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Using a signature function to determine resonant and attenuant 2-cycles in the Smith–Slatkin population model

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We study the responses of discretely reproducing populations to periodic fluctuations in three parameters: the carrying capacity and two demographic characteristics of the species. We prove that small 2-periodic fluctuations of the three parameters generate 2-cyclic oscillations of the population. We develop a signature function for predicting the responses of populations to 2-periodic fluctuations. Our signature function is the sign of a weighted sum of the relative strengths of the oscillations of the three parameters. Periodic environments are deleterious for populations when the signature function is negative, while positive signature functions signal favorable environments. We compute the signature function for the Smith–Slatkin model, and use it to determine regions in parameter space that are either favorable or detrimental to the species.

Keywords: Attenuant; Periodic forcing; Resonant; Signature function; Smith–Slatkin model

1. Introduction

Franke and Yakubu, in a recent paper, used classical parametric single species discrete-time population models to study the responses of populations to periodic fluctuations in two parameters, the carrying capacity and the demographic characteristic of the population (growth rate) [19]. In constant environments, many classical discrete-time single species population models have three parameters, the carrying capacity and two demographic characteristics of the species [1–25,27–43]. Examples of such 3-parameter single species models include the Smith–Slatkin, Hassell, Bobwhite quail and Maynard-Smith models [1,3–5,19–21,33–36,43]. In this paper, we focus on the effects of 2-periodic forcing of the carrying capacity and *two* demographic characteristics on populations governed by discrete-time models. Many of our arguments are similar to those in the two parameter paper [19] but are more complicated because of the third parameter.

Periodic environments are known to be deleterious for populations governed by the logistic differential or difference equations [6,39]. That is, the average of the resulting oscillations in the periodic environment is less than the average of the carrying capacities in corresponding constant environments (attenuance). Cushing and Henson obtained similar results for 2-periodic monotone models [6]. Elaydi and Sacker [9–12], Franke and Yakubu [15–19], Kocic [27], and

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Kon [29,30] have since extended these results to include *p-periodic* Beverton–Holt population models with or without age–structure, where $p > 2$. These results are known to be model-dependent [6]. However, in almost all the theoretical studies, with only a few exceptions (see [9–12,19]), *only* two parameters are periodically-forced: the carrying capacity of the species and one demographic characteristic of the species.

Unimodal maps under period-2 forcing in two parameters routinely have up to three coexisting 2-cycles (see [31,38] for examples). We use the Smith–Slatkin model to illustrate multiple 2-cycles in maps under period-2 forcing in three parameters. Also, we construct a signature function, $\mathcal{R}_d$, for determining whether the average total biomass is suppressed via attenuant stable 2-cycles or enhanced via resonant stable 2-cycles. As in Ref. [19], $\mathcal{R}_d$ is the sign of a weighted sum of the relative strengths of the oscillations of carrying capacity and the two demographic characteristics of the species. We use the 3-parameter Smith–Slatkin model to illustrate that, in the presence of periodic forcing, an inverse relationship between the carrying capacity and one of the demographic characteristics of the species can lead to a decrease in the population biomass (attenuance). However, large values of the carrying capacity and one of the demographic characteristics of the species can lead to an increase in the population biomass (resonance). Consequently, a change in relative strengths of oscillations of carrying capacity and at least one of the demographic characteristics of a species is capable of shifting population dynamics from attenuant to resonant cycles and vice versa. It is know that this dramatic shift is not possible in population models with a single fluctuating parameter [19,22,23].

Section 2 introduces our framework for studying the impact of environmental fluctuations on discrete-time population models with three fluctuating parameters. In Section 3, we prove that small 2-periodic perturbations of the carrying capacity and the demographic characteristics of the unforced system produce 2-cycle populations. The signature function, $\mathcal{R}_d$, for predicting resonant and attenuant 2-cycles that perturb from the equilibrium given by the carrying capacity of the unforced system is introduced in Section 4. $\mathcal{R}_d$ for the Smith–Slatkin model, and regions in parameter space for the support of attenuant or resonant 2-cycles that perturb from the equilibrium given by the carrying capacity are given in Section 5. In Sections 3–5, we assume that a 2-cycle must, for small forcing, be close to the carrying capacity. However, the carrying capacity does not have to be the only source of 2-cycles.

To compute $\mathcal{R}_d$ for the other coexisting 2-cycles, in Sections 6 and 7 we assume that two 2-cycles perturb from (the two different phases of) a 2-cycle in the unforced model. In Section 6, we prove that small 2-periodic perturbations of a 2-cycle of the unforced system produce two 2-cycle populations. Signature functions, $\mathcal{R}_d$, for 2-species Kolmogorov type discrete-time population models with 2-periodic forcing of 2-cycles are introduced in Section 7. $\mathcal{R}_d$ for the Smith–Slatkin model, and regions in parameter space for the support of attenuant or resonant coexisting 2-cycles in the model are also given in Section 7. The implications of our results are discussed in Section 8.

2. Population models with three parameters

Theoretical ecology literature is filled with single species discrete-time population models that have three parameters. Table 1 is a list of specific classical examples of population models with three parameters.

Table 1. Examples of three-parameter population models.

Model $f_{k,m,n}(x) =$	*Parameters giving stable carrying capacity,* $k > 0$	*References*
$\frac{(1+(mk)^n)x}{1+(mx)^n}$	$0 < n < 2$ or $0 < m < \frac{1}{k}\left(\frac{2}{n-2)^{1/n}}\right)$	Smith–Slatkin (1950) [3–5,19–21]
$\frac{mk^n x}{(k+(m)^{1/n}-1)x)^n}$	$0 < n\left(1 - \frac{1}{m^{1/n}}\right) < 2$	Hassell (1954) [3–5,19–21]
$\frac{k^n mx}{k^n+(m-1)x^n)}$	$1 < m, n(m-1) < 2m$	Maynard-Smith (1974) [3–5,19–21]

In Ref. [19], Franke and Yakubu studied the combined effects of 2-periodic forcing of two model parameters, the carrying capacity and a demographic characteristic of the species. To study the impact of 2-periodic forcing of three model parameters, we consider population models of the general form

$$x(t+1) = x(t)g(k, m, n, x(t)), \tag{1}$$

where $x(t)$ is the population size at generation t, m and n are demographic characteristics of the species and k is the carrying capacity, i.e. $g(k, m, n, k) = 1$. The per capita growth rate $g \in C^3(\mathring{\mathbb{R}}_+ \times \mathring{\mathbb{R}}_+ \times \mathring{\mathbb{R}}_+ \times \mathbb{R}_+, \mathbb{R}_+)$, where $\mathbb{R}_+ = [0, \infty)$ and $\mathring{\mathbb{R}}_+ = (0, \infty)$. To simplify the notation we will let $P(x) = (k, m, n, x)$.

For each triple of positive constants k, m and n, define

$$f_{k,m,n} : \mathbb{R}_+ \longrightarrow \mathbb{R}_+$$

by

$$f_{k,m,n}(x) = xg(P(x)).$$

The set of iterates of $f_{k,m,n}$ is equivalent to the set of density sequences generated by Model (1).

Table 1 lists the classic Smith–Slatkin, Hassell and Maynard-Smith models [3–5,19–21] that we denote as Models I, II and III, respectively. In Model I, the carrying capacity ($k > 0$) is an attracting positive fixed point whenever either $0 < n < 2$ or $m < (1/k)(2/n - 2)^{1/n}$. However, in Models II and III, the carrying capacity is an attracting positive fixed point when $0 < n(1 - (1/(m)^{1/n})) < 2$ and $1 < m, n(m-1) < 2m$, respectively (see column 2 of table 1 for stability conditions).

When the carrying capacity, k, as well as both of the demographic characteristics, m and n, are 2-periodically forced, then equation (1) becomes

$$x(t+1) = x(t)g(k(1 + \alpha(-1)^t),\ m(1 + \beta(-1)^t),\ n(1 + \gamma(-1)^t), x(t)), \tag{2}$$

where the relative strengths of the perturbations $\alpha, \beta, \gamma \in (-1, 1)$. Unimodal maps with period-2 forcing routinely have up to three coexisting 2-cycles. For two-parameter discrete-time population models, these results were obtained by Franke–Yakubu [19], Kot–Schaffer [31] and Rodriguez [38]. In Sections 5 and 7, we use the Smith–Slatkin model, Model I in table 1, to illustrate specific examples of equation (2).

