environmental fluctuation depending on the initial population size. The theory has been tested successfully in the laboratory by subjecting cultures of the flour beetle *Tribolium* to habitat periodicity of various amplitudes.

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1. Introduction

Although all natural populations suffer temporal environmental fluctuations on some scale, experimental and theoretical studies of population response to habitat fluctuation remain relatively rare. Few controlled experimental studies address the effect of time-varying habitats, and most mathematical population models are autonomous. In recent years, nonautonomous versions of classical model equations have been investigated in order to determine the extent to which fundamental theoretical principles remain valid in fluctuating environments, e.g., see [1]. However, few connections exist between controlled, replicated experimental data and rigorously validated models.

An exception is the controlled laboratory experiment of Jillson [2] and the subsequent model-based explanation, predictions, and further experimentation of Henson and Cushing [3], Costantino et al. [4], and Henson et al. [5]. Jillson placed flour beetles in volumes of flour that periodically alternated between 32 and 8 g every two weeks.

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The control cultures remained in a constant volume of 20 g. Total population numbers in the alternating habitat were more than twice those in the constant habitat even though the average flour volume was the same in both environments.

Henson and Cushing [3] and Costantino et al. [4] extended the modeling hypotheses of the LPA *Tribolium* model of Dennis et al. [6,7] and Costantino et al. [8,9] to include habitat periodicity. The resulting “periodic LPA model” explained the increased average biomass observed in the 32–8 g habitat as a type of resonance in which the inherent biological oscillation resonates with the periodic habitat [4]. Furthermore, the periodic LPA model generated unexpected new predictions which were then tested in the laboratory [5]. When the relative amplitude of oscillating flour volume in the periodic LPA model was set at 40% to simulate a 28–12 g alternating habitat, the model predicted multiple attracting final states: two different 2-cycles out of phase with each other and differing in average magnitude of animal numbers. This model forecast was successfully tested in the laboratory by placing beetle cultures in the different (model predicted) basins of attraction of the two locally stable 2-cycles.

The resonance and multiple attractor predictions of the periodic LPA model constitute one incarnation of a general nonlinear phenomenon. This paper presents general results concerning multiple attractors and resonance in periodically forced discrete dynamical systems. The contextual application will be periodic habitats in population biology.

Discrete autonomous (semi)dynamical systems with periodic solutions admit multiple oscillatory solutions in the advent of periodic forcing. In general, the multiple cycles are mutually out of phase, and some of the cycle averages may increase with the forcing amplitude while others decrease. In terms of population biology, a population which cycles in a constant habitat is predicted to have multiple attracting oscillatory final states in the presence of habitat periodicity. The multiple cycles differ in phase, and may differ in average total population size as well. Thus, Let B denote the set of p

Note the identity

$$x_0^i.t+j/=x_0^{.i+j/\,\mathrm{mod}\,p}.t/: \tag{4}$$

If p is the minimal period of $\mathbf{x}_0^0$, then the p phase shifts $\mathbf{x}_0^0; \mathbf{x}_0^1; :::; \mathbf{x}_0^{p-1}$ will be distinct. If the minimal period is $q < p;$ then the first q phase shifts $\mathbf{x}_0^0; \mathbf{x}_0^1; :::; \mathbf{x}_0^{q-1}$ will be distinct, while the rest will be duplicates under the identity $\mathbf{x}_0^j=\mathbf{x}_0^{j\,\mathrm{mod}\,q}:$ In this case identity (4) becomes

$$x_0^i.t+j/=x_0^{.i+j/\,\mathrm{mod}\,q}.t/: \tag{5}$$

Stability results will require a hyperbolicity assumption:

(A4) The matrix

$$\prod_{t=p-1}^{0} F_x.1; x_0^0.t//;$$

where F_x is the Jacobian of F, has no eigenvalues of modulus one.

A weaker hypothesis may be substituted for (A4) when results are independent of stability:

(A4*) The matrix

$$\mathbf{I}-\prod_{t=p-1}^{0} F_x.1; x_0^0.t//$$

is invertible.

