Phase switching in population cycles

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Oscillatory populations may exhibit a phase change in which, for example, a high–low periodic pattern switches to a low–high pattern. We propose that phase shifts correspond to stochastic jumps between basins of attraction in an appropriate phase space which associates the different phases of a periodic cycle with distinct attractors. This mechanism accounts for two-cycle phase shifts and the occurrence of asynchronous replicates in experimental cultures of Tribolium.

Keywords: periodic time-series; stochasticity; phase switching; basins of attraction; nonlinear population dynamics; Tribolium

1. INTRODUCTION

Many biological populations, when carefully studied in the laboratory, display temporal cycling in numbers (Hassell & May 1990). Examples include paramecia (Gause 1964), blow flies (Nicholson 1957), bean weevils (Utida 1957), and flour beetles. Indeed, most continuously cultured laboratory populations of the flour beetle Tribolium exhibit sustained oscillations (Costantino & Desharnais 1991).

Noise is always present in population data and prevents oscillatory data from being exactly periodic. Any mathematical property of periodicity (phase, amplitude, average, etc.) can be affected by stochastic perturbations. In this paper, we are concerned with the relationship between stochasticity and phase. In particular, we propose one possible causal mechanism for the phenomenon of phase switching in oscillating data.

§2 presents time-series data illustrating the phenomenon of phase switching in a variety of contexts. §3 uses the famous Ricker model to exemplify the mathematical theory proposed for a possible explanation of phase shifting. In §4, we apply the theory to a multivariate map for Tribolium dynamics and use it to explain specific occurrences of phase switching and asynchronous replicates in laboratory cultures of Tribolium.

2. OBSERVED PHASE SWITCHING IN POPULATION DATA

A common phenomenon observed in oscillating laboratory cultures of Tribolium is a change of phase in which, for example, a high–low periodic pattern ‘chicken-steps’ (skips) to a low–high pattern. Phase switching often leads to asynchronous replicates.

Phase shifts occur in many of the Tribolium castaneum time-series published in Desharnais & Costantino (1980). Figure 1a displays larval numbers for two of the control replicates. The cultures were shown to be oscillating with period two (Dennis et al. 1995). Phase shifts occur in both replicates, eventually leading to asynchrony.

A phenomenologically similar Tribolium example comes from an experiment conducted using a different strain in another laboratory under significantly different experimental protocols. Figure 1b plots larval numbers for two replicate time-series reported in Costantino et al. (1995). These cultures were also shown to be in a two-cycle regime (Dennis et al. 1997). One of the replicates appearing in figure 1b shifts phase, and at that particular time the replicates become asynchronous.

An example with a different animal can be seen in the data recorded by Gause (1964; tab. 3). Figure 1c presents time-series data for two replicate Paramecium caudatum cultures grown separately. Both replicates show two-cycle oscillations followed by several phase shifts.

A final example illustrates the phenomenon of phase switching in data cycling with period three. Three replicate time-series for Tribolium castaneum, as reported in Costantino et al. (1997), are shown in figure 1d. All three replicate cultures display three-cycle (high–low–low) behaviour, and two of the replicates shift phase. By the end of the time-series, all three replicates are oscillating out of phase.

3. THEORETICAL PHASE SWITCHING IN POPULATION MODELS

In this section we use a discrete univariate map to introduce and illustrate the mathematical ideas central to
Figure 1. (a) Tribolium castaneum two-cycle data from Desharnais & Costantino (1980). Replicate A (circles) changes phase at week 8. Replicate B (squares) changes phase at weeks 8 and 28. After week 28, the replicates are asynchronous. (b) Tribolium castaneum two-cycle data from Costantino et al. (1995). Replicate A (squares) does not change phase. Replicate D (circles) changes phase at week 20. After week 20, the replicates are asynchronous. (c) Paramaecium caudatum two-cycle data from Gause (1957). Numbers of individuals per 0.5 cm² are plotted against the number of days elapsed, with transient data (days zero to eight) omitted. Replicate no. 2 (circles) exhibits phase changes at days 14 and 16. Replicate no. 4 (squares) exhibits phase changes at days 13 and 17. (d) Tribolium castaneum three-cycle data from Costantino et al. (1997). Transient weeks zero to eight are omitted. All replicates display three-cycle behaviour (high-low-low). Replicate no. 23 (squares) does not shift phase. Replicate no. 3 (circles) changes phase once, at week 16. Replicate no. 18 (triangles) changes phase at week 26, at which time it becomes synchronized with replicate no. 3. At week 36, replicate no. 18 changes phase once more. From week 36 onwards, all three replicates remain out of phase. (In fact, this situation persists until the end of the experiment, at week 80.)

our explanation of phase switching. For simplicity, we restrict our attention to cycles of period two.