When

$$x_1 = x_0 g(k(1 + \alpha), m(1 + \beta), n(1 + \gamma), x_0) \quad \text{and}$$

$$x_0 = x_1 g(k(1 - \alpha), m(1 - \beta), n(1 - \gamma), x_1),$$

then $\{x_0, x_1\}$ is a 2-cycle for equation (2). Depending on model parameters, 2-periodic dynamical systems have globally stable 2-cycles [15–19]. In the next section, we obtain conditions for the global stability of the 2-cycle of equation (2) under the assumption that the 2-cycle must, for small forcing, be close to the carrying capacity. In general, the carrying capacity does not have to be the only source of 2-cycles. For example, in the logistic and Ricker maps with two parameters, the other two 2-cycles perturb from the 2-cycle of the unforced system.

As in Ref. [19], when a 2-cycle perturbs from the equilibrium given by the carrying capacity k, we use the following definition to compare the average of the 2-cycle with the carrying capacity k.

Definition 1. *A 2-cycle of equation (2) is attenuant (resonant) if its average value is less (greater) than the carrying capacity k* [6].

Next, we introduce similar definitions for attenuant and resonance 2-cycles that are perturbations of 2-cycles. When a 2-cycle perturbs from the 2-cycle of the unforced model, $\{\bar{x}, \bar{y}\}$, we use the following definition from Ref. [19] to compare the average of the 2-cycle with the average of $\{\bar{x}, \bar{y}\}$.

Definition 2. *A 2-cycle of equation (2) is attenuant (resonant) if its average value is less (greater) than $(\bar{x} + \bar{y}/2)$.*

When two 2-cycles perturb from the 2-cycle of the unforced model, $\{\bar{x}, \bar{y}\}$, we use the following definition to compare the average of the two 2-cycles together with the average of $\{\bar{x}, \bar{y}\}$.

Definition 3. *Let $\{\bar{x}_0, \bar{x}_1\}$ and $\{\bar{y}_0, \bar{y}_1\}$ denote two coexisting 2-cycles of equation (2) that perturb from $\{\bar{x}, \bar{y}\}$. Together, $\{\bar{x}_0, \bar{x}_1\}$ and $\{\bar{y}_0, \bar{y}_1\}$, are attenuant (resonant) if their average value*

$$\frac{\bar{x}_0 + \bar{y}_0 + \bar{x}_1 + \bar{y}_1}{4}$$

is less (greater) than $(\bar{x} + \bar{y}/2)$.

These definitions of attenuant and resonant cycles refer to a decrease and an increase in average total population sizes, respectively [19].

3. 2-Cycle perturbations from unforced carrying capacity: 2-cycle attractor

It is known that small 2-periodic perturbations of a single parameter can generate population cycles of period 2 in population models with either one or two parameters [14,19,23]. In this section, we illustrate that small 2-periodic perturbations of the carrying capacity, k, and the two demographic characteristics of the population governed by equation (2), m and n, produce 2-cycle populations, $\{x_0, x_1\}$ with x_0 and x_1 near k. This 2-cycle reduces to the carrying capacity in the absence of period-2 forcing in the parameters. To simplify the notation, throughout the paper we let

$$P(k) = (k, m, n, k), \quad P(\mathbf{0}, x) = (0, 0, 0, k, m, n, x)$$

and

$$P(\boldsymbol{\alpha}, x) = (\alpha, \beta, \gamma, k, m, n, x).$$

THEOREM 4. *Suppose*

$$\left.\frac{\partial g}{\partial x}\right|_{P(k)} \neq 0 \quad \text{and} \quad \left.\frac{\partial g}{\partial x}\right|_{P(k)} \neq -\frac{2}{k}.$$

Then for all sufficiently small $|\alpha|, |\beta|$ *and* $|\gamma|$, *equation* (2) *has a* 2-*cycle population*

$$\{x_0 = x_0(\alpha, \beta, \gamma), \;\; x_1 = x_1(\alpha, \beta, \gamma)\},$$

where

$$\lim_{(\alpha,\beta,\gamma)\to(0,0,0)} x_0(\alpha, \beta, \gamma) = \lim_{(\alpha,\beta,\gamma)\to(0,0,0)} x_1(\alpha, \beta, \gamma) = k$$

and $x_0(\alpha, \beta, \gamma), x_1(\alpha, \beta, \gamma)$ *are* C^3 *with respect to* α, β *and* γ. *If the carrying capacity, k, is locally asymptotically stable* (*unstable*), *then the* 2-*cycle is locally asymptotically stable* (*unstable*).

Proof. Let

$$F(P(\boldsymbol{\alpha}, x)) = f_{k(1-\alpha),m(1-\beta),n(1-\gamma)} \circ f_{k(1+\alpha),m(1+\beta),n(1+\gamma)}(x).$$

To prove this result, we look for fixed points of the composition map

$$\begin{aligned} F(P(\boldsymbol{\alpha}, x)) &= f(k(1-\alpha), m(1-\beta), n(1-\gamma), f(k(1+\alpha), m(1+\beta), n(1+\gamma), x)) \\ &= xg(\hat{k}, \hat{m}, \hat{n}, x)g(\tilde{k}, \tilde{m}, \tilde{n}, xg(\hat{k}, \hat{m}, \hat{n}, x)), \end{aligned}$$

where $\hat{k} = k(1+\alpha)$, $\hat{m} = m(1+\beta)$, $\hat{n} = n(1+\gamma)$, $\tilde{k} = k(1-\alpha)$, $\tilde{m} = m(1-\beta)$ and $\tilde{n} = n(1-\gamma)$.

Note that $F(P(0, x)) = k$ and

$$\left.\frac{\partial F}{\partial x}\right|_{P(\mathbf{0},x)} = \left(1 + k\left.\frac{\partial g}{\partial x}\right|_{P(k)}\right)^2.$$

Since

$$\left.\frac{\partial g}{\partial x}\right|_{P(k)} \neq 0 \quad \text{and} \quad \left.\frac{\partial g}{\partial x}\right|_{P(k)} \neq -\frac{2}{k}, \quad \left.\frac{\partial F}{\partial x}\right|_{P(\mathbf{0},k)} \neq 1.$$

These partial derivative conditions on g are equivalent to $f_{(k,m,n)}$ being hyperbolic at k. The theorem follows from a direct application of the Implicit Function Theorem to F. □

The carrying capacity, k, is a hyperbolic fixed point of $f_{k,m,n}$ if $|(\mathrm{d}f_{k,m,n}/\mathrm{d}x)(k)| \neq 1$. When k is a hyperbolic fixed point of $f_{k,m,n}$ then $(\partial g/\partial x)|_{P(k)} \neq 0$, $(\partial g/\partial x)|_{P(k)} \neq -(2/k)$ and the following result is immediate.

Corollary 5. *If the carrying capacity is a hyperbolic fixed point of equation* (1)*, then for all sufficiently small* $|\alpha|, |\beta|$ *and* $|\gamma|$*, equation* (2) *has a 2-cycle population*

$$\{x_0 = x_0(\alpha, \beta, \gamma), x_1 = x_1(\alpha, \beta, \gamma)\},$$

where

$$\lim_{(\alpha,\beta,\gamma)\to(0,0,0)} x_0(\alpha, \beta, \gamma) = \lim_{(\alpha,\beta,\gamma)\to(0,0,0)} x_1(\alpha, \beta, \gamma) = k$$

and $x_0(\alpha, \beta, \gamma), x_1(\alpha, \beta, \gamma)$ *are* C^3 *with respect to* α, β *and* γ*. If the carrying capacity, k, is locally asymptotically stable* (*unstable*)*, then the 2-cycle is locally asymptotically stable* (*unstable*).

By Corollary (5), table 1 gives parameter regimes for the occurrence of a locally stable 2-cycle in three specific three-parameter population models under small period-2 perturbations of the carrying capacity and the two demographic characteristics of the species. Since these population models can have up to 3 coexisting 2-cycles (two stable and one unstable), these are not the only such parameter regimes.