(A4) implies (A4*). Since the set of eigenvalues of the product matrix **AB** is the same as the set of eigenvalues of **BA** [10], each of the p matrices $\prod_{t=p-1}^{0} F_x.1; x_0^i.t// = \prod_{t=p-1}^{0} F_x.1; x_0^0.t+i//; i=0; 1; :::; p-1;$ of permuted Jacobian products has the same set of eigenvalues. This fact has two relevant consequences. First, since (A4*) holds if and only if the matrix $\prod_{t=p-1}^{0} F_x.1; x_0^0.t//$ does not have an eigenvalue of one, assumption (A4*) is equivalent to the invertibility of each of the matrices $\mathbf{I}-\prod_{t=p-1}^{0} F_x.1; x_0^i.t//$ for $i=0; 1; :::; p-1$. Second, since the stability of the cycle $\mathbf{x}_0^i$ depends on the eigenvalues of $\prod_{t=p-1}^{0} F_x.1; x_0^i.t//$, all of the phase shifted solutions $\mathbf{x}_0^1; \mathbf{x}_0^2; :::; \mathbf{x}_0^{p-1}$ must have the same stability properties when they are hyperbolic (see, e.g., [11], Theorem 9.14):

Theorem 1. *Assume* (A1)–(A4). *The phase shifted solutions* $\mathbf{x}_0^0; \mathbf{x}_0^1; :::; \mathbf{x}_0^{p-1}$ *are either all locally asymptotically stable, or they are all unstable.*

2.1. Multiple perturbed cycles

When small amplitude periodic forcing is introduced into the habitat of an oscillating population, the population is perturbed to a new oscillatory state. The next theorem guarantees each phase shifted p-cycle solution $\mathbf{x}=\mathbf{x}_0^i$ of the autonomous equation $K.0; \boldsymbol{\beta}; \mathbf{x}/=\mathbf{0}$ is perturbed into a continuous -branch $\mathbf{x}^i$ of p-cycle solutions of the nonautonomous equation $K. \;; \boldsymbol{\beta}; \mathbf{x}/=\mathbf{0}$ as is increased from zero.

Theorem 2. *Assume* (A1)–(A3) *and* $.\mathrm{A4}^*/$. *Let* $i \in \{0; 1; :::; p-1\}$. *Then there exist* $\;>0$ *and* $\gamma\;>0$ *and a* C^1 *function* $\;: .-\;;\;/ \to H^n$

Proof. The result follows from the Implicit Function Theorem as long as the Frechét derivative of K with respect to $\mathbf{x}$ evaluated at $\varepsilon = 0$ and $\mathbf{x} = \mathbf{x}_0^i$ is nonsingular, and K is C^1 in $\mathbf{x}$ and ε.

The Frechét derivatives of $K(\varepsilon, \boldsymbol{\beta}, \mathbf{x})$ with respect to $\mathbf{x}$ and ε are the linear operators $L_x : H_p^n \to H_p^n$ and $L_\varepsilon : R \to H_p^n$ defined by

$$\Delta\mathbf{x} \overset{L_x}{\mapsto} \{\Delta x(t+1) - F_x(1+\varepsilon\beta(t), x(t))\Delta x(t)\}_{t=0}^{p-1},$$
$$\Delta\varepsilon \overset{L_\varepsilon}{\mapsto} \{-F(1+\varepsilon\beta(t), x(t))\beta(t)\Delta\varepsilon\}_{t=0}^{p-1},$$

which are continuous in x and ε by (A1).

The Frechét derivative of $K(\varepsilon, \boldsymbol{\beta}, \mathbf{x})$ with respect to $\mathbf{x}$ evaluated at $\varepsilon = 0$ and $\mathbf{x} = \mathbf{x}_0^i$ is the linear operator L defined by

$$\Delta\mathbf{x} \overset{L}{\mapsto} \{\Delta x(t+1) - F_x(1, x_0^i(t))\Delta x(t)\}_{t=0}^{p-1}.$$

