

## The Effects of Seasonality on Discrete Models of Population Growth

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The effects of seasonality on the dynamics of a bivoltine population with discrete, nonoverlapping generations are examined. It is found that large seasonality is inevitably destabilizing but that mild seasonality may have a pronounced stabilizing effect. Seasonality also allows for the coexistence of alternative stable states (equilibria, cycles, chaos). These solutions may be seasonally in-phase, out-of-phase, or asynchronous. In-phase solutions correspond to winter regulation of population density, whereas out-of-phase solutions correspond to summer regulation. Analysis suggests that summer regulation is possible only in mildly seasonal habitats. © 1984 Academic Press, Inc.

### 1. INTRODUCTION

Nonlinear difference equations have been used for many years in the study of the growth of populations. They have appeared as models for populations with discrete, nonoverlapping generations (e.g., Nicholson & Bailey, 1935) and as approximate growth equations for species with continuous reproduction and mortality (Ricker, 1954). More recently (May, 1974, 1975, 1976; May & Oster, 1976; Guckenheimer *et al.*, 1977; Rodgers, 1981), scientists have focused attention on the wide range of dynamics inherent in these equations. It is now known that even first order, one dimensional, difference equations may exhibit "chaotic" solutions. Chaotic trajectories are asymptotically aperiodic. They are often visually indistinguishable from a sequence of random variables (Bunow & Weiss, 1979) and the existence of these trajectories raises interesting philosophical and biological questions (May & Oster, 1976).

Does chaos occur in nature? Several authors (Hassel *et al.*, 1976; Bellows, 1981) have addressed this question. The conclusion has emerged that natural populations are well damped and not susceptible to complex dynamics. These studies, however, are weighted toward temperate zone insects with a

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turnover time of one year. We hope to show that a much stronger potential for complex dynamics exists for multivoltine species in a seasonally fluctuating environment.

The logistic difference equation

$$N_{t+1} = (1 + r) N_t - (r/K) N_t^2 \quad (1)$$

(Maynard-Smith, 1968; May, 1972) is typical of many "chaotic" models. This equation maps population density at time  $t$ ,  $N_t$ , into  $N_{t+1}$ ;  $r$  measures the potential for population increasing at zero density; and  $K$  is the carrying capacity of the environment. From a dynamical systems viewpoint,  $r$  is the important parameter inasmuch as it tunes the severity of the density dependence and thus determines the asymptotic dynamics.  $K$ , on the other hand, merely scales  $N$ . Accordingly, Eq. (1) is often rescaled by letting

$$X_t = \{r/[(1 + r) K]\} N_t. \quad (2)$$

Equation (1) then takes on the simpler form

$$X_{t+1} = sX_t(1 - X_t), \quad (3)$$

where  $s = (1 + r)$ .

As written,  $r$  and  $K$  have fixed values. This implies a constant environment. Many species, however, live in environments which are seasonal with regard to factors such as temperature and rainfall (Fretwell, 1972). For such species, one expects predictable changes in physiology and condition over the course of the year, and thus seasonal variation in  $r$  and  $K$ . For continuous systems, it has been shown that seasonal variation may affect dynamics (Rosenblat, 1980; Cohen & Rosenblat, 1982; Nisbet & Gurney, 1982). In general, periodic coefficients may lead to parametric resonance (Arnold, 1978; Nayfeh, 1979). Little, however, has been done with discrete models (but see May & Oster, 1976, Appendix C). In particular, whether seasonality favors higher order, cycles, and chaos is a question that has not been addressed. To consider this question, we proceed as follows: In Section 2, we develop a simple model of seasonality—two seasons (good, bad)—for species with two nonoverlapping generations per year. This model has interesting features (Sect. 3) which may be examined analytically (Sect. 4) or geometrically (Sect. 5). Some of the features appear quite robust. Their biological significance is discussed in Section 6.

## 2. A SIMPLE MODEL OF SEASONAL GROWTH

Consider an insect with two discrete, nonoverlapping generations each year. The population is censused at the beginning of fall and spring. We

assume that there exists a logistic map with one set of parameters to account for the events of summer and a similar map with different parameters for the winter. If  $N_\phi$  and  $N_\sigma$  represent fall and spring densities, we then have

$$N_\phi = (1 + r) N_\sigma - (r/K) N_\sigma^2 \quad (4a)$$

$$N_\sigma = (1 + \tilde{r}) N_\phi - (\tilde{r}/\tilde{K}) N_\phi^2. \quad (4b)$$

For convenience let

$$N_s = \{r/[(1 + r)K]\} N_\sigma \quad (5a)$$

$$N_f = \{\tilde{r}/[(1 + \tilde{r})\tilde{K}]\} N_\phi. \quad (5b)$$

In terms of these new variables, Eqs. (4a) and (4b) become

$$N_f = a N_s (1 - N_s) \quad (6a)$$

$$N_s = b N_f (1 - N_f). \quad (6b)$$

Here,

$$a = \frac{(1 + r)^2 \tilde{r} K}{(1 + \tilde{r}) r \tilde{K}} \quad (7a)$$

$$b = \frac{(1 + \tilde{r})^2 r \tilde{K}}{(1 + r) \tilde{r} K}. \quad (7b)$$

We also introduce new parameters,  $\bar{s}$  and  $\varepsilon$  defined by

$$a = \bar{s} \frac{(1 + \varepsilon)}{(1 - \varepsilon)} \quad (8a)$$

$$b = \bar{s} \frac{(1 - \varepsilon)}{(1 + \varepsilon)}. \quad (8b)$$

Note that  $\bar{s}$  is the geometric mean of  $a$  and  $b$ , and that  $\varepsilon$ , which we take as our measure of seasonality, gauges the deviation of  $a$  and  $b$  from  $\bar{s}$ . As defined,  $\varepsilon$  lies between plus and minus one. Switching the sign of  $\varepsilon$  simply interchanges  $a$  and  $b$ . We take system (6) with  $a$  and  $b$  as in (8) as our fundamental system of equations.