4. 2-Cycle perturbation from unforced carrying capacity: signature function

In this section, we show that small perturbations of the carrying capacities and the two demographic characteristics of the species generate both attenuant and resonant 2-cycles, depending on the relative strengths of the fluctuations. As in the previous section, we assume that the 2-cycle must, for small forcing, be close to the carrying capacity. For this 2-cycle, we develop a signature function, $\mathcal{R}_d$, for determining whether the average total biomass is suppressed via attenuance or enhanced via resonance.

When the carrying capacity, k, is a hyperbolic fixed point of $f_{k,m,n}$ then Corollary (5) guarantees that the 2-cycle solution of equation (2) can be expanded in terms of α, β and γ as follows:

$$x_0(\alpha, \beta, \gamma) = k + \hat{x}_0(\alpha, \beta, \gamma) + x_{013}\alpha\gamma + x_{022}\beta^2 + x_{023}\beta\gamma + x_{033}\gamma^2 + R_0(\alpha, \beta, \gamma) \tag{3}$$

where

$$\hat{x}_0(\alpha, \beta, \gamma) = x_{01}\alpha + x_{02}\beta + x_{03}\gamma + x_{011}\alpha^2 + x_{012}\alpha\beta,$$

$x_{01}, x_{02}, x_{03}, x_{011}, x_{012}, x_{013}, x_{022}, x_{023}$, and x_{033} are the coefficients and $\lim_{(\alpha,\beta,\gamma)\to(0,0,0)}$ $(R_0(\alpha, \beta, \gamma)/\alpha^2 + \beta^2 + \gamma^2) = 0$ The expansion of the second point in the 2-cycle in terms of α, β and γ is as follows:

$$x_1(\alpha, \beta, \gamma) = k + \hat{x}_1(\alpha, \beta, \gamma) + x_{113}\alpha\gamma + x_{122}\beta^2 + x_{123}\beta\gamma + x_{133}\gamma^2 + R_1(\alpha, \beta, \gamma) \tag{4}$$

where

$$\hat{x}_1(\alpha, \beta, \gamma) = x_{11}\alpha + x_{12}\beta + x_{13}\gamma + x_{111}\alpha^2 + x_{112}\alpha\beta,$$

$x_{11}, x_{12}, x_{13}, x_{111}, x_{112}, x_{113}, x_{122}, x_{123}$ and x_{133} are the coefficients and

$$\lim_{(\alpha,\beta,\gamma)\to(0,0,0)} \frac{R_1(\alpha, \beta, \gamma)}{\alpha^2 + \beta^2 + \gamma^2} = 0.$$

We will use the following two auxiliary lemmas concerning the coefficients in equations (3) and (4) to establish the following expression for the average of the 2-cycle:

$$\frac{x_0(\alpha,\beta,\gamma)+x_1(\alpha,\beta,\gamma)}{2} = k + \frac{(x_{011}+x_{111})}{2}\alpha^2 + \frac{(x_{012}+x_{112})}{2}\alpha\beta + \frac{(x_{013}+x_{113})}{2}\alpha\gamma + \frac{R_0(\alpha,\beta,\gamma)+R_1(\alpha,\beta,\gamma)}{2}.$$

LEMMA 6. *In equations* (3) *and* (4),

$$x_{02} = x_{03} = x_{12} = x_{13} = x_{022} = x_{023} = x_{033} = x_{122} = x_{123} = x_{133} = 0.$$

Proof. When $\alpha = 0$,

$$x_0(0,\beta,\gamma) = k + x_{02}\beta + x_{03}\gamma + x_{022}\beta^2 + x_{023}\beta\gamma + x_{033}\gamma^2 + R_0(0,\beta,\gamma) \quad \text{and}$$

$$x_1(0,\beta,\gamma) = k + x_{12}\beta + x_{13}\gamma + x_{122}\beta^2 + x_{123}\beta\gamma + x_{133}\gamma^2 + R_1(0,\beta,\gamma).$$

However, the fixed point of $f_{k,m(1\pm\beta),n(1\pm\gamma)}$ is k. Thus,

$$f_{k,m(1-\beta),n(1-\gamma)} \circ f_{k,m(1+\beta),n(1+\gamma)}(k) = k \quad \text{and} \quad x_0(0,\beta,\gamma) = x_1(0,\beta,\gamma) = k.$$

Therefore,

$$x_{02} = x_{03} = x_{12} = x_{13} = x_{022} = x_{023} = x_{033} = x_{122} = x_{123} = x_{133} = 0.$$

□

By this result, the coefficients of the relative strength β, γ, β^2 and γ^2 in equations (3) and (4) are zero. The next result establishes that the sum of the coefficients of the relative strength α in equations (3) and (4) is zero.

LEMMA 7. *In equations* (3) *and* (4)*, if*

$$\left.\frac{\partial g}{\partial x}\right|_{P(k)} \neq 0,$$

then

$$x_{01} + x_{11} = 0.$$

Proof. Since

$$x_1(\alpha,\beta,\gamma) = f_{k(1+\alpha),m(1+\beta),n(1+\gamma)}(x_0(\alpha,\beta,\gamma)) = x_0(\alpha,\beta,\gamma)g(\hat{k},\hat{m},\hat{n},x_0(\alpha,\beta,\gamma)),$$

where $\hat{k} = k(1+\alpha), \hat{m} = m(1+\beta)$ and $\hat{n} = n(1+\gamma)$.

Therefore,

$$x_{11} = \left.\frac{\partial[x_0(\alpha,\beta,\gamma)g(\hat{k},\hat{m},\hat{n},x_0(\alpha,\beta,\gamma))]}{\partial\alpha}\right|_{P(\boldsymbol{\alpha},x)=P(\mathbf{0},k)}.$$

Similarly,

$$x_0(\alpha, \beta, \gamma) = f_{k(1-\alpha),m(1-\beta),n(1-\gamma)}(x_1(\alpha, \beta, \gamma))$$

$$= x_1(\alpha, \beta, \gamma)g(\tilde{k}, \tilde{m}, \tilde{n}, x_1(\alpha, \beta, \gamma)),$$

$$\text{where } \tilde{k} = k(1-\alpha), \tilde{m} = m(1-\beta) \text{ and } \tilde{n} = n(1-\gamma).$$

Therefore,

$$x_{01} = \left.\frac{\partial[x_1(\alpha, \beta, \gamma)g(\bar{k}, \bar{m}, \bar{n}, x_1(\alpha, \beta, \gamma))]}{\partial\alpha}\right|_{P(\boldsymbol{\alpha},x)=P(\mathbf{0},k)}.$$

Hence,

$$x_{11} = x_{01}\left(1 + k\left.\frac{\partial g}{\partial x}\right|_{P(k)}\right) + k^2\left.\frac{\partial g}{\partial k}\right|_{P(k)} \quad \text{and} \quad x_{01} = x_{11}\left(1 + k\left.\frac{\partial g}{\partial x}\right|_{P(k)}\right) - k^2\left.\frac{\partial g}{\partial k}\right|_{P(k)}.$$

Adding produces

$$(x_{01} + x_{11})k\left.\frac{\partial g}{\partial x}\right|_{P(k)} = 0.$$

Since $k \neq 0$ and $(\partial g/\partial g)|_{P(k)} \neq 0$,

$$x_{01} + x_{11} = 0.$$

□

Let

$$\mathcal{R}_d = \begin{cases} \text{sign}(w_1\alpha + w_2\beta + w_3\gamma) & \text{if} \quad \alpha > 0 \\ 0 & \text{if} \quad \alpha = 0 \\ -\text{sign}(w_1\alpha + w_2\beta + w_3\gamma) & \text{if} \quad \alpha < 0 \end{cases},$$

where

$$w_1 = \frac{(x_{011} + x_{111})}{2}, \quad w_2 = \frac{(x_{012} + x_{112})}{2} \quad \text{and} \quad w_3 = \frac{(x_{013} + x_{113})}{2}.$$

$\mathcal{R}_d$ is the sign of a weighted sum of the relative strengths of the oscillations of the carrying capacity and the two demographic characteristics of the species. A compact expression for $\mathcal{R}_d$ is

$$\mathcal{R}_d = \text{sign}(\alpha(w_1\alpha + w_2\beta + w_3\gamma)).$$

In the following result, we show that $\mathcal{R}_d$ determines when the 2-cycle is either attenuant or resonant.