If $\mathbf{w} \in H_p^n$ is in the kernel of L, it must satisfy the recursion formula

$$w(t+1) = F_x(1, x_0^i(t))w(t)$$

for $t = 0, 1, \ldots, p-1$. Thus

$$w(0) = \left[\prod_{t=p-1}^{0} F_x(1, x_0^i(t))\right] w(0)$$

and so

$$\left(\mathbf{I} - \prod_{t=p-1}^{0} F_x(1, x_0^i(t))\right) w(0) = 0.$$

Since $\mathbf{I} - \prod_{t=p-1}^{0} F_x(1, x_0^i(t))$ is invertible by assumption (A4*), $w(0) = 0$, which implies $\mathbf{w} = \mathbf{0}$. Hence the operator L is nonsingular. □

Denote $(\varepsilon) = \mathbf{x}_\varepsilon^i$. Then for small ε, $\mathbf{x}_\varepsilon^i$ is a C^1 ε-branch of solutions of $K(\varepsilon, \boldsymbol{\beta}, \mathbf{x}) = \mathbf{0}$ for which $\lim_{\varepsilon \to 0} \mathbf{x}_\varepsilon^i = \mathbf{x}_0^i$. The branch may be expanded in ε as $\mathbf{x}_\varepsilon^i = \mathbf{x}_0^i + \mathbf{u}^i\varepsilon + O(\varepsilon^2)$. Properties of the first-order term $\mathbf{u}^i$ will play a large role in our study of the perturbed cycles.

If the inherent cycle $\mathbf{x}_0^0$ has minimal period $q \le p$, then the q distinct phase shifted solutions $\mathbf{x}_0^i$ are perturbed into q distinct branches $\mathbf{x}_\varepsilon^i$ of p-cycle solutions as ε increases from zero. By continuity, the cycles on each branch $\mathbf{x}_\varepsilon^i$ are in phase with the parent cycle $\mathbf{x}_0^i$; hence, the q distinct p-cycles are mutually out of phase. Furthermore, if assumption (A4) holds, then by an eigenvalue continuity argument the q perturbed cycles are locally asymptotically stable (unstable) if $\mathbf{x}_0^0$ is locally asymptotically stable (unstable).

Now suppose the inherent cycle $\mathbf{x}_0^i$ has minimal period q and the input oscillation $\boldsymbol{\beta}$ has minimal period r. The smallest value of p for which Theorem 2 applies is the least common multiple of q and r: $p = \operatorname{lcm}(q, r)$. Thus, the inherent q-cycle is perturbed into q out of phase p-cycles as ε increases from zero. Two questions are in order. First, what is the *minimal*

The autonomous map ($= 0$) has exactly one periodic solution: the equilibrium $x = 0$ (period $q = 1$). When forcing of minimal period $r = 2$ is introduced into the map (> 0), the equilibrium $x = 0$ remains as the only periodic solution. In particular, there are no solutions of minimal period $2 = \text{lcm}.1; 2/$. The problem is that the function $F. \;\; ; x/ = 3 \;\; x$ is independent of when $x = 0$. These kinds of degeneracies are ruled out if F, when evaluated at the inherent cycle, is invertible as a function of . This is condition (6) in the next lemma and theorem.

With regard to the second question, condition (6) also implies $\text{gcd}.q; r/$ of the perturbed cycles are distinct modulo phase shifts, where $\text{gcd}.q; r/$ denotes the least common divisor of q and r. We now turn to the proof of these remarks.

Lemma. *Assume* (A1)–(A3) *and* (A4*). *Suppose the* $\mathbf{x}_0^i$ *have minimal period* q *and* $\boldsymbol{\beta}$ *has minimal period* r, *and that* $\mathbf{x}^i; i = 0; 1; 2; \ldots; q-1;$ *are the* q *perturbed branches of* p*-cycles guaranteed by Theorem 2, where* $p = l\text{cm}.q; r/$. *Assume further that*

$$F. \;\; _1; x^i .t// = F. \;\; _2; x^i .t// \Rightarrow \;\; _1 = \;\; _2; \tag{6}$$

for all t *and all* $i = 0; 1; 2; \ldots; q-1$ *and all sufficiently small* . *Then for sufficiently small* ; *a phase shift* $x^i .t + m/$ *of a solution* $x^i .t/$ *of (2) is itself a solution if and only if* m *is a multiple of* r.