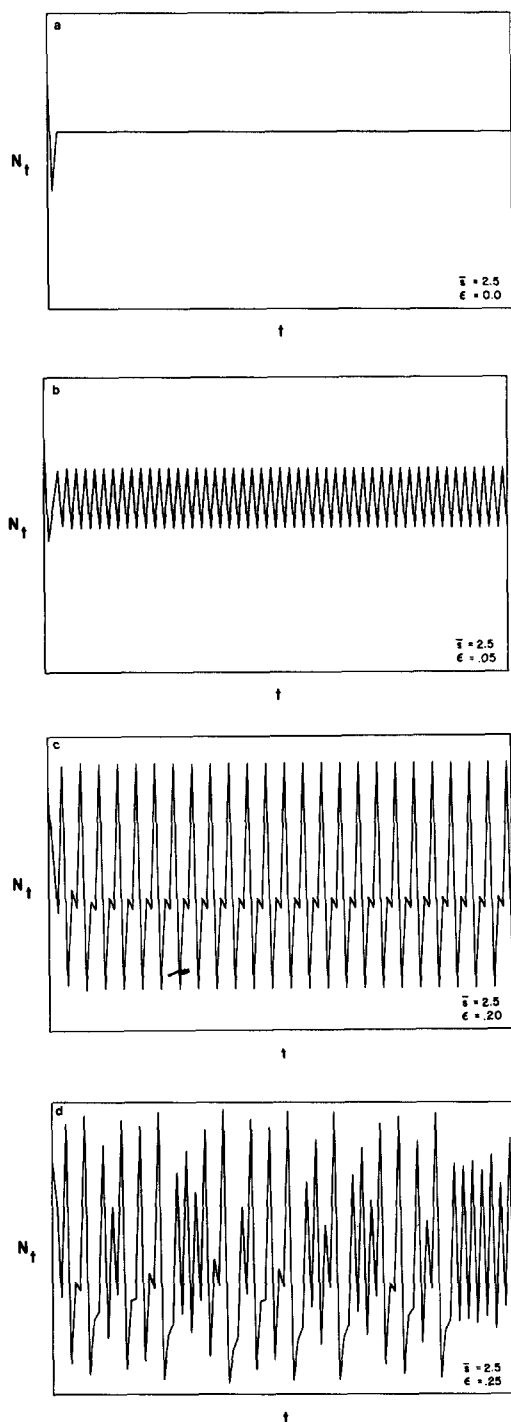


FIG. 1. Increasing  $\epsilon$  for low values of  $\bar{s}$  results in cycles of increasing period and eventually chaos.

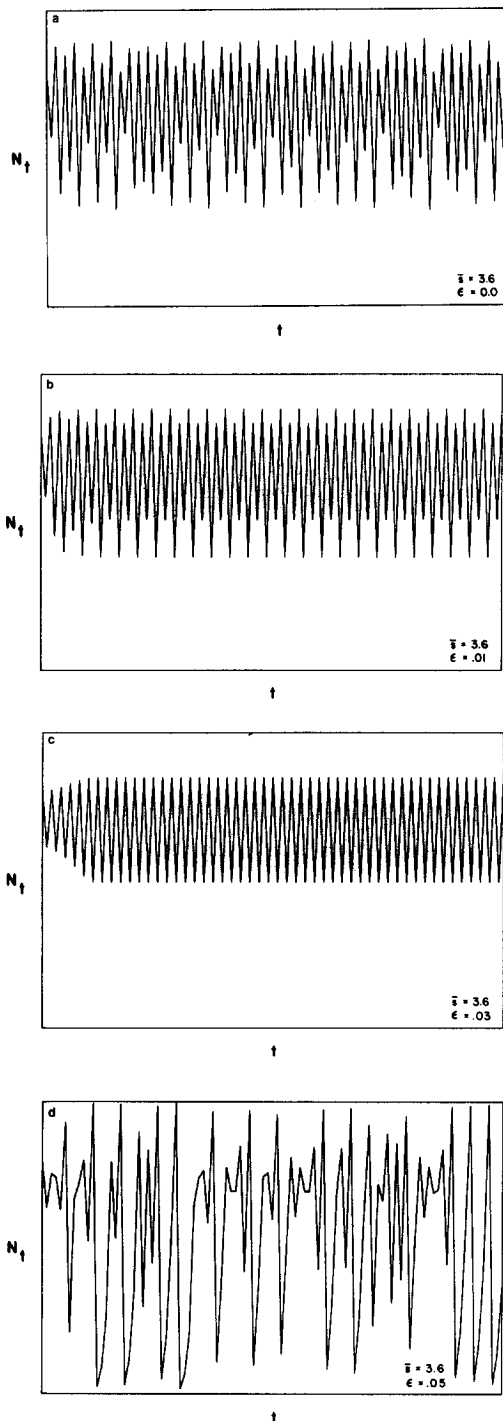


FIG. 2. Increasing  $\epsilon$  for high values of  $\bar{s}$ . Initially, solutions are stabilized, but then extreme chaos abruptly appears.

## 3. NUMERICAL RESULTS

The following patterns have been detected numerically for system (6):

(1) In less productive environments (i.e.,  $1 < \bar{s} < 3$ ), seasonality is destabilizing. For increasing  $\varepsilon$  one sees bifurcations leading from an equilibrium to a 2-cycle to higher order cycles to chaos (Fig. 1).

(2) For more productive environments (i.e.,  $3 < \bar{s} < 4$ ), a small amount of seasonality may be very stabilizing! Indeed, increasing  $\varepsilon$  through small values results in a reverse cascade from chaos (or a higher order cycle) to a stable 2-cycle (Fig. 2a, b, c). Further increases in seasonality, however, quickly reintroduce chaos (Fig. 2d).

(3) Stable periodic and/or chaotic solutions may coexist. With  $\bar{s} = 3.5$  and  $\varepsilon = 0.008$ , for example, a stable 2-cycle and a stable 8-cycle both occur (Fig. 3). (In contrast, (1) never has more than a single stable periodic solution (Singer, 1978).) Each coexisting cycle has a distinct domain of attraction, and each cycle undergoes its own cascade of bifurcations with increasing  $\bar{s}$ .