The Ricker map \( x_{t+1} = f(x_t) \) given by

\[
 x_{t+1} = bx_t e^{-cx_t},
\]

is a well-known population model which generates cycles at many choices of parameters \( b \) and \( c \). For example, when \( b = 9 \) and \( c = 1 \), the two-cycle sequence \( x_0 = 1.099, x_1 = 3.296, x_2 = 1.099, x_3 = 3.296, \ldots \) is a solution (to four significant figures). Initial conditions near \( x_0 = 1.099 \) generate solution sequences which converge to this two-cycle; hence the two-cycle solution is labelled locally stable. The out-of-phase sequence \( x_0 = 3.296, x_1 = 1.099, x_2 = 3.296, x_3 = 1.099, \ldots \) is also a locally stable two-cycle solution.

The set of points (1.099, 3.296) on the real line is an 'attractor' for the map; both of the two-cycle solutions mentioned above 'live' on this attractor. (Note that, mathematically speaking, the attractor is not a solution of the Ricker map; the attractor is just a set of two points, not a sequence of points.) The set of initial conditions which generate solutions converging on either of the two-cycles on this attractor is denoted by \( B \) and is called the basin of attraction for the attractor. A solution starting in \( B \) will remain in \( B \) throughout time.

The basin of attraction \( B \) is composed of two noteworthy subsets: the subset \( B_1 \) of initial conditions that generate solutions converging to the first two-cycle ('up' on odd-numbered \( t \)), and the set \( B_2 \) of initial conditions that generate solutions converging to the second, out-of-phase two-cycle ('up' on even-numbered \( t \)). In this sense, each of the two-cycle solutions have their own 'basin of attraction', even though neither cycle is an 'attractor' by mathematical definition.

There is a classical way, in fact, to view the two cycles of opposite phase as separate mathematical attractors in order to bring to bear the powerful tools and concepts of a dynamical systems theory. The idea is to look at the population at every other time-step by constructing the so-called 'composite' map (e.g. see May & Oster 1976).
For the Ricker model, the population density \( x_{t+2} \) at time \( t+2 \) is projected from \( x_t \) by two successive applications of the Ricker map
\[
x_{t+2} = f(x_{t+1}) = f(f(x_t)).
\]
This is the expression we would use to calculate the population density at every second time-step. If we redefine a unit of time to be two of the original units of time, we have the composite Ricker map \( x_{t+1} = f(f(x_t)) \):
\[
x_{t+1} = b[x_t e^{-\alpha t}] e^{-[b(x_t e^{-\alpha t})]}.
\]
Given an initial condition \( x_0 \), the solution sequence of the composite map corresponds to every other step of the solution sequence of the Ricker map. For example, the locally stable two-cycle solution \( x_0 = 1.099, x_1 = 3.296, x_2 = 1.099, x_3 = 3.296, \ldots \), of the Ricker map corresponds to a locally stable constant solution \( x_0 = 1.099, x_1 = 1.099, x_2 = 1.099 \) (i.e., a locally stable fixed point \( x_0 = 1.099 \)) of the composite Ricker map. Similarly, the locally stable two-cycle solution \( x_0 = 3.296, x_1 = 1.099, x_2 = 3.296, x_3 = 1.099, \ldots \), of the Ricker map corresponds to a locally stable fixed point \( x_0 = 3.296 \) of the composite map. The composite Ricker map thus has two separate fixed-point attractors \( \{x_0\} \) and \( \{x_2\} \).

The set \( B_0 \) of initial conditions leading to composite map solutions which converge to the fixed-point \( x_0 \), is the basin of attraction for the attractor \( \{x_0\} \). The basin of attraction \( B_0 \) of \( \{x_2\} \) is defined similarly. A solution of the composite map starting in \( B_0 \) remains in \( B_0 \) throughout time. A similar statement holds for \( B_2 \).