Proof. Consider the phase shift $z \;\; .t/ = x^i .t + m/;$ with $m = kr$ and $k \in \{0; 1; 2; \ldots; .p{=}r/ - 1\}$. Then

$$z \;\; .t + 1/ = x^i .t + kr + 1/ = F.1 + \;\;\; .t + kr/; x^i .t + kr// = F.1 + \;\;\; .t/; z \;\; .t//;$$

and so $z \;\; .t/$ is a solution.

Conversely, if $z.t/ = x^i .t + m/$ is a solution, then

$$\begin{aligned} &F.1 + \;\;\; .t/; x^i .t + m// = F.1 + \;\;\; .t/; z.t// = z.t + 1/ = x^i .t + m + 1/ \\ &= F.1 + \;\;\; .t + m/; x^i .t + m// \end{aligned}$$

for all t, and so $\;\; .t/ = \;\; .t + m/$ for all t by (6). Hence m is a multiple of r since $\boldsymbol{\beta}$ has minimal period r. □

Theorem 3. *Under the assumptions of the preceding lemma, for sufficiently small* *the perturbed cycles* $\mathbf{x}^i$ *have minimal period* $p = \text{lcm}.q; r/$. *Moreover, modulo phase shifts,* $\text{gcd}.q; r/$ *of these perturbed cycles are distinct*.

Proof. Suppose $\mathbf{x}^i$ has minimal period m. Then

$$\begin{aligned} &F.1 + \;\;\; .t/; x^i .t// = x^i .t + 1/ = x^i .t + m + 1/ = F.1 + \;\;\; .t + m/; x^i .t + m// \\ &= F.1 + \;\;\; .t + m/; x^i .t// \end{aligned}$$

for all t, and so $\;\; .t/ = \;\; .t + m/$ for all t by (6). Since $\boldsymbol{\beta}$ has minimal period r, we conclude m must be a multiple of r. Also, $\lim_{\;\to 0} \mathbf{x}^i = \mathbf{x}_0^i$ has period m by continuity, and so m must also be a multiple of q since $\mathbf{x}_0^i$ has minimal period q. Since $\mathbf{x}^i \qquad + m/; x$

For example, suppose the inherent 6-cycle $(q = 6)$ with phases $\mathbf{x}_0^0, \mathbf{x}_0^1, \ldots, \mathbf{x}_0^5$ is perturbed by 4-periodic forcing $(r = 4)$ into six out of phase 12-cycles $\mathbf{x}^0, \mathbf{x}^1, \ldots, \mathbf{x}^5$ $(p = \mathrm{lcm}(6, 4) = 12)$. Then there are $\mathrm{gcd}(6, 4) = 2$ equivalence classes modulo phase shifts: $\{\mathbf{x}^0, \mathbf{x}^4, \mathbf{x}^2\}$ and $\{\mathbf{x}^1, \mathbf{x}^5, \mathbf{x}^3\}$.

Roughly speaking, Theorem 3 says the result of forcing with minimal period r an inherent oscillation of minimal period q is the creation of q out of phase cycles of minimal period $\mathrm{lcm}(q, r)$ which live on $\mathrm{gcd}(q, r)$ different attractors. Two extremes deserve mention. First, if an inherent cycle of minimal period p is forced with minimal period p, the result is p out of phase p-cycles, none of which are related by phase shifts. Second, if an inherent cycle of minimal period q is forced with minimal period r where q and r are relatively prime, the result is q out of phase qr-cycles, all of which are phase shifts of each other.

Thus if a population oscillates with minimal period q in a constant habitat, it will, according to its initial state, settle on one of q possible out of phase oscillations when it is placed in a habitat fluctuating with small amplitude and phaseinwhichd r perjandof ph73dcshifts.8dof,[(c)8d5Dbe on $(q; r$ pcomfts.8dareycles th5m43.4a305. 1 (th5;nd)-1 Tfyt2D2nft8ractors[(out) or

$$x^{i}\,.t/ = x_0^{i}.t/ + u^{i}.t/\quad + \mathrm{O}.\quad {}^{2}/ = x_0^{0}.t+i/ + u^{i}.t/\quad + \mathrm{O}.\quad {}^{2}/$$

for all t.

