A Simple Model of Cannibalism

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ABSTRACT

A simple nonlinear discrete model is derived for the dynamics of a two-age class population consisting of juveniles and adults that includes cannibalism of juveniles by adults. The model is investigated analytically and numerically. It is shown how even this very simple model, by incorporating the negative and positive feedbacks due to cannibalism, can account for several important phenomena concerning the dynamics of cannibalistic populations that have been discussed and studied in the literature. These include the possibilities that the practice of cannibalism can (1) in certain circumstances be a form of self-regulation that promotes stable equilibration, while in other circumstances it can lead to population oscillations; (2) result in a viable population in circumstances when its absence would otherwise result in extinction; and (3) be the source of multiple stable equilibria and hysteresis effects.

1. INTRODUCTION

In an environment with limited resources the natural propensity for biological populations to grow exponentially is ultimately regulated in some manner or another. In classical models of population dynamics, such as the famous logistic equation, this "density self-regulation" is expressed through an assumption that the net per capita growth rate (births minus deaths) is a decreasing function of total population size. Usually there is no attempt in such models to account precisely for this regulation mechanism, and only its gross qualitative properties at the high aggregate level of total population numbers, with individual organisms treated as identical, are specified. The facts that individual organisms within a species often differ significantly in important physiological and behavioral characteristics and that self-regulation often occurs because of interactions between individual organisms (e.g., intraspecific competition and predation) imply that a more complete understanding of a population's dynamics often requires a "struc-

tured population" model in which appropriate classes or categories of individuals are distinguished (see Werner and Gilliam [21]).

Although the modeling methodology for the dynamics of structured populations is well established (see Metz and Diekmann [16] and Caswell [2]), the study of intraspecific interaction models is still in its infancy. Some examples of intraspecific competition models that have been recently studied include age-structured models of competition between juveniles and adults in which either juvenile survival or adult fecundity are adversely affected by interclass competition [3, 4, 7, 8, 14, 15, 19]. Other examples include the size-structured models of Ebenman [9] and of Cushing and Li [5] that include density-dependent individual body size growth rates, which in turn affect size at maturity and hence adult fertility.

Another potential regulatory interaction between members of a species is intraspecific predation or cannibalism. The two survey articles of Fox [10] and Polis [18] discuss the importance of cannibalism in a wide diversity of animals, across many taxa, and its effects on the dynamics and evolution of cannibalistic species. Some of the important consequences that cannibalism can have on the dynamics of populations, which can be found in this and other literature, include the following. Cannibalism can be an effective mechanism for the regulation and equilibration of population density. On the other hand, for some species and some environmental circumstances, cannibalism can result in population oscillations (even to the extent of wiping out entire age classes). Thus, cannibalism can promote either equilibration or oscillations depending upon the exact circumstances under which it is practiced. Second, in some cases cannibalism can be a crucial mechanism for population survival. The so-called lifeboat strategy asserts that the resources obtained from cannibalism can permit a population to survive during periods of noncannibalistic resource scarcity or in other circumstances under which it could not otherwise survive [18, 20]. For example, the cannibalism of young by adults may provide access to re- sources available to young individuals that are otherwise unavailable to adults. Third, the interplay between the negative and positive feedbacks inherent in cannibalism can result in multiple steady states and hence hysteresis effects. This hysteresis can lead to catastrophic crashes to lower equilibrium levels, as population parameters are changed below critical values, that cannot be reversed by increasing the parameters back above their critical values. This fact has been used by Botsford [1], for example, to explain the collapse of certain harvested fish populations and their failure to return to preharvested levels after harvesting is ceased (although other explanations are possible, such as evolutionary effects as studied, for example, by Law and Grey [11]).

Only a handful of dynamical models for populations practicing cannibal- ism appear in the literature. There have been some studies of the extreme

case of egg cannibalism that address the destabilization effect of cannibalism (e.g., [6], [12]). The possibility of oscillations in a discrete age-structured cannibalism model was studied by Landahl and Hansen [13] (their model does not incorporate a positive feedback of cannibalism on adult fertility, however). Botsford [1] used some continuous age-structured models to study the multiple steady-state and hysteresis phenomena. Van den Bosch et al. [20] studied the lifeboat strategy using a continuous age-structured model involving integro-partial differential equations.

Our primary purpose here is to show that the effects of cannibalism discussed above can all be found in a very simple discrete age-structured model, one that is both analytically and numerically very tractable. A point to be made, then, is that one does not need a complicated model in order to capture all of these dynamical phenomena. The simplicity of the model suggests that these phenomena are very likely to be common in model cannibalistic populations and consequently might also be expected to occur in more sophisticated models.