If, however, noise were added to the system, a solution of the composite map lying in basin \( B_0 \) might be stochastically bumped into basin \( B_2 \) at some point in time. In terms of the original Ricker map, this would correspond to a solution approaching the first two-cycle being stochastically bumped into an approach to the second (out-of-phase) two-cycle solution. If the solution was originally in phase with the first two-cycle, such a stochastic perturbation would, at least in the long run, cause a change in the phase of oscillation.

For example, consider the stochastic Ricker map
\[
x_{t+1} = b x_t e^{-\alpha t} + \sigma E_t,
\]
where \( E_t \) is a normal random variable with a mean zero and variance one (Dennis & Taper 1994). Figure 2 shows one stochastic-realization switching (composite) attractor basins and temporal phase at time \( t = 7 \) and thereafter oscillating out of phase with the deterministic two-cycle solution.

The general concept of stochastic basin jumping is an explanation we propose for the phenomenon of phase switching in time-series data.

4. THE THEORY APPLIED TO EXPERIMENTAL DATA

In this section we apply our proposed theoretical explanation of phase switching to the control treatments (see figure 1a) reported in Desharnais & Costantino (1980). Briefly, the experimental protocol was as follows. Cultures of Tribolium castaneum, homozygous for the corn-oil sensitive allele (os/os), were initiated with 64 young adults, 15 pupae, 20 large larvae, and 70 small larvae. Each population was contained in a half-pint milk bottle with 20 g of corn-oil media (90% wheat flour, 5% brewer’s yeast, and 5% liquid corn oil) and kept in an unlit incubator at 33±1 °C and 56±11% relative humidity. Every two weeks all stage classes, except eggs, were censused and all stage classes, including eggs, were placed in fresh media. This procedure was followed for 38 weeks. A complete listing of the census data is given in tab. 2 in Desharnais & Liu (1987).

(a) The LPA model

The discrete stage-structured ‘LPA’ Tribolium model of Dennis et al. (1995) has successfully explained and predicted nonlinear phenomena in a variety of contexts, including the transitions between dynamic regimes (such as equilibria, two-cycles, three-cycles, invariant loops, and chaos), multiple attractors, and saddle influences (Costantino et al. 1995, 1997, 1998; Cushing 1996, 1998; Dennis et al. 1995, 1997; Desharnais et al. 1997; Henson et al. 1999). We now use the LPA model to explain the chicken-steps observed in Desharnais & Costantino (1980) and Dennis et al. (1995).

A stochastic version of the LPA model is given by the equations
\[
L_{t+1} = b A_t \exp \left( -\epsilon_{os} A_t - \epsilon_{ct} L_t \right) \exp (E_{Lt}),
\]
\[
P_{t+1} = L_t (1 - \mu) \exp (E_{Pt}),
\]
\[
A_{t+1} = [P_t \exp (\epsilon_{pt} A_t) + A_t (1 - \mu_p)] \exp (E_{At}),
\]
where $L$ denotes the number of (feeding) larvae, $P$ denotes the number of pupae (non-feeding larvae, pupae, and
callow adults), and $A$ denotes the number of adults. The
discrete time interval is two weeks. The coefficient $b > 0$
denotes the average number of larvae recruited per adult per
unit of time in the absence of cannibalism, $0 < \mu_a, \mu_l < 1$
are the adult and larval probabilities of dying from causes
other than cannibalism, and the exponentials
\[ \exp(-c_{oa} a_i - c_{pa} p_i) \] and
\[ \exp(-c_{pa} p_i) \] represent the probabilities that individuals survive cannibalism in one unit of
time, with 'cannibalism coefficients' $c_{oa}$, $c_{pa}$, $c_{pa} > 0$.
$E_i = [E_{i1}, E_{i2}, E_{i3}]$ is a random vector assumed to have a
trivariate normal distribution with mean vector zero and variance–covariance matrix $\Sigma$. $E_{i1}, E_{i2}, ..., $ are assumed to
be uncorrelated. We refer to the deterministic skeleton of
the stochastic LPA model (obtained by setting $E_i = 0$) as the
'LPA model'. Relevant mathematical theorems concerning
properties of the LPA model appear in Henson & Cushing
(1997). Local stability results for both the LPA model and
its composite are obtained using standard linearization
techniques (Cushing 1998; Guckenheimer & Holmes 1983).