Thus, the resonance or attenuation of $\mathbf{x}^i$ at $= 0$ is determined by

$$\left.\frac{\mathrm{d}\lceil \mathbf{x}^i\ \rceil}{\mathrm{d}}\right|_{=0} = \frac{1}{p}\sum_{t=0}^{p-1}\left.\frac{\mathrm{d}\lceil x^i\,.t/\rceil}{\mathrm{d}}\right|_{=0} = \frac{1}{p}\sum_{t=0}^{p-1}\left\lceil \left.\frac{\mathrm{d}x^i\,.t/}{\mathrm{d}}\right|_{=0}\right\rceil = \frac{1}{p}\sum_{t=0}^{p-1}\lceil u^i.t/\rceil = \lceil \mathbf{u}^i\rceil:$$

If $\lceil \mathbf{u}^i\rceil > 0;\ \mathbf{x}^i$ is resonant at $= 0$; if $\lceil \mathbf{u}^i\rceil < 0;\ \mathbf{x}^i$ is attenuant. If $\lceil \mathbf{u}^i\rceil = 0$, higher order terms must be calculated.

and

$$\mathbf{D} = \operatorname{diag}[F(0), F(1), \ldots, F(p-1)],$$

with

$$F(t) = \operatorname{diag} F(1, x_0^0(t))$$

and

$$\mathbf{v}^i = \begin{pmatrix} u^i(p-i) \\ u^i(p-i+1) \\ \vdots \\ u^i(2p-i-1) \end{pmatrix},$$

$$\mathbf{1} = \begin{bmatrix} 1 \\ \vdots \\ 1 \end{bmatrix} \in R^n,$$

$$\boldsymbol{\beta}^i = \begin{bmatrix} \mathbf{1}(p-i) \\ \mathbf{1}(p-i+1) \\ \vdots \\ \mathbf{1}(2p-i-1) \end{bmatrix}.$$

Here the Jacobians $F_x(t)$ and the identity **I** are $n \times n$ matrices, and so the block matrix $\boldsymbol{9}$ is $np \times np$. $F(1, x_0^0(t))$ is a column vector in R^n, so $F(t)$ is an $n \times n$ diagonal matrix with the elements of $F(1, x_0^0(t))$ on the diagonal. Thus, **D** is a $np \times np$ diagonal matrix. $\mathbf{v}^i$ and $\boldsymbol{\beta}^i$ are column vectors in R^{np}. Note that $\sum_{i=0}^{p-1} \boldsymbol{\beta}^i = \mathbf{0}$ and $\lceil \mathbf{v}^i \rceil = \lceil \mathbf{u}^i \rceil$.

It is straightforward to check that $[\boldsymbol{9}]^{-1} = \mathbf{MP}$, where

$$\mathbf{M} = \operatorname{diag}\left(\left[\mathbf{I} - \prod_{t=p-1+j}^{j} F_x(t)\right]^{-1}\right)_{j=0}^{p-1},$$

$$\mathbf{P} = \left(\begin{matrix} \prod_{t=p-1}^{1} F_x(t) & \prod_{t=p-1}^{2} F_x(t) & \cdots & F_x(p-1) & \mathbf{I} \\ \mathbf{I} & \prod_{t=p}^{2} F_x(t) & \cdots & & F_x(p) \\ F_x(p+1) & \mathbf{I} & \cdots & & \prod_{t=p+1}^{p} F_x(t) \\ \vdots & & & & \\ & & & & \end{matrix}\right.$$

Proof.

$$\sum_{i=0}^{p-1}\lceil \mathbf{u}^i \rceil = \sum_{i=0}^{p-1}\lceil \mathbf{v}^i \rceil = \sum_{i=0}^{p-1}\lceil \mathbf{MPD}\boldsymbol{\beta}^i \rceil = \left\lceil \mathbf{MPD}\sum_{i=0}^{p-1}\boldsymbol{\beta}^i \right\rceil = \lceil \mathbf{0} \rceil = 0.$$