Cannibalism, like interspecies predation, is most commonly practiced by larger individuals on smaller individuals [18, 21]. If we assume that age correlates with body size, then a simple model could be built by distinguishing just two age classes, a juvenile class and an adult class, such as is done in the simple model for intraspecific competition introduced by Ebenman [7]. The building of a model for the dynamics of the population involves the building of submodels for juvenile survival and adult fecundity. Under the assumption that adults cannibalize juveniles, the juvenile survival rate would be lowered (from its inherent level) by adult cannibalism. Adult fecundity would in turn be a function of the energy obtained from the practice of cannibalism as well as from noncannibalistic sources (for which there could also be intraspecific competition among adults). These assumptions form the basis for the simple discrete model derived in Section 2. An analysis of the model, its equilibria, and its cycles is given in Section 3. We do not attempt a complete and full analysis of the dynamics implied by the model but limit ourselves simply to demonstrating that the dynamical features discussed above can be found. A discussion of these issues can be found in Section 4.

2. THE MODEL EQUATIONS

Let $J(t)$ and $A(t)$ denote the number or density of juveniles and adults, respectively, at times $t = 0, 1, 2, \ldots$ in a population in which adults cannibalize juveniles. Let the "inherent" probability (i.e., the probability at low juvenile population densities) that a juvenile will be cannibalized during one unit of time when the adult population has density A be denoted by $\Psi^*(A)$. This fraction, which necessarily vanishes when $A = 0$, will be

assumed to monotonically approach a limiting (maximal) value c, $0 \leqslant c \leqslant 1$, as $A \to +\infty$. We write $\Psi^*(A) = c\Psi(A)$, where Ψ is a continuously differentiable function of $A \in [0, +\infty)$ that satisfies

$$0 \leqslant \Psi(A) \leqslant 1, \qquad \Psi(0) = 0, \qquad \Psi'(A) > 0, \qquad \Psi(+\infty) = 1. \quad (2.1)$$

Under this assumption, the coefficient c is the maximal possible inherent probability of being cannibalized. It will be referred to in this paper as the *cannibalism coefficient*. The assumption in (2.1) that $\Psi(+\infty) = 1$ is indicative of a "contest" (or "interference") competition between adults for juvenile "prey." For the case of "scramble" (or "exploitative") competition between adults, one would want $\Psi(+\infty) = 0$, in which case Ψ would not be monotonically increasing. Most of our analytical results remain valid for scramble competition. Specifically, Theorems 2–7 (Section 3) remain valid only under the assumption that $\Psi'(0) > 0$. Only the *global* existence of positive equilibria (for all $r > r_m$ in Theorem 1) is in doubt if $\Psi(A)$ decreases for large $A > 0$. We restrict our attention here to contest competition, noting that scramble competition is less common in animals than plants ([17], p. 252).

Since cannibalism rates can be affected by changes in juvenile density in the same way that predator responses are affected by heterospecific prey density [18], we assume that adult cannibalism saturates as a function of increasing juvenile density (as, for example, in Holling type II or III functional responses). If $\phi(J)$ denotes the fractional reduction in the inherent probability of being cannibalized when the juvenile population density is $J > 0$, then the probability of being cannibalized at juvenile and adult population levels J and A is $c\Psi(A)\phi(J)$. If $1 - p$ is the probability that a juvenile will die of causes other than cannibalism during one unit of time, then (treating survival from cannibalism and from death by these other causes as independent) the probability that a juvenile survives one unit of time is $p[1 - c\Psi(A)\phi(J)]$. It follows that the number of surviving, and hence maturing, juveniles is

$$p[1 - c\Psi(A)\phi(J)]J = p[J - c\Psi(A)\Phi(J)],$$

where $\Phi(J) = \phi(J)J$. It is assumed that ϕ and Φ are continuously differentiable functions of $J \in [0, +\infty)$ that satisfy

$$0 \leqslant \phi(J) \leqslant 1, \qquad \phi(0) = 1, \qquad \phi'(J) < 0,$$
$$\Phi'(J) > 0, \qquad \Phi(+\infty) < +\infty. \quad (2.2)$$

For times $t = 0, 1, 2, \ldots$ we now have that

$$A(t+1) = p[J(t) - c\Psi(A(t))\Phi(J(t))] + sA(t). \quad (2.3)$$

Here s is the survival probability of an adult over one unit of time.