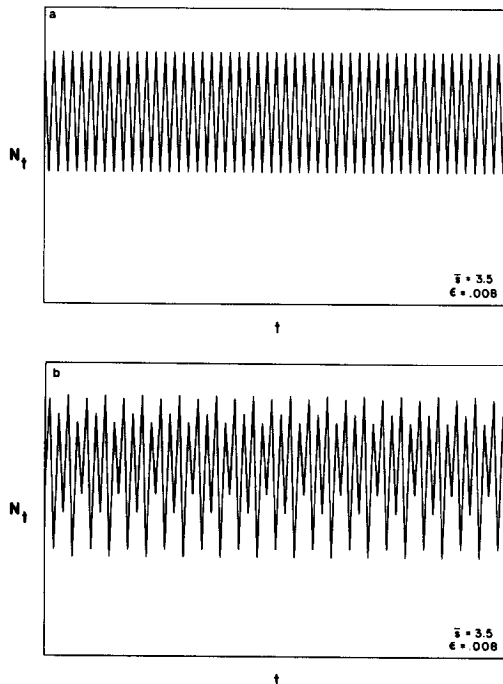


FIG. 3. For high values of  $\bar{s}$  and small  $\varepsilon$ , two stable periodic and/or chaotic solutions may coexist.

The rest of this paper will be concerned with expanding upon these observations.

#### 4. ANALYSIS

System (6) may be reformulated as a pair of uncoupled equations. Alternately composing (6a) with (6b) and (6b) with (6a), we obtain two uncoupled annual maps

$$N_f' = F(N_f) \quad (9a)$$

$$N_s' = G(N_s), \quad (9b)$$

where

$$F(N_f) = -ab^2N_f^4 + 2ab^2N_f^3 - ab(b+1)N_f^2 + abN_f \quad (10a)$$

$$G(N_s) = -a^2bN_s^4 + 2a^2bN_s^3 - ab(a+1)N_s^2 + abN_s. \quad (10b)$$

(' refers simply to the next value. No differentiation is implied.)

For

$$|\varepsilon| < \frac{(4 - \bar{s})}{(4 + \bar{s})} \quad (11)$$

both (9a) and (9b) map the unit interval into itself. In other words, in addition to being autonomous, these maps are endomorphic. As such, they may be analyzed in the usual way (May & Oster, 1976; Chang *et al.* 1981, 1982). Equilibria of the annual maps (2-cycles of (6)) are the fixed points of (9),

$$N_f^* = F(N_f^*) \quad (12a)$$

$$N_s^* = G(N_s^*); \quad (12b)$$

$n$ -cycles of the annual maps ( $2n$ -cycles of (6)) are made up of fixed points of the  $n$ -fold compositions

$$N_f^* = F^{(n)}(N_f^*) \quad (13a)$$

$$N_s^* = G^{(n)}(N_s^*). \quad (13b)$$

Equilibria and  $n$ -cycles are stable if their associated eigenvalues,

$$\lambda_f = [\partial F(N_f)/\partial N_f]_{N=N_f^*} \quad (14a)$$

$$\lambda_s = [\partial G(N_s)/\partial N_s]_{N=N_s^*} \quad (14b)$$

or

$$\lambda_f = [\partial F^{(n)}(N_f)/\partial N_f]_{N=N_f^*} \quad (15a)$$

$$\lambda_s = [\partial G^{(n)}(N_s)/\partial N_s]_{N=N_s^*} \quad (15b)$$

lie between plus and minus one.

For our system, the nontrivial equilibria of the annual maps appear as roots of

$$ab^2N_f^{*3} - 2ab^2N_f^{*2} + ab(b+1)N_f^* + (1-ab) = 0. \quad (16a)$$

$$a^2bN_s^{*3} - 2a^2bN_s^{*2} + ab(a+1)N_s^* + (1-ab) = 0. \quad (16b)$$

Associated with these dual cubics is the cusp

$$\varepsilon^2 = \frac{(\bar{s}+1)(\bar{s}-3)^3}{(\bar{s}-1)(\bar{s}+3)^3} \quad (17)$$

in  $\bar{s} - \varepsilon$  parameter space. For  $\bar{s} > 1$ , and  $\varepsilon$  above this cusp, (6) has a single nontrivial 2-cycle. As one passes through (17) an additional pair of 2-cycles appear. The fact that these 2-cycles coexist follows from the bimodality of (9a) and (9b) for  $b > 2$  and  $a > 2$  (Chang *et al.*, 1981, 1982; see also Skjolding *et al.*, 1983).

In Section 5, we will use graphs to show how the actual values for the 2-cycles vary with  $\varepsilon$ . One may also approximate these 2-cycles using elementary perturbation techniques (Nayfeh, 1981). In particular, one may expand  $N_s$  or  $N_f$  in (16) in powers of  $\varepsilon$  and perturb off the known solutions for  $\varepsilon = 0$ . The resulting power series breaks down for

$$(\bar{s} - 3) = O(\varepsilon^{1/3}). \quad (18)$$

In this region it is necessary to expand  $N_s$  and  $N_f$  in powers of  $\varepsilon^{1/3}$ .

The bifurcation curves for the 2-cycles may be obtained analytically by eliminating  $N_s$  or  $N_f$  between (12) and (14). For  $\lambda_s, \lambda_f = 1$ , we obtain (17)—the 2-cycles which appear as one crosses the cusp appear via a saddle-node or tangent bifurcation. For  $\lambda_s, \lambda_f = -1$ , we obtain

$$\varepsilon^2 = P(\bar{s})/P(-\bar{s}), \quad (19)$$

where

$$P(\bar{s}) = (\bar{s}^2 - 2\bar{s} - 5)^2(-3\bar{s}^4 + 12\bar{s}^3 - 10\bar{s}^2 - 20\bar{s} + 25). \quad (20)$$

As one passes through this latter bifurcation curve, a stable 2-cycle of (6) undergoes a pitchfork bifurcation and is supplanted by a stable 4-cycle.



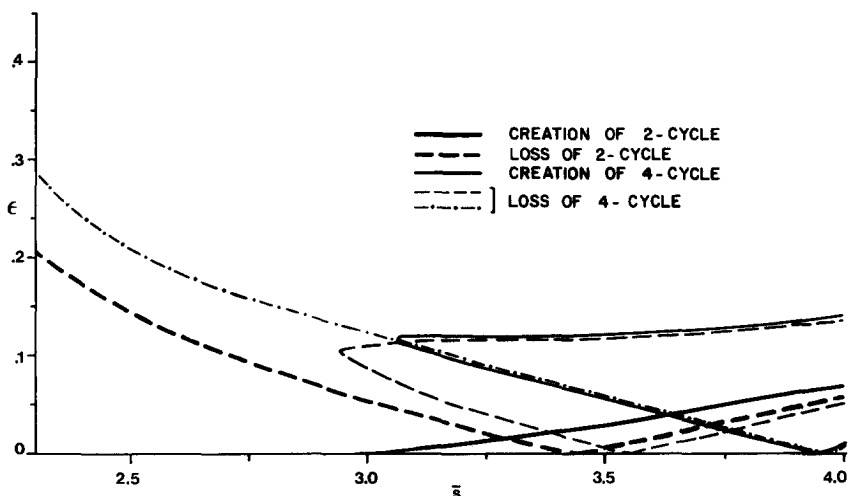


FIG. 4. Bifurcation curves corresponding to birth and loss of stable 2 and 4-cycles for system (6).