Thus, there exist $j, k \in \{0, 1, \dots, p-1\}$ such that $\lceil \mathbf{u}^j \rceil > 0$ and $\lceil \mathbf{u}^k \rceil < 0$. □

In our application, Theorem 4 asserts that (generically speaking) the average total population size for at least one of the multiple attracting oscillatory states in the periodic habitat *exceeds* the total population size in the constant habitat. Furthermore, at least one of the multiple attracting states in the periodic habitat has average total population size *less than* that in the constant habitat. These results hold only for “small” forcing amplitudes; however, in many situations the resonant and/or attenuant cycles may persist for significantly large values of , as illustrated in Examples 1 and 2.

3. Example 1: a one-dimensional map

Let $F : R^1_+ \times R^1_+ \to R^1_+$ be the generalized Ricker map $F(\, ; x) = b \, x e^{-cx} + (1 - \,)x$, and $\, (t) = (-1)^t$. In this example, $n = 1$ and $p = 2$. Eq. (2) becomes

$$x(t+1) = b[1 + \, (-1)^t]x(t)\mathrm{e}^{-cx(t)} + (1 - \,)x(t).$$

$x(t)$ is the population size at time t, the per capita probability of dying during one time interval, $\mathrm{e}^{-cx(t)}$ the fractional reduction of new recruits due to density dependent effects, and $b[1 + \, (-1)^t]$ the seasonal recruitment rate, which fluctuates around an average of b with period $r = 2$ and relative amplitude $\in [0, 1)$.

When $= 0$, the autonomous model predicts 2-cycles at many values of its parameters $(q = 2)$. For example,

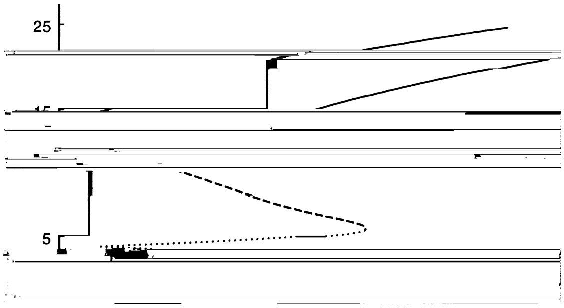
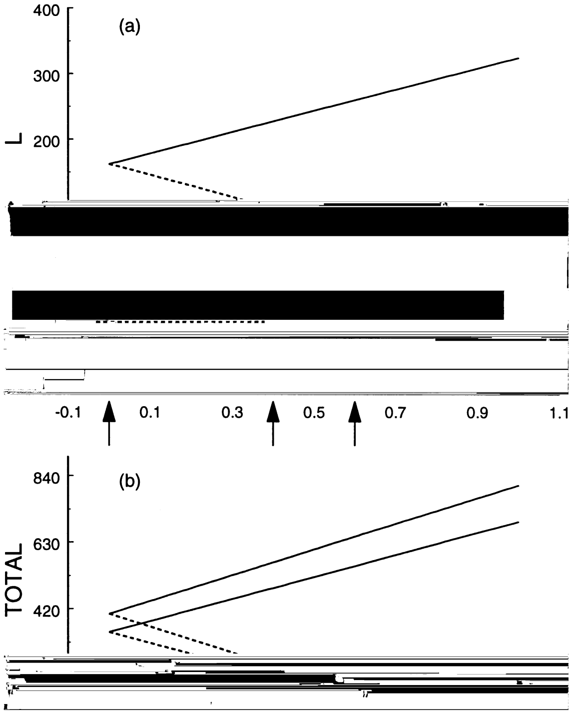


Fig. 1. 2-cycle solutions of the periodically forced Ricker-type map, shown as functions of amplitude . When = 0, there are two stable 2-cycles which are simply time shifts of each other, and an unstable fixed point. As increases from zero, one of the two locally stable 2-cycles increases in average (solid lines), while the other decreases in average (dashed lines). The unstable fixed point is perturbed into an unstable 2-cycle (dotted lines). The attenuant stable cycle and the unstable cycle annihilate each other in a saddle-node bifurcation, while the resonant stable cycle persists for all < 1.