THEOREM 8. *If the carrying capacity is a hyperbolic fixed point of equation* (1)*, then for all sufficiently small* $|\alpha|$, $|\beta|$ *and* $|\gamma|$*, equation* (2) *has an attenuant* (*a resonant*) 2*-cycle if* $\mathcal{R}_d$ *is negative* (*positive*)*.*

Proof. Lemmas (6) and (7) establish that the average of the 2-cycle predicted in Corollary (5) satisfies the equation

$$\begin{aligned}\frac{x_0(\alpha,\beta,\gamma)+x_1(\alpha,\beta,\gamma)}{2} &= k+\frac{(x_{011}+x_{111})}{2}\alpha^2+\frac{(x_{012}+x_{112})}{2}\alpha\beta\\ &\quad+\quad\frac{(x_{013}+x_{113})}{2}\alpha\gamma+\frac{R_0(\alpha,\beta,\gamma)+R_1(\alpha,\beta,\gamma)}{2}\\ &= k+\alpha(w_1\alpha+w_2\beta+w_3\gamma)+\frac{R_0(\alpha,\beta,\gamma)+R_1(\alpha,\beta,\gamma)}{2}.\end{aligned}$$

Since,

$$\lim_{(\alpha,\beta,\gamma)\to(0,0,0)}\frac{R_0(\alpha,\beta,\gamma)}{\alpha^2+\beta^2+\gamma^2}=\lim_{(\alpha,\beta,\gamma)\to(0,0,0)}\frac{R_1(\alpha,\beta,\gamma)}{\alpha^2+\beta^2+\gamma^2}=0,$$

the sign of

$$\frac{x_0(\alpha,\beta,\gamma)+x_1(\alpha,\beta,\gamma)}{2}-k$$

is the same as the sign of $\alpha(w_1\alpha+w_2\beta+w_3\gamma)$ which is $\mathcal{R}_d$, for all sufficiently small $|\alpha|$, $|\beta|$ and $|\gamma|$ and $\mathcal{R}_d\neq 0$. If $(x_0(\alpha,\beta,\gamma)+x_1(\alpha,\beta,\gamma)/2)-k>0$, then the 2-cycle is resonant and if $(x_0(\alpha,\beta,\gamma)+x_1(\alpha,\beta,\gamma)/2)-k<0$, then the 2-cycle is attenuant. □

When the demographic characteristics are fluctuating but the carrying capacity is constant (that is, $\alpha=0,\beta\neq 0$ and $\gamma\neq 0$), then the 2-cycle degenerates into a fixed point at the carrying capacity. However, when the demographic characteristics are constant but the carrying capacity is fluctuating ($\alpha\neq 0$, $\beta=0$ and $\gamma=0$) Theorem (8) and the definition of $\mathcal{R}_d$ give the following result.

Corollary 9. *If the carrying capacity is a hyperbolic fixed point of equation* (1) *and only the carrying capacity is fluctuating* ($\beta=0$ *and* $\gamma=0$)*, then for all sufficiently small* $|\alpha|$*,*

$$\mathcal{R}_d=\operatorname{sign}(w_1)$$

and equation (2) *has an attenuant* (*a resonant*) 2-*cycle if* w_1 *is negative* (*positive*).

Population models with 3 parameters which are 2-periodically forced are capable of experiencing both resonance and attenuance. We formalize this in the following result.

Corollary 10. *If the carrying capacity is a hyperbolic fixed point of equation* (1)*, then for all sufficiently small* $|\alpha|$, $|\beta|$ *and* $|\gamma|$, *equation* (2) *has an attenuant* (*a resonant*) 2-*cycle if* $\alpha>0$, $w_2+w_3>0$ *and* $\max\{\beta,\gamma\}<-(w_1/w_2+w_3)\alpha$ ($\min\{\beta,\gamma\}>-(w_1/w_2+w_3)\alpha$). *Also, equation* (2) *has an attenuant* (*a resonant*) 2-*cycle if* $\alpha>0$, $w_2+w_3<0$ *and* $\min\{\beta,\gamma\}>-(w_1/w_2+w_3)\alpha$ ($\max\{\beta,\gamma\}<-(w_1/w_2+w_3)\alpha$). *Consequently, if* $w_2+w_3\neq 0$ *the model has both attenuant and resonant cycles.*

Proof. If $w_2+w_3>0,\alpha>0$ and $\max\{\beta,\gamma\}<-(w_1/w_2+w_3)\alpha$, then $w_2\beta+w_3\gamma<-w_1\alpha$, $w_1\alpha+w_2\beta+w_3\gamma<0,\alpha(w_1\alpha+w_2\beta+w_3\gamma)<0$ and $\mathcal{R}_d$ is negative. Thus, Theorem (8) gives that the 2-cycle is attenuant. Similar arguments establish the rest of the proof. □

5. 2-Cycle perturbation from unforced carrying capacity: Smith–Slatkin model

In this section, we use our theorems to study the impact of the combined effects of a fluctuating carry capacity and demographic characteristics on the average total biomass of populations that are governed by the Smith–Slatkin model (table 1). Specifically, we compute $\mathcal{R}_d$ and use it to investigate parameter regimes of attenuance and resonance of the 2-cycle that perturbs from the equilibrium given by the carrying capacity.

When the carrying capacity and both of the demographic characteristics are 2-periodically forced, then the classic Smith–Slatkin model becomes

$$x(t+1) = x(t)\frac{1+(m(1+(-1)^t\beta)k(1+(-1)^t\alpha))^{n(1+(-1)^t\gamma)}}{1+(m(1+(-1)^t\beta)x(t))^{n(1+(-1)^t\gamma)}}. \tag{5}$$

From table 1, in constant environment, the carrying capacity, k, is asymptotically stable when $n < 2$ or $m < (1/k)(2/n-2)^{1/n}$. In either of these cases, Corollary (5) predicts a stable 2-cycle in Model (5).

Let $A = (1-n+4(mk)^n - 4(mk)^n n + 4(mk)^{3n} - (mk)^{4n} n + (mk)^{4n}$, $B = (mk)^n n^2 - 6(mk)^{2n} n - 4(mk)^{3n} n + 6(mk)^{2n} + 2(mk)^{2n} n^2 + (mk)^{3n} n^2$ and $C = (mk)^{3n} + 2(mk)^n n \ln(mk) + (mk)^{2n} n \ln(mk) + n\ln(mk)$. To determine the effects of periodicity on the 2-cycle, we obtain that $\mathcal{R}_d = \operatorname{sign}(\alpha(w_1\alpha + w_2\beta + w_3\gamma))$, where

$$w_1 = \frac{-4k(A+B)}{(1+(mk)^n)^2(-2-2(mk)^n+(mk)^n n)^2},$$

$$w_2 = \frac{-4kn}{-2-2(mk)^n+(mk)^n n},$$

$$w_3 = \frac{-4k(3(mk)^n+3(mk)^{2n}+1+C)}{(1+(mk)^n)^2(-2-2(mk)^n+(mk)^n n)}.$$

When $n = 1$,

$$w_1 = -\frac{4mk^2}{(2+mk)^2},$$

$$w_2 = \frac{4k}{2+mk},$$

$$w_3 = \frac{4k(mk+1+\ln(mk))}{2+mk}.$$

If $mk + 1 + \ln(mk) > 0$, $\alpha > 0$, $\beta < 0$ and $\gamma < 0$, then $\mathcal{R}_d < 0$ and the 2-cycle is attenuant. That is, a periodic environment is detrimental to the species when the fluctuations in the carrying capacity are out of phase with the fluctuations in the demographic characteristics of the species. Since $(w_1/w_2) = -(mk/2 + mk)$, if $\beta > -(w_1/w_2)\alpha = (mk/2 + mk)\alpha$ and all the three fluctuations are in phase, then $\mathcal{R}_d > 0$ and the 2-cycle is resonant (Figure 1).