The higher order cycles are more difficult to handle. For a piecewise linear, trapezoidal approximation to the logistic (e.g., Hsu and Yee, 1975), the higher order bifurcations may be obtained analytically (see the Appendix). For the seasonal logistic map, however, it is more useful to treat  $\bar{s}$  as an independent variable, to differentiate say (13a) and (15a) with respect to  $\bar{s}$ , and to solve for  $dN_j^*/d\bar{s}$  and  $d\epsilon/d\bar{s}$ . One may then integrate these differential equations numerically to obtain the higher order bifurcation curves.

Figure 4 shows the bifurcation curves which correspond to the birth and loss of stable 2-cycles and 4-cycles of (6). These curves are entirely consistent with the simulations of Section 3. Above the cusp (creation of 2-cycle curve in Fig. 4), there is a single nontrivial 2-cycle which undergoes a cascade of period-doubling bifurcations with increasing  $\epsilon$ . As one crosses the cusp from above, a new stable 2-cycle appears (as does an unstable 2-cycle). This cycle bifurcates for decreasing  $\epsilon$  and/or increasing  $\bar{s}$ . The resulting striae in parameter space overlap to yield regions of coexisting periodic solutions.

The curves in Fig. 4 can be traced back to the well-understood (May, 1976; Collet & Eckmann, 1980) bifurcations in the seasonless ( $\epsilon = 0$ ) logistic model. Some of these bifurcations lie in the chaotic region (e.g., the tangent birth of a 4-cycle at  $\bar{s} = 3.961$ ,  $\epsilon = 0$ ). All of the curves in Fig. 4 may be obtained from either the spring-to-spring map or the fall-to-fall map. This follows from the topological conjugacy (Metropolis *et al.*, 1973; Collet & Eckmann, 1980; Chang *et al.*, 1981) of (9a) and (9b).

## 5. GRAPHICAL ANALYSIS

Equation (6) may also be viewed as a coupled system in the  $N_s - N_f$  phase plane. This approach is widely used in mathematical economics (e.g., Baumol, 1959) and was suggested to us by E. L. Charnov. In Figs. 5, 7, and 8, we have plotted  $N_s$  and  $N_f$  against each other for various parameter values. Intersections of the two curves typically correspond to 2 point cycles, that is annual cycles with different densities in the spring and fall. However, in the special case where the intersection occurs on the  $45^\circ$  line, the intersection will be an equilibrium. Population trajectories are obtained from the figures by alternately reflecting between the two graphs (This is shown most clearly in Fig. 7b.). Notice that if a trajectory is entirely above the  $45^\circ$  line, we may say that the orbit is in-phase with the pattern of seasonal changes; that is,  $N_f$  always exceeds  $N_s$ . Conversely, trajectories lying below the  $45^\circ$  line are out-of-phase with the environment. Note also, that increasing  $\bar{s}$  steepens both  $N_s$  and  $N_f$ , whereas increasing  $\varepsilon$  steepens  $N_f$  but pulls  $N_s$  in and to the left. These observations allow for a qualitative understanding of the bifurcation curves (Fig. 4) previously discussed.

*Seasons Identical*

We begin our analysis by supposing that the two seasons are identical. Thus,  $N_s$  and  $N_f$  are identical, and plotting  $N_s$  and  $N_f$  against each other (Fig. 5) yields a graph which is symmetric about the  $45^\circ$  line. Note, that the origin is always a trivial equilibrium and that it is stable for  $\bar{s} < 1$ . For  $\bar{s} > 1$ , there is a second nontrivial equilibrium (Fig. 5) at

$$N_s^* = N_f^* = 1 - (1/\bar{s}). \quad (21)$$

From the traditional (nonseasonal) viewpoint, this latter equilibrium bifurcates to a single 2-cycle at  $\bar{s} = 3$ . From the seasonal perspective, we see that as  $\bar{s}$  exceeds 3, the nontrivial fixed point is destabilized, and *two* 2-cycles appear (Fig. 5b). One of these lies above the  $45^\circ$  line, the other below. Thus, even though the new 2-cycles are identical in amplitude, they are out of phase. Thus, introducing a sense of seasons, that is, an absolute time frame, allows us to distinguish between seasonally in-phase and seasonally out-of-phase cycles.

If we continue to increase  $\bar{s}$ , the intersections of  $N_s$  and  $N_f$  are forced off the peaks, the eigenvalues increase in magnitude and the 2-cycles eventually give way to 4-cycles. Figure 5c shows a seasonally in-phase 4-cycle. A symmetric, out-of-phase 4-cycle surrounds the now unstable, out-of-phase 2-cycle. Further increases in  $\bar{s}$  yield higher order cycles (Fig. 5d) and chaotic orbits (Fig. 5e). Initially trajectories are contained within invariant regions (Fig. 6) that lie entirely above or below the  $45^\circ$  line. As a result, all solutions