Suppose that in the absence of competition the environment would provide each adult individual in the population an amount ρ of (noncannibalistic) food resources per unit time. We assume that adults do compete for these resources, however, and consequently that the amount of noncannibalistic resources consumed by an adult (per unit time) is actually $\rho f(A)$. Here $f(A)$ is the fractional decrease in resource consumption (per adult) due to competition. We assume that

$$0 \leqslant f(A) \leqslant 1, \qquad f(0) = 1, \qquad f'(A) < 0, \qquad f(+\infty) = 0. \quad (2.4)$$

If we denote the energy derived from one unit of resource by e_ρ, then the number of juvenile offspring produced by an adult population from these energy sources is $\zeta e_\rho \rho f(A)A$, where ζ is the conversion factor that gives the number of offspring produced by adults per unit energy.

In addition to affecting juvenile survival, cannibalism affects adult fertility by providing an additional source of energy. Suppose that e_c is the energy accrued to the adult population for each juvenile cannibalized. Then the number of juveniles produced per unit time due to cannibalism is $\zeta e_c c \Psi(A)\Phi(J)$. Thus, for $t = 0,1,2,\ldots,$

$$J(t+1) = \zeta e_\rho \rho f(A(t))A(t) + \zeta e_c c \Psi(A(t))\Phi(J(t)). \quad (2.5)$$

Equations (2.3) and (2.5) determine the dynamics of the juvenile and adult classes. In general, the survival probabilities p and s could depend on energy consumed, as we have assumed that fertility does. We will not consider this more general case here, however, but instead concentrate on the positive feedback loop formed by the effect of cannibalism on adult fertility and by the negative effect of cannibalism on juvenile survival. Toward this end we take p and s to be constants. Thus, we ignore intraspecific competitive effects on juvenile survival and assume that juvenile food resources are always in ample supply. We will also assume for simplicity (as in Ebenman [7, 8]) that $s = 0$, that is, that adults do not survive longer than one unit of time. [Equations (2.3) and (2.5) can be viewed as a modification, to include cannibalism, of a simple version of Ebenman's intraspecific competition model, namely of Ebenman's model when juvenile survival is density-independent.]

Under the assumptions above, Equations (2.3) and (2.5) can be rewritten as

$$J(t+1) = \frac{r}{p}\left[f(A(t)) + \frac{\beta c}{\rho}\psi(A(t))\Phi(J(t))\right]A(t)$$

$$A(t+1) = p[1 - c\Psi(A(t))\phi(J(t))]J(t),$$

where we have introduced the notation

$$r = p\zeta e_\rho \rho, \qquad \beta = e_c / e_\rho, \qquad \psi(A) = \Psi(A)/A.$$

We assume that $\psi(A)$ is a continuously differentiable function of $A \in [0, +\infty)$. The assumptions previously made on Ψ imply that $0 \leqslant \psi(A)$, $\psi(+\infty) = 0$. The coefficient r is the *inherent net reproductive number*, the expected number of offspring per adult per lifetime at low population levels or, in other words, in the absence of competition and cannibalism. The coefficient β is the ratio of the energy obtained by an individual adult from one cannibalized juvenile to the energy obtained from one unit of noncannibalistic food resource.

These model equations can be further simplified by specifying certain units. If one unit of noncannibalistic food resource is defined in such a way that it supplies the same energy as one cannibalized juvenile, then $\beta = 1$. Furthermore, p can effectively be set equal to 1 by assuming that the adult population is measured in units according to the number of juveniles necessary to result in one adult (in the absence of cannibalism). That is to say, if we define $\bar{A}(t) = A(t)/p$ and $\bar{f}(\bar{A}) = f(p\bar{A})$, $\bar{\Psi}(\bar{A}) = \Psi(p\bar{A})$, then the model equations become (upon dropping the bars)

$$J(t+1) = r\left[f(A(t)) + \frac{c}{\rho}\psi(A(t))\Phi(J(t))\right]A(t), \qquad (2.6a)$$

$$A(t+1) = \left[1 - c\Psi(A(t))\phi(J(t))\right]J(t). \qquad (2.6b)$$

The new functions $f(A)$, $\Psi(A)$, and $\psi(A)$ satisfy all of the conditions given above that the original functions do.

In the next section we study the asymptotic dynamics implied by Equations (2.6) as they depend upon the parameters r, c, and ρ and the nonlinearities determined by f, Ψ, and Φ.