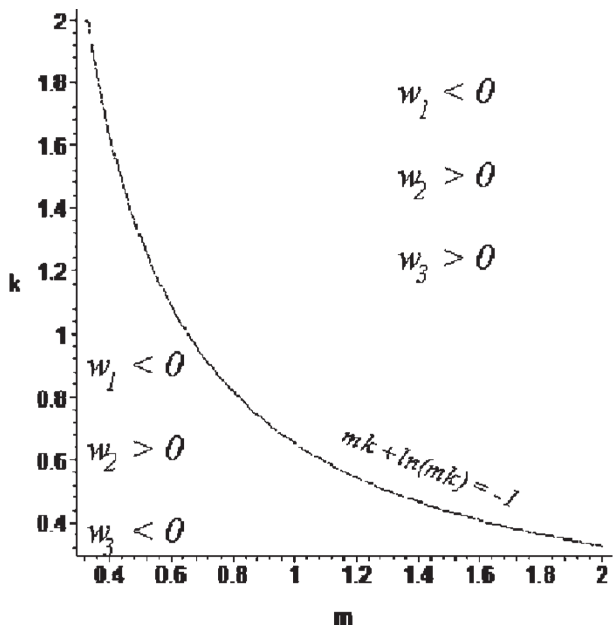

Figure 1. Regions in the *km*-plane where w_1, w_2 and w_3 are positive and negative for the 2-periodic Smith–Slatkin model, where $n = 1$.

When $n = 3$,

$$w_1 = \frac{4k(2m^3k^3 - 1)}{m^3k^3 - 2},$$
$$w_2 = -\frac{12k}{m^3k^3 - 2},$$
$$w_3 = -\frac{4k(m^3k^3 + 1 + 3\ln mk)}{m^3k^3 - 2}.$$

If $(1/\sqrt[2]{3}) < mk < \sqrt[2]{3}$, then $w_1 < 0$, $w_2 > 0$ and $w_3 > 0$ (Figure 2). If, in addition, the fluctuations in the carrying capacity are out of phase with the fluctuations in the demographic characteristics of the species, then $\mathcal{R}_d < 0$ and the 2-cycle is attenuant. That is, in the presence of periodic forcing, an inverse relationship between the carrying capacity and one of the demographic characteristics of the species can lead to a decrease in the population biomass. If $mk > \sqrt[2]{3}$, then $w_1 > 0$, $w_2 < 0$ and $w_3 < 0$ (Figure 2). If, in addition, the fluctuations in the carrying capacity are out of phase with the fluctuations in the demographic characteristics of the species, then $\mathcal{R}_d > 0$ and the 2-cycle is resonant. That is, in the presence of periodic forcing, large values of the carrying capacity and one of the demographic characteristics of the species can lead to an increase in the population biomass.

As in the case when $n = 3$, any time $n > 2$ there are two hyperbolas, $mk = c_1$ and $mk = c_2$ with $c_1 < c_2$, in the first quadrant of the m,k-plane such that $w_1 > 0$, $w_2 < 0$ and $w_3 < 0$ above the higher curve and $w_1 > 0$, $w_2 > 0$ and $w_3 < 0$ below the lower curve. This shows that if $n > 2$ in the Smith–Slatkin model, out of phase forcing of the carrying capacity and the demographic characteristics leads to an increase in the average population biomass whenever *km* is large. However, if the forcing is in phase and the forcing of the demographic characteristics are strong enough then the average population biomass decreases. In the

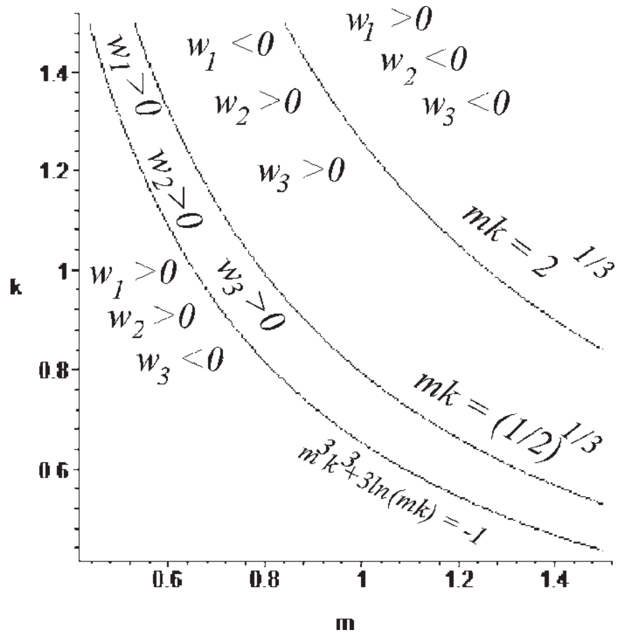

Figure 2. Regions in the km-plane where w_1, w_2 and w_3 are positive and negative for the 2-periodic Smith–Slatkin model, where $n = 3$.

region where km is small, in phase fluctuations of k and n together with out of phase fluctuations in m lead to an increase in the average total population biomass.

6. 2-Cycle perturbation from unforced 2-cycle: two coexisting 2-cycles

The classic Smith–Slatkin model, a unimodal map, is capable of undergoing period-doubling bifurcations route to chaos. In this section, we illustrate that small 2-periodic perturbations of a 2-cycle of equation (1), denoted by $\{\bar{x}, \bar{y}\}$, produce two 2-cycle populations, $\{\bar{x}_0, \bar{x}_1\}$ and $\{\bar{y}_0, \bar{y}_1\}$ with $\bar{x}_0$, $\bar{y}_1$ near $\bar{x}$ and $\bar{x}_1$, $\bar{y}_0$ near $\bar{y}$. These two 2-cycles reduce to the 2-cycle $\{\bar{x}, \bar{y}\}$ in the absence of period-2 forcing in the parameters.

Recall that in the absence of period-2 forcing our general model, equation (1), is

$$f_{k,m,n}(x) = f(P(x)) = xg(P(x)).$$

Unlike the previous sections, we now assume throughout that $f_{k,m,n}(x)$ has a 2-cycle, $\{\bar{x}, \bar{y}\}$. Next, we proceed as in Corollary 5 and use the Implicit Function Theorem to show that, for small forcing, two coexisting 2-cycles perturb from $\{\bar{x}, \bar{y}\}$. In this result,

$$F(P(\boldsymbol{\alpha}, x)) = f_{k(1-\alpha),m(1-\beta),n(1-\gamma)} \circ f_{k(1+\alpha),m(1+\beta),n(1+\gamma)}(x).$$

THEOREM 11. *Assume $f_{k,m,n}$ has a hyperbolic 2-cycle, $\{\bar{x}, \bar{y}\}$. Then for all sufficiently small $|\alpha|$ $|\beta|$ and $|\gamma|$, equation (2) has a pair of 2-cycle populations*

$$\{\bar{x}_0 = \bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1 = \bar{x}_1(\alpha, \beta, \gamma)\}$$

and

$$\{\bar{y}_0 = \bar{y}_0(\alpha, \beta, \gamma), \bar{y}_1 = \bar{y}_1(\alpha, \beta, \gamma)\}$$

where

$$\lim_{(\alpha,\beta,\gamma)\to(0,0,0)} \bar{x}_0(\alpha, \beta, \gamma) = \bar{x}, \qquad \lim_{(\alpha,\beta,\gamma)\to(0,0,0)} \bar{x}_1(\alpha, \beta, \gamma) = \bar{y}, \qquad \lim_{(\alpha,\beta,\gamma)\to(0,0,0)} \bar{y}_1(\alpha, \beta, \gamma) = \bar{x},$$

$$\lim_{(\alpha,\beta,\gamma)\to(0,0,0)} \bar{y}_0(\alpha, \beta, \gamma) = \bar{y},$$

and $\bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1(\alpha, \beta, \gamma)$, $\bar{y}_0(\alpha, \beta, \gamma), \bar{y}_1(\alpha, \beta, \gamma)$ *are* C^3 *with respect to* α, β *and* γ. *If the* 2-*cycle,* $\{\bar{x}, \bar{y}\}$, *is locally asymptotically stable* (*unstable*), *then the two* 2-*cycles are locally asymptotically stable* (*unstable*).