In Dennis et al. (1995), the maximum likekly parameters
estimated from the control replicates reported in Desharnais
& Costantino (1980) were $b = 1.1772$, $\mu_l = 0.5129$,
$c_{pa} = 0.0178$, $c_{oa} = 0.0110$, $c_{ml} = 0.0093$, and $\mu_a = 0.1108$, with
\[
\Sigma = \begin{pmatrix}
0.2771 & 0.0279 & 0.0098 \\
0.0279 & 0.4284 & -0.0081 \\
0.0098 & -0.0081 & 0.0111
\end{pmatrix}.
\]

At these parameter values, the LPA model admits an
unstable fixed point (rounded to the nearest beetle) of
$[L, P, A] = [124, 60, 97]$.

This fixed point is stable in some directions and unstable
in other directions (i.e. it is a saddle point; see Cushing et al.
(1998)). The LPA model also predicts two locally stable
two-cycle solutions: one determined by the stage vectors
$[L_0, P_0, A_0] = [18, 158, 106]$, $[L_0, P_0, A_0] = [325, 9, 118]$, and
the other given by the phase-shifted cycle $[L_0, P_0, A_0] = [325, 9, 118]$, $[L_0, P_0, A_0] = [18, 158, 106]$.

Because they 'live' on the same attractor $([18, 158, 106],
[325, 9, 118])$, the two different two-cycle solutions listed
above are indistinguishable when plotted in $[L, P, A]$ space
(phase space). However, these solutions do determine
different phases for each component. For example, the first
cycle determines a low–high oscillation in the larval component $L$, while the second determines a high–
low oscillation in $L$. In order to differentiate between
these out-of-phase two-cycle solutions as separate attractors
with distinct basins of attraction, we turn to the
composite of the LPA model.

(b) The composite LPA model

The 'composite LPA model' (the composite map, in
which the solutions correspond to even time-steps of solutions
of the LPA model) identifies the above two-cycle
solutions as two different fixed point attractors given by
the stage vectors $[L, P, A] = [18, 158, 106]$, and
$[L, P, A] = [325, 9, 118]$. 

Figure 3. LPA model predictions.
(a) Deterministic model time-series with the
initial condition $[70, 35, 64]$ approaches a stable two-cycle. The
composite time-series consists of the even
time-steps (solid triangles). (b) A time-series realization of the stochastic LPA
model with the initial condition $[70, 35, 64]$ suffers phase shifts at $t = 7$
and $t = 15$. (c) In composite phase space, the corresponding deterministic model
orbit (solid triangles) approaches the composite fixed point attractor
$[L, P, A] = [18, 158, 106]$, remaining well to the left of the basin boundary.
The basin-boundary surface is indicated by cross-sections in the $P = 0, 60, 120$ and
180 planes. The cross on the boundary marks the saddle point, and the solid
circle represents the composite fixed-point attractor $[L, P, A] = [325, 9, 118]$.
(d) In composite phase space, the stochastic time-series phase shifts appear
as crossings of the basin boundary. Open triangles represent triples in the basin of
$[L, P, A] = [18, 158, 106]$; open circles represent triples in the basin of
$[L, P, A] = [325, 9, 118]$. 


Figure 4. Data. Replicates A (a) and (c) and B (b) and (d) from Desharnais & Costantino (1980) plotted as time-series and as orbits in composite phase space using the same format as in figure 3. Open triangles represent triples in the basin of $[L, P, A]_G = [18, 158, 106]$ (solid triangle); open circles represent triples in the basin of $[L, P, A]_O = [325, 9, 118]$ (solid circle). Boundary crossings in phase space correspond to time-series phase shifts.

(Note the subscripts $\Delta$ and $\bigcirc$ are used to label the two attractors.) The saddle point of the LPA map (labelled with the subscript $+$) is also a saddle point $[L, P, A]_s = [124, 60, 97]$, of the composite map.