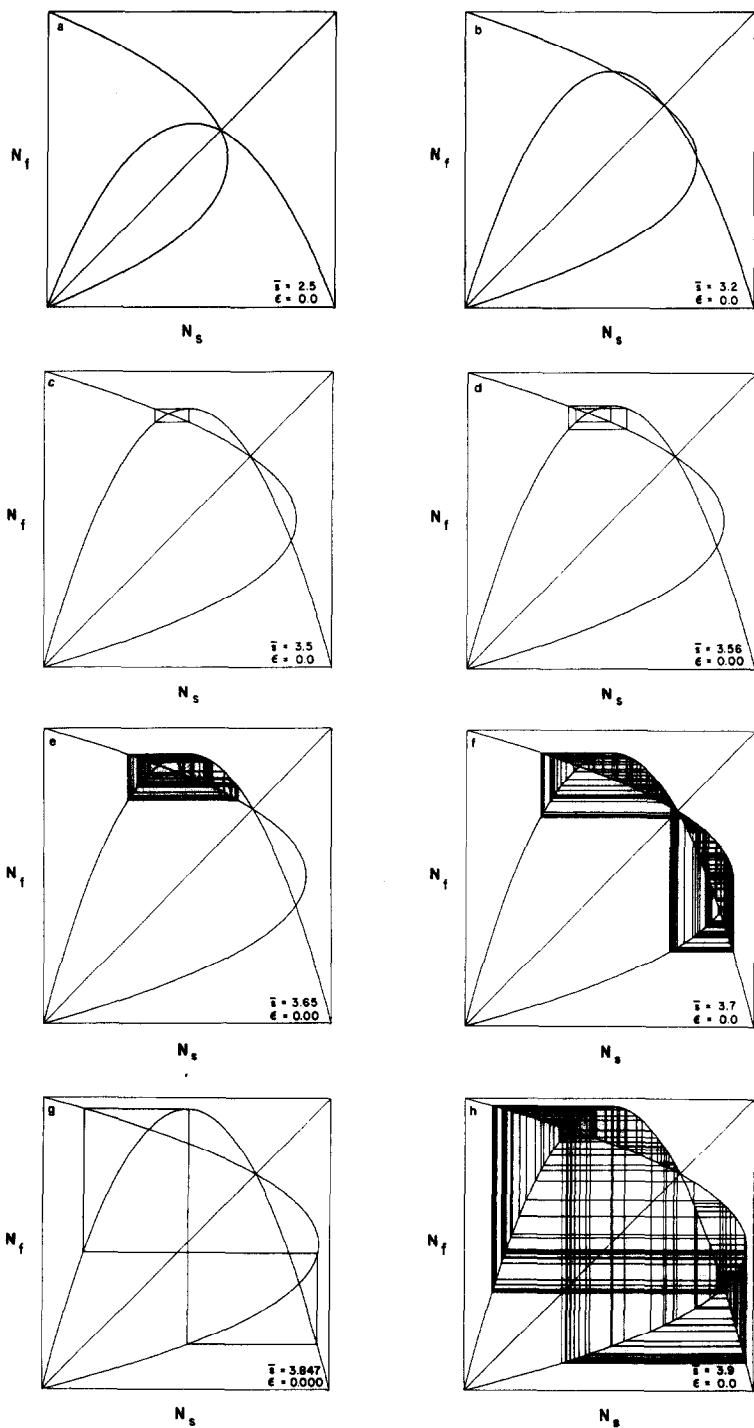


FIG. 5. Phase plane representation of system (6) for  $\epsilon = 0$ . At  $\bar{\epsilon} = 3$ , the stable fixed point becomes unstable and two symmetric and stable 2-cycles appear. Further increases in  $\epsilon$  lead to higher order cycles and chaos. A stable 6-cycle in the chaotic regime is shown in Fig. 5g.

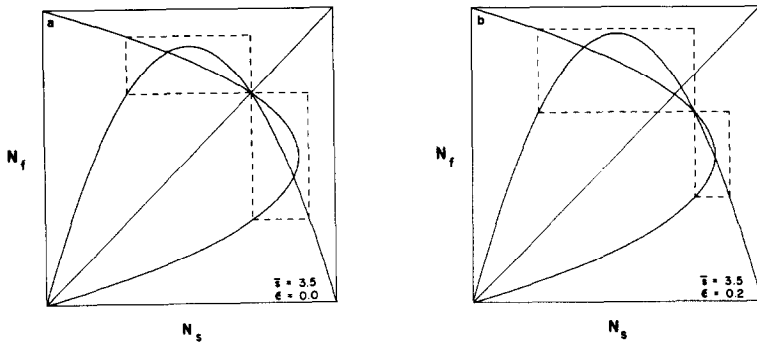


FIG. 6. Invariant regions (dashed lines) for phase plane representations of system (6). Trajectories entering these regions never leave. (a)  $\epsilon = 0$ . The regions are symmetric and correspond to strictly in-phase and out-of-phase dynamics. (b)  $\epsilon > 0$ . The regions are no longer symmetric and the formerly in-phase region now contains points which are out-of-phase.

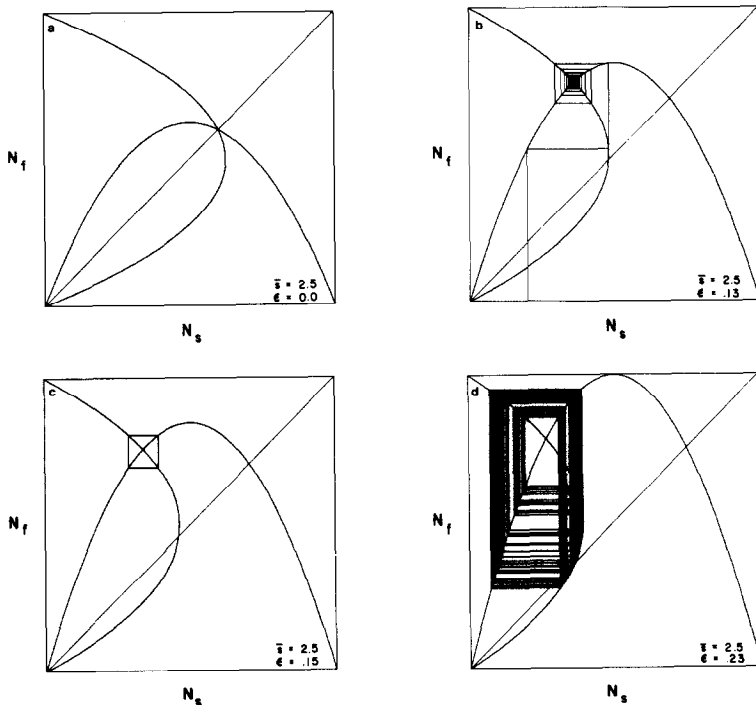


FIG. 7. Phase plane representation of (6) for  $\epsilon > 0$ , low  $\bar{\epsilon}$ . Increasing  $\epsilon$  leads to higher order cycles and chaos.

continue to exhibit an in-phase or out-of-phase character. However, beyond  $\bar{s} = 3.67\dots$ , invariance is lost and trajectories now shuttle back and forth across the  $45^\circ$  line (Fig. 5f–h). Note that this loss of invariance does not preclude the existence of periodic solutions. Indeed, from the nonseasonal viewpoint, loss of invariance occurs at that value of  $\bar{s}$  for which odd-period cycles first appear (e.g., May, 1976).