Proof.

$$F(P(\alpha, x)) = xg(\hat{k}, \hat{m}, \hat{n}, x)g(\tilde{k}, \tilde{m}, \tilde{n}, xg(\hat{k}, \hat{m}, \hat{n}, x)),$$

where $\hat{k} = k(1 + \alpha)$, $\hat{m} = m(1 + \beta)$, $\hat{n} = n(1 + \gamma)$, $\tilde{k} = k(1 - \alpha)$, $\tilde{m} = m(1 - \beta)$ and $\tilde{n} = n(1 - \gamma)$. Thus, $F(P(0, \bar{x})) = \bar{x}$ and $F(P(0, \bar{y})) = \bar{y}$. The 2-cycle, $\{\bar{x}, \bar{y}\}$, is a hyperbolic fixed point of $f^2_{k,m,n}$ if

$$\left|\frac{\partial f^2_{k,m,n}}{\partial x}(\bar{x})\right| = \left|\frac{\partial f_{k,m,n}}{\partial x}(\bar{x}) \cdot \frac{\partial f_{k,m,n}}{\partial x}(\bar{y})\right| \neq 1.$$

Hence,

$$\left.\frac{\partial F}{\partial x}\right|_{P(\mathbf{0},\bar{x})} = \left.\frac{\partial f_{k,m,n}}{\partial x}\right|_{(\bar{y})} \cdot \left.\frac{\partial f_{k,m,n}}{\partial x}\right|_{(\bar{x})} = \left.\frac{\partial F}{\partial x}\right|_{P(\mathbf{0},\bar{y})} \neq 1.$$

As in the proof of Theorem 4 and Corollary 5, we apply the Implicit Function Theorem at $P(0, \bar{x})$ and $P(0, \bar{y})$ to get

$$\bar{x}_0 = \bar{x}_0(\alpha, \beta, \gamma) \quad \bar{y}_0 = \bar{y}_0(\alpha, \beta, \gamma)$$

as two 3-parameters families of fixed points of F

Hence, $\bar{x}_0(\alpha, \beta, \gamma)$ and $\bar{y}_0(\alpha, \beta, \gamma)$ each gives us a 2-cycle for the 2-periodic dynamical system

$$\{f_{k(1-\alpha),n(1-\beta),n(1-\gamma)}(x), f_{k(1+\alpha),n(1+\beta),n(1+\gamma)}(x)\}.$$

Let

$$\bar{x}_1(\alpha, \beta, \gamma) = f_{k(1+\alpha),n(1+\beta),n(1+\gamma)}(\bar{x}_0(\alpha, \beta, \gamma))$$

and

$$\bar{y}_1(\alpha, \beta, \gamma) = f_{k(1-\alpha),n(1-\beta),n(1-\gamma)}(\bar{y}_0(\alpha, \beta, \gamma)).$$

Then

$$\bar{x}_0(\alpha, \beta, \gamma) = f_{k(1-\alpha),n(1-\beta),n(1-\gamma)}(\bar{x}_1(\alpha, \beta, \gamma)) \quad \text{and}$$

$$\bar{y}_0(\alpha, \beta, \gamma) = f_{k(1+\alpha),n(1+\beta),n(1+\gamma)}(\bar{y}_1(\alpha, \beta, \gamma)).$$

7. 2-Cycle perturbation from unforced 2-cycle: signature function

In this section, we obtain a signature function, $\mathcal{R}_d$, under the assumption that a 2-cycle must, for small forcing, be close to the 2-cycle $\{\bar{x}, \bar{y}\}$ of equation (1). When the 2-cycle $\{\bar{x}, \bar{y}\}$ is hyperbolic, Theorem (11) guarantees the four three-parameter families,

$$\bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1(\alpha, \beta, \gamma), \bar{y}_0(\alpha, \beta, \gamma) \quad \text{and} \quad \bar{y}_1(\alpha, \beta, \gamma),$$

where

$$\bar{x}_1(\alpha, \beta, \gamma) = f_{k(1+\alpha),n(1+\beta),n(1+\gamma)}(\bar{x}_0(\alpha, \beta, \gamma))$$

and

$$\bar{y}_1(\alpha, \beta, \gamma) = f_{k(1+\alpha),n(1+\beta),n(1+\gamma)}(\bar{y}_0(\alpha, \beta, \gamma)).$$

Note that

$$\bar{x}_0(\alpha, \beta, \gamma) = f_{k(1-\alpha),n(1-\beta),n(1-\gamma)}(\bar{x}_1(\alpha, \beta, \gamma)) \quad \text{and}$$

$$\bar{y}_0(\alpha, \beta, \gamma) = f_{k(1-\alpha),n(1-\beta),n(1-\gamma)}(\bar{y}_1(\alpha, \beta, \gamma)).$$

Let the linear expansion of these four 3-parameter families about $(\alpha, \beta, \gamma) = (0, 0, 0)$ be

$$\bar{x}_0(\alpha, \beta, \gamma) \approx \bar{x} + x_{01}\alpha + x_{02}\beta + x_{03}\gamma \quad \bar{x}_1(\alpha, \beta, \gamma) \approx \bar{y} + x_{11}\alpha + x_{12}\beta + x_{13}\gamma$$

$$\bar{y}_0(\alpha, \beta, \gamma) \approx \bar{y} + y_{01}\alpha + y_{02}\beta + y_{03}\gamma \quad \bar{y}_1(\alpha, \beta, \gamma) \approx \bar{x} + y_{11}\alpha + y_{12}\beta + y_{13}\gamma.$$

Next, we state the formulas for the coefficients.

$$x_{01} = -\frac{\frac{\partial F}{\partial \alpha}\Big|_{P(\mathbf{0},\bar{x})}}{\frac{\partial F}{\partial x}\Big|_{P(\mathbf{0},\bar{x})} - 1} = -\frac{-k\frac{\partial f}{\partial k}\Big|_{P(\bar{y})} + \frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \left(k\frac{\partial f}{\partial k}\Big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} - 1},$$

$$x_{02} = -\frac{\frac{\partial F}{\partial \beta}\Big|_{P(\mathbf{0},\bar{x})}}{\frac{\partial F}{\partial x}\Big|_{P(\mathbf{0},\bar{x})} - 1} = -\frac{-m\frac{\partial f}{\partial m}\Big|_{P(\bar{y})} + \frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \left(m\frac{\partial f}{\partial m}\Big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} - 1},$$

$$x_{03} = -\frac{\frac{\partial F}{\partial \gamma}\Big|_{P(\mathbf{0},\bar{x})}}{\frac{\partial F}{\partial x}\Big|_{P(\mathbf{0},\bar{x})} - 1} = -\frac{-n\frac{\partial f}{\partial n}\Big|_{P(\bar{y})} + \frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \left(n\frac{\partial f}{\partial n}\Big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} - 1},$$

and

$$y_{01} = -\frac{\frac{\partial F}{\partial \alpha}\Big|_{P(\mathbf{0},\bar{y})}}{\frac{\partial F}{\partial x}\Big|_{P(\mathbf{0},\bar{y})} - 1} = -\frac{-k\frac{\partial f}{\partial k}\Big|_{P(\bar{x})} + \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} * \left(k\frac{\partial f}{\partial k}\Big|_{P(\bar{y})}\right)}{\frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} - 1},$$

$$y_{02} = -\frac{\frac{\partial F}{\partial \beta}\Big|_{P(\mathbf{0},\bar{y})}}{\frac{\partial F}{\partial x}\Big|_{P(\mathbf{0},\bar{y})} - 1} = -\frac{-m\frac{\partial f}{\partial m}\Big|_{P(\bar{x})} + \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} * \left(m\frac{\partial f}{\partial m}\Big|_{P(\bar{y})}\right)}{\frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} - 1},$$

$$y_{03} = -\frac{\frac{\partial F}{\partial \gamma}\Big|_{P(\mathbf{0},\bar{y})}}{\frac{\partial F}{\partial x}\Big|_{P(\mathbf{0},\bar{y})} - 1} = -\frac{-n\frac{\partial f}{\partial n}\Big|_{P(\bar{x})} + \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} * \left(n\frac{\partial f}{\partial n}\Big|_{P(\bar{y})}\right)}{\frac{\partial f}{\partial x}\Big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\Big|_{P(\bar{x})} - 1}.$$

To get the other 6 coefficients, we let $\bar{F}(\alpha,\beta,\gamma,k,m,n,x) = F(-\alpha,-\beta,-\gamma,k,m,n,x)$. Then

$$\bar{F}(\alpha,\beta,\gamma,k,m,n,\bar{x}_1(\alpha,\beta,\gamma)) = \bar{x}_1(\alpha,\beta,\gamma) \quad \text{and}$$

$$\bar{F}(\alpha,\beta,\gamma,k,m,n,\bar{y}_1(\alpha,\beta,\gamma)) = \bar{y}_1(\alpha,\beta,\gamma).$$