The basins of attraction of the two stable fixed points of the composite LPA model are sets in three-dimensional phase space and are computed numerically. In this particular example, the basins are fairly simple sets. Throughout a large portion of phase space, they are separated by a two-dimensional surface (containing the saddle) which forms part of the ‘basin boundary’. Initial conditions on one side of the boundary lead to composite map solutions which approach $[L, P, A]_G$, while initial conditions on the other side generate composite map solutions approaching $[L, P, A]_O$. Solutions starting on the basin boundary near the saddle point tend to the saddle $[L, P, A]$, (locally, the boundary is the ‘stable manifold’ of the unstable saddle). Indeed, near the saddle, the stable manifold of this unstable entity forms the watershed geometrical feature of phase space. Near the origin, however, the basin boundary becomes much more complicated; but this will not concern us.

(c) Model predictions and data

Figures 3a and 3b exhibit the larval stage time-series of both the deterministic prediction of the LPA model, and a stochastic realization of the stochastic LPA model using the initial condition $[70, 35, 64]$ of the experiment described above. In figures 3c and 3d appear corresponding composite phase-space plots of every other step in the time-series.

The deterministic time-series approaches the two-cycle $[L_O, P_O, A_O] = [18, 158, 106]$, $[L_s, P_s, A_s] = [325, 9, 118]$, and, in composite phase space, the corresponding solution of the composite LPA map approaches the fixed point $[L, P, A]_G = [18, 158, 106]$.

The stochastic time-series, on the other hand, shifts phase at time $t=7$ and again at $t=15$. In composite phase space, the phase changes in this example occur exactly when the basin boundary is crossed.

Figure 4 presents data from the experiment using the same format as figure 3. As the LPA model predicts, phase switching occurs in the time-series data precisely when the data cross the model predicted basin boundary in composite phase space.

5. DISCUSSION

Populations often exhibit temporal oscillations, and sometimes these oscillations shift phase. We offer an explanation for phase shifts by means of a mix of stochastic and deterministic elements. Namely, we
hypothesize that phase shifts may correspond to stochastic jumps between basins of attraction in an appropriate phase space which associates the different phases of a periodic cycle with distinct attractors. We showed how this explanation accounts for phase shifts observed in two-cycle oscillations of *Tribolium* populations, as reported in Desharnais & Costantino (1980). In this case, phase shifts correspond exactly to stochastic jumps between the basins of attraction of two stable fixed points of the first composite of the deterministic LPA model.

More generally, for discrete autonomous models, p-cycle attractors of minimal period p admit p distinct phases, and hence correspond to p distinct (out-of-phase) attracting p-cycle solutions. Each of these p solutions corresponds to a different fixed-point attractor of the (p−1)-composite map (i.e. the map composed with itself p−1 times). If noise is added to the system, a solution of the composite map lying in a basin of attraction of one of the fixed points can be stochastically bumped into one of the other p−1 basins. In terms of the original map the corresponding solution, which should approach a certain p-cycle is stochastically bumped into an approach of an out-of-phase p-cycle. If the solution is originally in phase with the first cycle, such a stochastic perturbation causes (at least in the long run) a change in the phase of oscillation. The data at figure 1d provide an example of p=3'-cycle phase shifting, although the basins of the second-composite map are not analyzed here.

Deterministic attractors alone do not account for the phase-switching mechanism proposed. Unstable invariant sets such as basin boundaries and saddle points, along with stochasticity, play a key role. Deterministic attractors and unstable invariant sets define, in composite phase space, the geometry that determines the behaviour of stochastic time-series.

Finally, our explanation for phase switching may be further tested by experimental investigation of new hypotheses generated by the model. For example, the frequency of phase changes should be determined by the strength of the stochasticiy relative to basin sizes and shapes. Riddled or marbled basins with fractal boundaries might lead to perpetual phase shifting, disguising deterministic influences and making data fluctuations appear completely random. Even when the basins are simple, oscillations of small amplitude could contain so many phase shifts that the data would appear to be at noisy equilibrium. (This could occur, for example, because the attractors are close together in composite phase space, allowing frequent stochastic basin crossings.) On the other hand, oscillations of a large amplitude would be likely to suffer few phase shifts, depending on the size and location of the basin boundary. Specific model predictions such as these could be located in parameter space and tested in the laboratory.

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REFERENCES


Henson, S. M., Costantino, R. F., Cushing, J. M., Dennis, B. & Desharnais, R. A. 1999 Multiple attractors, saddles, and population dynamics in periodic habitats. (In preparation.)