The effect of seasonality is to break the symmetry in  $N_s$  and  $N_f$ . This also breaks the symmetry between the in-phase and out-of-phase cycles. In the case of three intersections, increasing  $\varepsilon$  shifts the unstable equilibrium to the right of the  $45^\circ$  line where it becomes a 2-cycle. Consequently the two invariant regions no longer correspond strictly to in-phase and out-of-phase solutions. In particular, trajectories which were wholly in-phase for  $\varepsilon = 0$ , may now include points which are marginally out-of-phase (Fig. 6b).

### Seasons Distinct

For  $\varepsilon = 0$  and low  $\bar{s}$  ( $1 < \bar{s} \leq 3$ ),  $N_s$  and  $N_f$  intersect but once (Fig. 7a). In this case, increasing  $\varepsilon$  forces the equilibrium up and to the left, that is, off

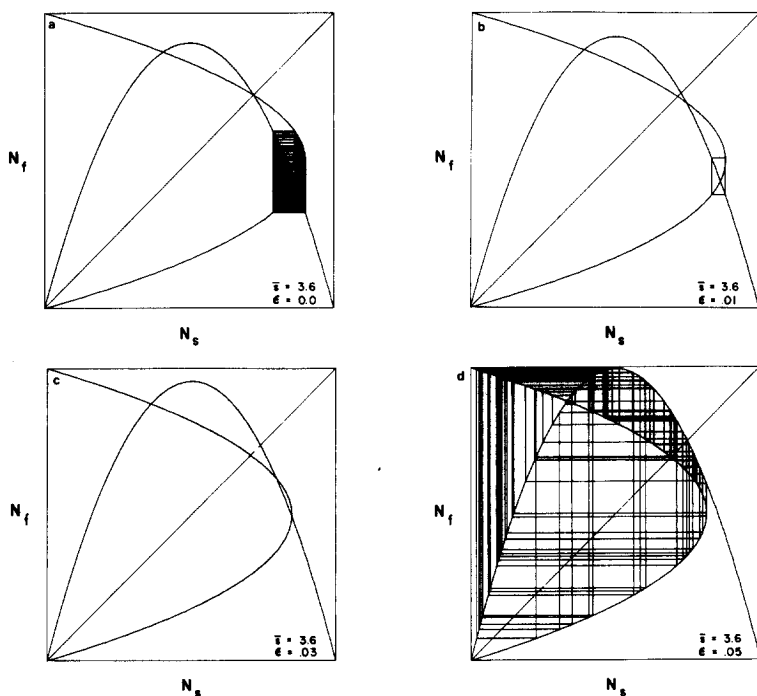


FIG. 8. Phase plane representation of (6) for  $\varepsilon > 0$ , high  $\bar{s}$ . Increasing  $\varepsilon$  stabilizes the out-of-phase trajectories until a stable 2-cycle appears. For sufficiently high values of  $\varepsilon$ , the two (stable and unstable) out-of-phase 2-cycles coalesce and only asynchronous chaos remains.

the 45° line and into the in-phase region. This gives a seasonally in-phase 2-cycle (Fig. 7b). Further increases in  $\varepsilon$  lead to a 4-cycle (Fig. 7c) which increases in amplitude and eventually yields to higher order cycles and chaos (Fig. 7d).

For  $\varepsilon = 0$  and high  $\bar{s}$  ( $3 < \bar{s} < 4$ ), there are three nontrivial intersections. One of these is an unstable equilibrium. Increasing  $\varepsilon$  forces this equilibrium off the 45° line and into the out-of-phase region; the equilibrium becomes an unstable, out-of-phase 2-cycle. The other two intersections are a pair of initially symmetric 2-cycles. These may or may not be stable. As before, the effect of increasing  $\varepsilon$  on the in-phase cycle is to force it away from the peak of  $N_f$  (where it is superstable (Collet & Eckmann, 1980)) and to destabilize. Conversely, increasing  $\varepsilon$  stabilizes the out-of-phase cycle by forcing it towards the peak in  $N_s$ . This pattern is illustrated in Fig. 8. As  $N_f$  is pulled out and  $N_s$  is tucked in, what is initially mild, seasonally out-of-phase chaos (Fig. 8a—there is, of course, symmetric, in-phase chaos) reduces to a 4-cycle (Fig. 8b) and then a 2-cycle (Fig. 8c). At some point, however, the two out-of-phase 2-cycles coalesce and disappear. This corresponds to being on the

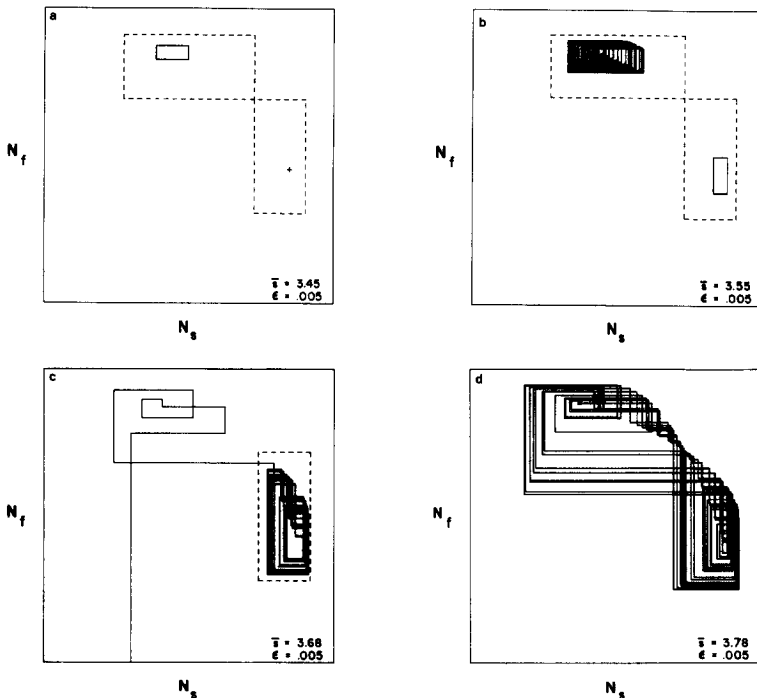


FIG. 9. Increasing  $\bar{s}$  for constant  $\varepsilon$  results in the loss of first one and then both invariant regions. When both regions have been destabilized, trajectories shuttle back and forth between the two former basins of attraction.