Consequently,

$$x_{11} = -\frac{\frac{\partial F}{\partial \alpha}\big|_{P(\mathbf{0},\bar{y})}}{\frac{\partial F}{\partial x}\big|_{P(\mathbf{0},\bar{y})}-1} = -\frac{-k\frac{\partial f}{\partial k}\big|_{P(\bar{x})}+\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\left(k\frac{\partial f}{\partial k}\big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\frac{\partial f}{\partial x}\big|_{P(\bar{x})}-1},$$

$$x_{12} = -\frac{\frac{\partial F}{\partial \beta}\big|_{P(\mathbf{0},\bar{y})}}{\frac{\partial F}{\partial x}\big|_{P(\mathbf{0},\bar{y})}-1} = -\frac{-m\frac{\partial f}{\partial m}\big|_{P(\bar{x})}+\frac{\partial f}{\partial x}\big|_{P(\bar{x})}*\left(m\frac{\partial f}{\partial m}\big|_{P(\bar{y})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\frac{\partial f}{\partial x}\big|_{P(\bar{x})}-1},$$

$$x_{13} = -\frac{\frac{\partial F}{\partial \gamma}\big|_{P(\mathbf{0},\bar{y})}}{\frac{\partial F}{\partial x}\big|_{P(\mathbf{0},\bar{y})}-1} = -\frac{-n\frac{\partial f}{\partial n}\big|_{P(\bar{x})}+\frac{\partial f}{\partial x}\big|_{P(\bar{x})}*\left(n\frac{\partial f}{\partial n}\big|_{P(\bar{y})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\frac{\partial f}{\partial x}\big|_{P(\bar{x})}-1},$$

and

$$y_{11} = -\frac{\frac{\partial F}{\partial \alpha}\big|_{P(\mathbf{0},\bar{x})}}{\frac{\partial F}{\partial x}\big|_{P(\mathbf{0},\bar{x})}-1} = -\frac{-k\frac{\partial f}{\partial k}\big|_{P(\bar{y})}+\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\left(k\frac{\partial f}{\partial k}\big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\frac{\partial f}{\partial x}\big|_{P(\bar{x})}-1},$$

$$y_{12} = -\frac{\frac{\partial F}{\partial \beta}\big|_{P(\mathbf{0},\bar{x})}}{\frac{\partial F}{\partial x}\big|_{P(\mathbf{0},\bar{x})}-1} = -\frac{-m\frac{\partial f}{\partial m}\big|_{P(\bar{y})}+\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\left(m\frac{\partial f}{\partial m}\big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\frac{\partial f}{\partial x}\big|_{P(\bar{x})}-1},$$

$$y_{13} = -\frac{\frac{\partial F}{\partial \gamma}\big|_{P(\mathbf{0},\bar{x})}}{\frac{\partial F}{\partial x}\big|_{P(\mathbf{0},\bar{x})}-1} = -\frac{-n\frac{\partial f}{\partial n}\big|_{P(\bar{y})}+\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\left(n\frac{\partial f}{\partial n}\big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})}*\frac{\partial f}{\partial x}\big|_{P(\bar{x})}-1}.$$

Let

$$\mathcal{R}_d(\bar{x}) = w_{1x}\alpha + w_{2x}\beta + w_{3x}\gamma \quad \text{and} \quad \mathcal{R}_d(\bar{y}) = w_{1y}\alpha + w_{2y}\beta + w_{3y}\gamma,$$

where

$$w_{ix} = x_{0i} + x_{1i}$$

and

$$w_{iy} = y_{0i} + y_{1i},$$

for each $i \in \{1,2,3\}$. As in our previous signature function, when the two 2-cycles perturb from the 2-cycle in the unforced model, the signature function $\mathcal{R}_d$ is a weighted sum of the relative strengths of the oscillations of the carrying capacity and the two demographic characteristic of the species.

LEMMA 12. *Assume $f_{k,m,n}$ has a hyperbolic 2-cycle, $\{\bar{x},\bar{y}\}$. Then for all sufficiently small $|\alpha|$, $|\beta|$ and $|\gamma|$, equation* (2) *has a pair of 2-cycle populations*

$$\{\bar{x}_0 = \bar{x}_0(\alpha,\beta,\gamma),\ \ \bar{x}_1 = \bar{x}_1(\alpha,\beta,\gamma)\}$$

and

$$\{\bar{y}_0 = \bar{y}_0(\alpha, \beta, \gamma),\ \ \bar{y}_1 = \bar{y}_1(\alpha, \beta, \gamma)\},$$

where $\mathcal{R}_d(\bar{x}) + \mathcal{R}_d(\bar{y}) = 0$*.*

Proof. By Theorem 11, the two coexisting 2-cycles exist. Next, we proceed to show that $\mathcal{R}_d(\bar{x}) + \mathcal{R}_d(\bar{y}) = 0$.

Note that,

$$\begin{aligned} x_{01} + x_{11} + y_{01} + y_{11} = &- \frac{-k\frac{\partial f}{\partial k}\big|_{P(\bar{y})} + \frac{\partial f}{\partial x}\big|_{P(\bar{y})} * \left(k\frac{\partial f}{\partial k}\big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\big|_{P(\bar{x})} - 1} - \frac{k\frac{\partial f}{\partial k}\big|_{P(\bar{x})} + \frac{\partial f}{\partial x}\big|_{P(\bar{x})} * \left(-k\frac{\partial f}{\partial k}\big|_{P(\bar{y})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\big|_{P(\bar{x})} - 1} \\ &- \frac{-k\frac{\partial f}{\partial k}\big|_{P(\bar{x})} + \frac{\partial f}{\partial x}\big|_{P(\bar{x})} * \left(k\frac{\partial f}{\partial k}\big|_{P(\bar{y})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\big|_{P(\bar{x})} - 1} - \frac{k\frac{\partial f}{\partial k}\big|_{P(\bar{y})} + \frac{\partial f}{\partial x}\big|_{P(\bar{y})} * \left(-k\frac{\partial f}{\partial k}\big|_{P(\bar{x})}\right)}{\frac{\partial f}{\partial x}\big|_{P(\bar{y})} * \frac{\partial f}{\partial x}\big|_{P(\bar{x})} - 1} \\ &= 0. \end{aligned}$$

Similarly $x_{02} + x_{12} + y_{02} + y_{12} = 0$ and $x_{03} + x_{13} + y_{03} + y_{13} = 0$. Hence, $\mathcal{R}_d(\bar{x}) + \mathcal{R}_d(\bar{y}) = 0$. □

Note that, $\mathcal{R}_d(\bar{x}) + \mathcal{R}_d(\bar{y}) = 0$ implies $w_{ix} = -w_{iy}$ for each $i \in \{1, 2, 3\}$. The next result shows that, typically, one of $\{\bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1(\alpha, \beta, \gamma)\}$ or $\{\bar{y}_0(\alpha, \beta, \gamma), \bar{y}_1(\alpha, \beta, \gamma)\}$ is attenuant while the other resonant.