In this example the dynamical system $x.t+1/=F.\;;x.t//$ is the periodic LPA model

$$\begin{pmatrix} L.t+1/ \\ P.t+1/ \\ A.t+1/ \end{pmatrix} = \left(\begin{array}{c} bA.t/\exp\left(\frac{-c_{\mathrm{el}}}{}L.t/-\frac{c_{\mathrm{ea}}}{}A.t/\right) \\ .1 \\ \\ \end{array} \right.$$


(a)
L
400
300
200
-0.1
0.1
0.3
0.5
0.7
0.9
1.1
(b)
TOTAL
840
630
420

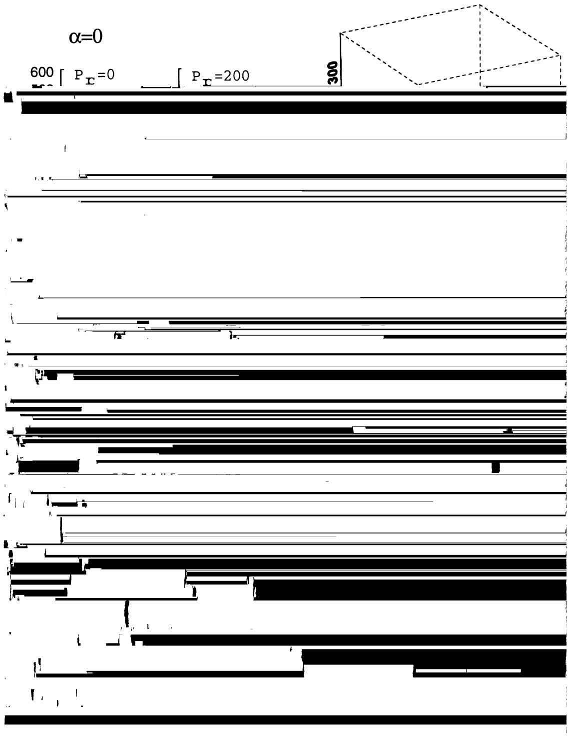


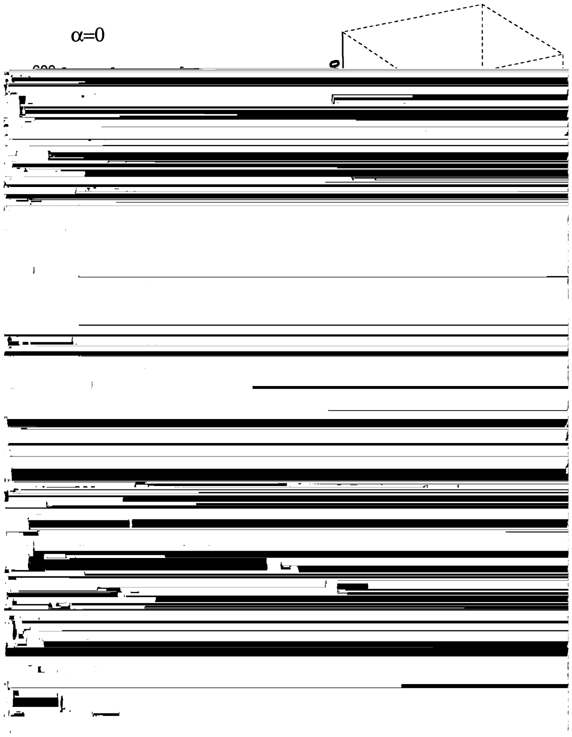
Fig. 3. Model predictions (including transients) for each of the six treatments, shown in L-stage time series and composite phase space. The squares correspond to times when flour volume is high. The solid circles in phase space represent equilibria of the first composite map. The upper (lower) composite fixed point for $\ = 0{:}4$ corresponds to the resonant (attenuant) 2-cycle.