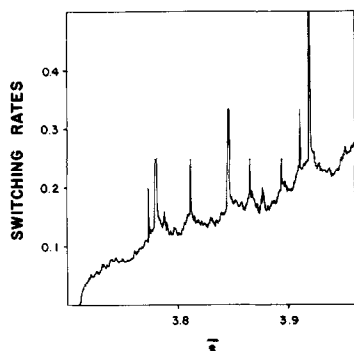


FIG. 10. Switching rate between two former basins of attraction plotted against  $\bar{s}$ . For each parameter value 250 initial conditions on  $(0, 1)$  were iterated 21,000 times. The number of switches for the last 1,000 iterations were counted;  $\bar{s}$  was increased in steps of 0.0005. The spikes correspond to periodic windows in the chaotic regime.

cusps. Beyond this point, one is left with large scale, asynchronous chaos (Fig. 8d). Thus, we retrieve the simulations and the outcome of Fig. 2.

#### *Effect of Increasing $\bar{s}$ for Fixed $\epsilon$*

If instead of varying  $\epsilon$ , we hold the degree of seasonality constant and vary  $\bar{s}$ , a final pattern emerges. Specifically, if we start with two distinct 2-cycles, one in-phase and one out-of-phase, and increase  $\bar{s}$ , first one and then the other cycle become unstable (Fig. 9a–b). Further increases in  $\bar{s}$  lead to the loss of in-phase invariance. Consequently, all initial conditions have out-of-phase limit sets (Fig. 9c). For a still higher value of  $\bar{s}$ , the out-of-phase invariance is also lost. Trajectories now shuttle back and forth between what were once basins of attraction (Fig. 9d). Figure 10 shows the dependence of the shuttling rate on  $\bar{s}$ . The overall pattern is one of increase. Superimposed, however, are sharp peaks which correspond to periodic “windows” (May, 1976) in the chaotic region.

## 6. DISCUSSION

### *Summer vs. Winter Regulation of Population Numbers*

Some years ago, Fretwell (1972; see also Pulliam & Parker, 1979; Ricklefs, 1980) suggested that the densities of many north temperate bird species are regulated primarily by competition for resources during the winter. That this may be true for overwintering birds is readily apparent, but it may also apply to migratory species (e.g., Willis, 1966; Karr, 1976). As a result, efforts (MacArthur, 1958) to detect niche partitioning and community structure on the breeding grounds might well be foredoomed.

Bird generations are not, of course, nonoverlapping, and system (6) is therefore inappropriate to the study of birds. On the other hand, one may ask whether species that do conform to the assumptions of (6) are summer or winter regulated. The resulting analysis suggests that Fretwell's thesis holds for many bivoltine insects. Specifically, it is possible to associate winter regulation with in-phase dynamics and summer regulation with out-of-phase fluctuations..

To see this, consider Fig. 11. At the left, we show the consequences of ameliorating the summer environment. That is, we increase  $N_f$  (dashed line) for all values of  $N_s$ . At the right, we show the effects of increasing  $N_s$ . For in-phase cycles, ameliorating winter (right) increases both spring and fall densities. Conversely, improving summer (left) increases fall densities but lowers spring population size. Thus for in-phase dynamics, winter acts as a bottleneck, and we may say that the population is "winter-regulated." Just the opposite situation results for out-of-phase dynamics. Here, increasing  $N_f$  (left) increases population size in both seasons, whereas increasing  $N_s$  increases spring numbers at the expense of numbers in the fall. Thus populations displaying out-of-phase dynamics are "summer-regulated."

To summarize, both types of regulation are possible. Recall, however, that out-of-phase dynamics occur only in mildly seasonal (low  $\varepsilon$ ) environments. For species which reside all year in temperate latitudes, low  $\varepsilon$  is clearly an unrealistic assumption. Thus for year round temperate zone residents, we expect winter regulation.

### Interpretation

On the basis of system (6), we have made predictions regarding in-phase and out-of-phase fluctuations, the occurrence of complex dynamics, and the possibility of multiple stable states. Numerical simulations suggest that these

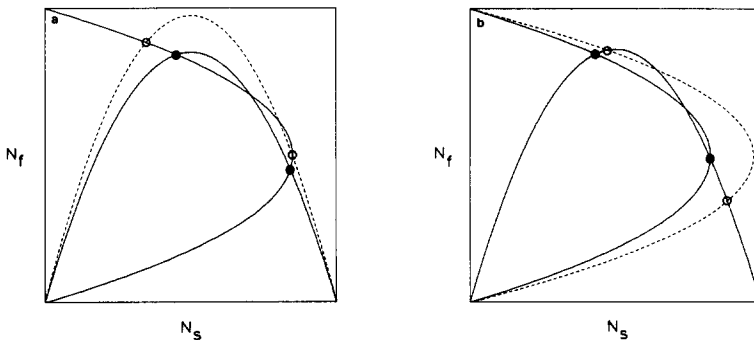


FIG. 11. In-phase 2-cycles are "winter-regulated" whereas out-of-phase 2-cycles are "summer-regulated". (a) The effects of an improved summer on spring and fall densities. (b) The effects of an ameliorated winter.



predictions hold if we allow more than two generations per year. Are these predictions biologically reasonable?

Let us begin by considering seasonally out-of-phase, i.e., summer-regulated, populations. Here a population does so well at the start of the summer that density dependent factors soon take over—the population crashes to below spring's level by summer's end. Such crashes will be favored by two factors: (1) a high growth rate in the summer, and (2) a summer carrying capacity which is not greatly in excess of winter capacity. Together, these permit the population to overshoot and crash before the summer's end.

In terms of  $\bar{s}$  and  $\varepsilon$ , we thus expect out-of-phase cycles in high  $\bar{s}$ , low  $\varepsilon$  environments, which is what our model predicts. Conversely, if the difference between seasons is greater, the likelihood of summer populations exceeding that season's carrying capacity is diminished. Hence, in-phase cycles should result. Note, that if the difference between summer and winter is too great, post-summer crashes may be so severe that more than a single season will be required for the onset of recovery. Thus for productive (high  $\bar{s}$ ) environments, we expect out-of-phase or in-phase dynamics to give way to asynchronous trajectories as one moves along a gradient of increasing seasonality say from the tropics to the poles. A similar transect through unproductive habitats should yield only in-phase and asynchronous cycles of increasing magnitude.