LEMMA 13. *If* $x_{01} + x_{11} \neq 0$*,* $x_{02} + x_{12} \neq 0$*, and* $x_{03} + x_{13} \neq 0$*, then for each fixed line through the origin in* (α, β, γ) *space not on the plane* $\mathcal{R}_d(\bar{x}) = (x_{01} + x_{11})\alpha + (x_{02} + x_{12})\beta + (x_{03} + x_{13})\gamma = 0$ *there is a neighborhood of* $(0, 0, 0)$ *such that on one side* $\{\bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1(\alpha, \beta, \gamma)\}$ *and* $\{\bar{y}_0(\alpha, \beta, \gamma), \bar{y}_1(\alpha, \beta, \gamma)\}$ *are respectively attenuant and resonant and on the other side they are respectively resonant and attenuant.*

Proof. To investigate the resonance or attenuance of $\{\bar{x}_0(\alpha, \beta, \gamma), x_1(\alpha, \beta, \gamma)\}$ we need to look at $\bar{x}_0(\alpha, \beta, \gamma) + \bar{x}_1(\alpha, \beta, \gamma) - (\bar{x} + \bar{y}) = \mathcal{R}_d(\bar{x}) +$ higher order terms. Approaching the origin from one side along a fixed line through the origin in (α, β, γ) space guarantees that the sign of $\mathcal{R}_d(\bar{x})$ does not change and that it eventually dominates the higher order terms. The sign of $\mathcal{R}_d(\bar{x})$ changes as we move to the other side of the origin. Thus, if $\mathcal{R}_d(\bar{x}) > 0$ on one side of the origin, $\{\bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1(\alpha, \beta, \gamma)\}$ is resonant on this side and attenuant on the other side. By the last lemma, $\mathcal{R}_d(\bar{x}) = -\mathcal{R}_d(\bar{y})$ and hence $\{\bar{y}_0(\alpha, \beta, \gamma), \bar{y}_1(\alpha, \beta, \gamma)\}$ will be attenuant on the side where $\{\bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1(\alpha, \beta, \gamma)\}$ is resonant and will be resonant on the side where $\{\bar{x}_0(\alpha, \beta, \gamma), \bar{x}_1(\alpha, \beta, \gamma)\}$ is attenuant. □

Example 14. In the Smith–Slatkin Model with periodic forcing, equation (5), set the following parameter values.

$$\alpha = \beta = \gamma = 0,\ \ k = 2, m = 0.7 \ \text{ and } \ n = 3.$$

Then there is an attracting 2-cycle at $\{1.2180, 2.8153\}$. Calculating derivatives at these points we obtain

$$w_{1x} = x_{01} + x_{11} = -9.407036455 + 9.407036504 = 4.9 \times 10^{-8}$$

$$w_{2x} = x_{02} + x_{12} = -2.068233172 + 3.665506391 = 1.5973$$

$$w_{3x} = x_{03} + x_{13} = -0.750678311 + 2.854772692 = 2.1041.$$

By the last lemma, a 2-periodic force applied to this system, usually leads to the emergence of two 2-cycles, where one of them is attenuant and the other is resonant.

Another interesting question is to compare the average of all four points on the two 2-cycles with the average of $\bar{x}$ and $\bar{y}$. Since $\mathcal{R}_d(\bar{x}) + \mathcal{R}_d(\bar{y}) = 0$, the answer to this question comes from a second order form in (α, β, γ). Let

$$\mathcal{R}_d(\bar{x}, \bar{y}) = w_{11}\alpha^2 + w_{12}\alpha\beta + w_{13}\alpha\gamma + w_{22}\beta^2 + w_{23}\beta\gamma + w_{33}\gamma^2,$$

where

$$w_{11} = x_{011} + x_{111} + y_{011} + y_{111}$$

$$w_{12} = x_{012} + x_{112} + y_{012} + y_{112}$$

$$w_{13} = x_{013} + x_{113} + y_{013} + y_{113}$$

$$w_{22} = x_{022} + x_{122} + y_{022} + y_{122}$$

$$w_{23} = x_{023} + x_{123} + y_{023} + y_{123}$$

$$w_{33} = x_{033} + x_{133} + y_{033} + y_{133}.$$

It is possible for $\mathcal{R}_d(\bar{x}, \bar{y})$ to be positive everywhere except at the origin. For example, $\mathcal{R}_d(\bar{x}, \bar{y}) > 0$ except at the origin whenever $w_{11}, w_{22}, w_{33} > 0$ and $w_{12} = w_{13} = w_{23} = 0$. In this case, the four points together generate resonance. It is also possible for $\mathcal{R}_d(\bar{x}, \bar{y})$ to be negative everywhere except at the origin. For example, $\mathcal{R}_d(\bar{x}, \bar{y}) < 0$ except at the origin whenever $w_{11}, w_{22}, w_{33} < 0$ and $w_{12} = w_{13} = w_{23} = 0$. In this case, the four points together generate attenuance.

In $(\alpha, \beta, \gamma) -$ space, the sign of $\mathcal{R}_d(\bar{x}, \bar{y})$ is constant on any ray starting at the origin. Thus, if $\mathcal{R}_d(\bar{x}, \bar{y}) > 0$ for some (α, β, γ), the four points are resonant for some small values of (α, β, γ). For other rays starting at the origin, $\mathcal{R}_d(\bar{x}, \bar{y})$ can be negative. Thus, the system can support both resonant and attenuant perturbations.

Next, we perturb the previous example and obtain two coexisting stable 2-cycles where one is attenuant and the other is resonant. In this example, the four points together are resonant.

Example 15. In Example 14, fix all parameters at their current values and set

$$\alpha = \beta = \gamma = 0.01.$$

As predicted by Theorem 11, the system has two coexisting 2-cycles, a resonant 2-cycle $\{1.115945, 2.958663\}$ and an attenuant 2-cycle $\{1.391256, 2.60988\}$. The average of the four points is 2.0189 and the average of the 2-cycle of the unperturbed system is 2.0166. Hence, together the four points are resonant.

Without knowing the coordinates of the two coexisting 2-cycles, one can use $\mathcal{R}_d(\bar{x}, \bar{y})$ to determine their attenuance or resonance. To illustrate this, we calculate second partials to determine the following values.

$$w_{11} = 115 \quad w_{12} = 150 \quad w_{13} = 200 \quad w_{22} = 15 \quad w_{23} = 36 \quad w_{33} = 13$$

$$\mathcal{R}_d(\bar{x}, \bar{y}) = w_{11}\alpha^2 + w_{12}\alpha\beta + w_{13}\alpha\gamma + w_{22}\beta^2 + w_{23}\beta\gamma + w_{33}\gamma^2 > 0.$$

As predicted above, $\mathcal{R}_d(\bar{x}, \bar{y}) > 0$ and the two 2-cycles together are resonant.

8. Conclusion

Many experimental and theoretical studies predict that populations are either enhanced or suppressed by periodic environments [2,6,9–12,14,15,18,19,22–27,29–31,37,40–43]. However, in most theoretical studies, with only a few exceptions (see [6,19,23,25,31,38]), only the carrying capacity or a demographic characteristic of the species (one or two parameters) are periodically forced. It is known that unimodal maps under period-2 forcing in two model parameters routinely have up to three coexisting 2-cycles [19,31,38]. Our results, on population models with three model parameters which are 2-periodically forced, support these predictions. We prove that small 2-periodic fluctuations of both the carrying capacity and two demographic characteristics of the species generate 2-cyclic population oscillations. Our results predict both attenuance and resonance in 2-periodically forced, three-parameter population models. As in Ref. [19], we derive a signature function, $\mathcal{R}_d$, for determining the response of discretely reproducing populations to periodic fluctuations of their carrying capacity and two demographic characteristics. $\mathcal{R}_d$ is the sign of a weighted sum of the relative strengths of the oscillations of the three parameters. Periodic environments are deleterious for the population when $\mathcal{R}_d$ is negative, and favorable when $\mathcal{R}_d$ is positive. A change in the relative strengths of the environmental and demographic fluctuations can shift the system from attenuance to resonance and vice versa.

We compute $\mathcal{R}_d$ for the Smith–Slatkin model, and determine regions in parameter space where its weights are positive and negative. Once the signs of the weights are known, $\mathcal{R}_d$ can be used to decide whether in phase or out of phase forcing of the three parameters is deleterious or beneficial for the population. When $n = 1$ and mk is large in the Smith–Slatkin model, a periodic environment is detrimental to the species when the fluctuations in the carrying capacity are out of phase with the fluctuations in the demographic characteristics of the species. However, when $n > 2$ and mk is large, these same fluctuations lead to an increase in the average population biomass.

In constant environments, unimodal maps are capable of supporting 2-cycles. We prove that small 2-periodic perturbations of a 2-cycle of the unforced three-parameter system produce two (coexisting) 2-cycle populations. As in Ref. [19], we compute $\mathcal{R}_d$ for the coexisting 2-cycles. Usually, one of the 2-cycles will be attenuant and the other will be resonant. We use examples to illustrate attenuant and resonant 2-cycles that perturb from a 2-cycle of the unforced classical Smith–Slatkin model.

Our analysis and examples illustrate that, the response of populations to periodic environments is a complex function of the period of the environments, the carrying capacities, all the demographic characteristics of the species, and the type and nature of the fluctuations.

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