The model therefore predicts three asymptotic regimes as indexed by the relative amplitude of the habitat fluctuation: for $\ = 0$, the stable cycle $\mathbf{x}_0^0$ and its time shift $\mathbf{x}_0^1$ of opposite phase; for $0 < \ < {}_0$, the locally stable resonant and attenuant cycles $\mathbf{x}^1$ and $\mathbf{x}^0$, respectively; and for $\ > {}_0$, the stable resonant cycle $\mathbf{x}^1$.

We studied three habitat sequences: a constant 20 g habitat ($\ = 0$), an alternating 28–12 g habitat ($\ = 0{:}4$), and an alternating 32–8 g habitat ($\ = 0{:}6$). In each of the three habitats, we used two initial conditions, $[150; 200; 150]^{\mathrm{T}}$ and $[150; 0; 150]^{\mathrm{T}}$, for a total of six treatments. There were three replicates in each of the six treatments for a total of 18 cultures. The detailed experimental protocol appears in [5].

The model predictions for each of the six treatments appear in Fig. 3. The model trajectories are presented both as time series and as orbits in “composite” phase space. The latter are actually orbits of the (autonomous) first composite map, and correspond to every other step of the time series. Black squares correspond to times when the flour volume is high. When $\ = 0;$ the model orbits for both initial conditions approach the inherent cycle $\mathbf{x}_0^0$. When $\ = 0{:}4;$ the initial condition $[150; 200; 150]^{\mathrm{T}}$ lies in the basin of attraction of the resonant 2-cycle $\mathbf{x}_{0:4}^1$, while $[150; 0; 150]^{\mathrm{T}}$ lies in the basin of attraction of the attenuant 2-cycle $\mathbf{x}_{0:4}^0$. When $\ = 0{:}6$, both initial conditions lead to model orbits approaching the resonant cycle $\mathbf{x}_{0:6}^1$.

Fig. 4 presents the first 40 weeks of data from six replicates, organized in the same format as Fig. 3. The multiple cycles are seen clearly in the data when $\ = 0{:}4$. The complete results of this experiment and those of a follow-up experiment are reported in detail in [5].


α=0

$$\mathbf{M}=\begin{pmatrix}[\mathbf{I}-F_x(1)F_x(0)]^{-1} & \mathbf{0}\\ \mathbf{0} & [\mathbf{I}-F_x(0)F_x(1)]^{-1}\end{pmatrix};$$

$$\mathbf{P}=\begin{pmatrix}F_x(1) & \mathbf{I}\\ \mathbf{I} & F_x(0)\end{pmatrix};$$

By Eq. (11) and the program Maple,

$$\mathbf{v}^0=\begin{pmatrix}u^0(0)\\ u^0(1)\end{pmatrix}=\begin{pmatrix}\begin{pmatrix}-162.2\\ 3.700\times 10^{-4}\\ -242.8\end{pmatrix}\\ \begin{pmatrix}4.656\times 10^{-4}\\ -128.8\\ -218.5\end{pmatrix}\end{pmatrix};$$

and

$$\mathbf{v}^1=\begin{pmatrix}u^1(1)\\ u^1(0)\end{pmatrix}=\begin{pmatrix}\begin{pmatrix}162.2\\ -3.700\times 10^{-4}\\ 242.8\end{pmatrix}\\ \begin{pmatrix}-4.656\times 10^{-4}\\ 128.8\\ 218.5\end{pmatrix}\end{pmatrix}.$$

Hence

$$\mathbf{u}^0=\begin{pmatrix}u^0(0)\\ u^0(1)\end{pmatrix}=\begin{pmatrix}\begin{pmatrix}-162.2\\ 3.700\times 10^{-4}\\ -242.8\end{pmatrix}\\ \begin{pmatrix}4.656\times 10^{-4}\\ -128.8\\ -218.5\end{pmatrix}\end{pmatrix};$$

$$\mathbf{u}^1=\begin{pmatrix}u^1(0)\\ u^1(1)\end{pmatrix}=\begin{pmatrix}\begin{pmatrix}-4.656\times 10^{-4}\\ 128.8\\ 218.5\end{pmatrix}\\ \begin{pmatrix}162.2\\ -3.700\times 10^{-4}\\ 242.8\end{pmatrix}\end{pmatrix}.$$

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