There are few long term data sets for multivoltine insects. A notable exception is the study by Biggy and Tapley (1969) of two species of coffee leaf miner, *Leucoptera coffeina* and *Leucoptera meyrichi*. The two species of leaf miner were found to have distinct generations with no appreciable overlap. They were censused daily for some seven years. The resulting time series are consistent with our model. Both species show signs of a biennial cycle. The cycle is particularly striking for *Leucoptera coffeina*. Bigger and Tapley claim that the same biennial periodicity may also be seen in an earlier study (Notley, 1948). Finally, both species show evidence of being summer-regulated. This is in keeping with their mildly seasonal tropical habitat.

At the opposite extreme, multi-annual, asynchronous cycles are observed in many high latitude species including insects (Baltensweiler, 1970), birds (Keith, 1963), and, in particular, mammals (Finnerty, 1980). But birds and mammals are generally thought of as having continuous reproduction and mortality. How then can we relate the results of the present discrete analysis to species whose dynamics are best represented by differential equations? The answer to this question is, of course, another paper. Here we merely observe that one dimensional difference equations of the sort considered in this paper *can*, in certain cases, be abstracted from higher order systems of differential equations (e.g., Shaw, 1981; Schaffer, 1985). The important and

nontrivial problem that remains is to determine the nature and biological significance of the circumstances for which such an abstraction is equivalent to the composition of a pair of 1-D equations.

#### APPENDIX

Maps described by trapezoidal or flat top functions seem to have almost all of the structural properties of the logistic map (Beyer & Stein, 1982a, b). Because they are piecewise linear, these maps are relatively easy to work with. In this Appendix, we propose a simple, two-season, trapezoid map. This map shares many of the features of the system (6).

The system that we wish to consider is

$$n_f = f(n_s) \quad (\text{A1a})$$

$$n_s = g(n_f), \quad (\text{A1b})$$

where

$$\begin{aligned} f(n_s) &= an_s, & 0 \leq n_s \leq 1 \\ &= a, & 1 \leq n_s \leq 3 \\ &= a(4 - n_s), & 3 \leq n_s \leq 4 \end{aligned} \quad (\text{A2a})$$

and

$$\begin{aligned} g(n_f) &= bn_f, & 0 \leq n_f \leq 1 \\ &= b, & 1 \leq n_f \leq 3 \\ &= b(4 - n_f), & 3 \leq n_f \leq 4. \end{aligned} \quad (\text{A2b})$$

As before, we also introduce the two parameters  $\bar{s}$  and  $\varepsilon$ ,

$$a = \bar{s} \frac{(1 + \varepsilon)}{(1 - \varepsilon)} \quad (\text{A3a})$$

$$b = \bar{s} \frac{(1 - \varepsilon)}{(1 + \varepsilon)} \quad (\text{A3b})$$

and let  $\varepsilon$  represent the degree of seasonality.

System (A1) is a piecewise linear approximation system (6), provided we identify the variables of (6) and (A1) as

$$n_s = 4N_s \quad (\text{A4a})$$

$$n_f = 4N_f. \quad (\text{A4b})$$

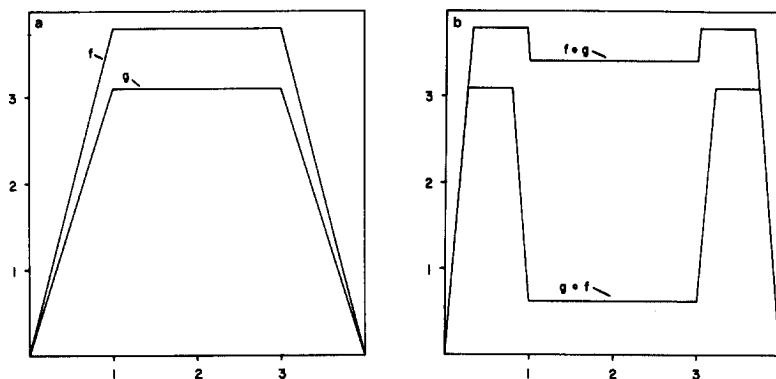


FIG. A1. Trapezoidal approximation to system (6). (a) Seasonal maps. (b) Annual (i.e., composed) maps.

In the absence of seasonality, (A1) reduces to a map first studied by Hsu and Yee (1975).

In looking for the annual cycles (2-cycles) of system (A1), we need consider the fixed points of the two annual maps  $f \circ g$  and  $g \circ f$ . As  $f$  and  $g$  are piecewise linear,  $f \circ g$  and  $g \circ f$  are also piecewise linear (e.g., Fig. A1). The same is true of higher order compositions. As a result, we may solve explicitly for the 2-cycles and higher order cycles of (A1).

As the various compositions consist entirely of flat segments with slope zero and slanted segments with slope greater than one in magnitude, we may

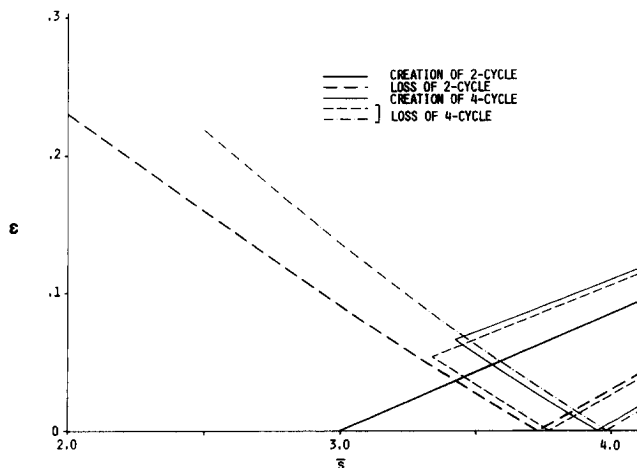


FIG. A2. Bifurcation curves corresponding to the birth and loss of stable 2-cycles and 4-cycles for the trapezoidal approximation to (6). Compare with Fig. 4.

also, to the extent of our patience, solve for the bifurcation curves of (A1). We look for those values of  $\bar{s}$  and  $\varepsilon$  for which the fixed points of given compositions first move from flat to sloped segments. Figure A2 shows the 2-cycle and 4-cycle bifurcation curves we have obtained in this way. The similarity to Fig. 4 is striking. The significance of Fig. A2 is that, whereas many of the curves in Fig. 4 were, of necessity, computed numerically, all of the curves in Fig. A2 were derived analytically.

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