3. ANALYSIS OF THE MODEL

3.1. *EQUILIBRIA*

Equations (2.6) clearly have the trivial equilibrium $J = A = 0$. Positive equilibria must satisfy the equations

$$J = r\left[f(A) + \frac{c}{\rho}\psi(A)\Phi(J)\right]A, \qquad (3.1a)$$

$$A = \left[1 - c\Psi(A)\phi(J)\right]J. \qquad (3.1b)$$

For each $J > 0$, the right-hand side of (3.1b) is a monotonically decreasing function of A that equals $J > 0$ at $A = 0$. Thus, (3.1b) has a unique solution

$A = A(J) > 0$, continuous in $J > 0$. Clearly, $A(0) = 0$ and $A(+\infty) = +\infty$. Equation (3.1a), which can be rewritten

$$1 = rn(J, A), \tag{3.2a}$$

$$n(J, A) = \left[f(A) + \frac{c}{\rho} \psi(A) \Phi(J) \right] [1 - c\Psi(A)\phi(J)], \tag{3.2b}$$

can then be used to define uniquely an $r = r(J) = 1/n(J, A(J)) > 0$ for which Equations (2.6) have the positive equilibrium $(J, A(J))$. Equation (3.2a) says biologically that at equilibrium the *net reproductive number* $rn(J, A)$ must be equal to 1. Note that $n(J, A)$ satisfies $n(0,0) = 1$, as is consistent with r being the *inherent* net reproductive number (technically, the net reproductive number at $J = A = 0$). Clearly, $r(J)$ is continuous for $J \geqslant 0$, $r(0) = 1$, and $r(+\infty) = +\infty$. Let $r_m = \min_{J \geqslant 0} r(J)$, which clearly satisfies $0 < r_m \leqslant 1$. These observations are summarized in the following theorem.

THEOREM 1

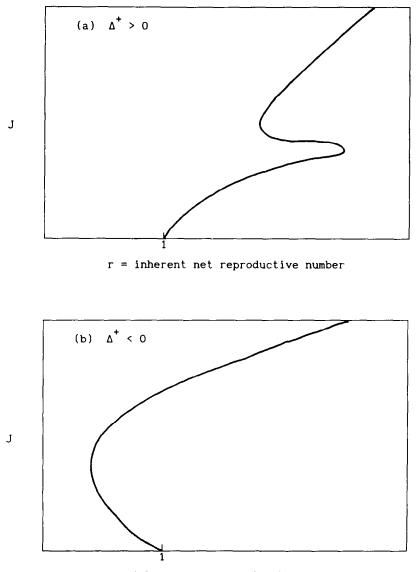There is a real number r_m satisfying $0 < r_m \leqslant 1$ such that Equations (2.6) have a positive equilibrium $J > 0$, $A > 0$ for and only for $r > r_m$. Both J and A tend to $+\infty$ as $r \to +\infty$, and there are equilibria such that both J and A tend to zero as $r \to 1$.

The set of pairs $(r(J), J)$, where $J > 0$ is the equilibrium value for the juvenile class when the inherent net reproductive number r equals $r(J)$, can be viewed as a curve C in the rJ plane that intersects the set of trivial equilibria $(r, 0)$ at, or bifurcates from, the point $(r, J) = (1, 0)$ corresponding to the trivial equilibrium at $r = 1$. This curve is unbounded in both its r and J components. (See Figure 1.) Note that Theorem 1 does not rule out the possibility that there could be more than one positive equilibrium for a given $r > r_m$. Also note that if $r_m < 1$ then there will exist positive equilibria for values of the inherent net reproductive number r *less than* 1. We will see below that both of these possibilities can occur.

The number r_m will definitely be less than 1 if $r'(0) < 0$, in which case there will exist positive equilibria for $r < 1$ but close to 1. In this case the bifurcation at $r = 1$ will be referred to as *subcritical*. In the opposite case, when $r'(0) > 0$, the bifurcation will be referred to as *supercritical*. Define the two quantities $\Delta^{\pm}, \Delta^{-} < \Delta^{+}$, by

$$\Delta^{\pm} = \frac{\rho - 1}{\rho} c\Psi'(0) \mp f'(0).$$

The fact that $r'(0) = \Delta^{+}$ can be deduced from (3.2a) [note that $A'(0) = 1$ follows from (3.1b)]. This yields the following result.
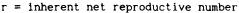
FIG. 1. If the quantity Δ^+ is positive, then the branch of positive equilibria of (2.6) bifurcates "supercritically" from the zero state at the critical value $r = 1$ of the inherent net reproductive number as schematically shown in (a), in which the juvenile components J of the equilibria are plotted against r. If $\Delta^+ < 0$, then the bifurcation is "subcritical" as shown in (b), and there exist positive equilibria for values of $r < 1$.

THEOREM 2

The curve C bifurcates supercritically *from the point* $(r, J) = (1, 0)$ *if* $\Delta^+ > 0$ *and* subcritically *if* $\Delta^+ < 0$.

Note that since by assumption we have $\Psi'(0) > 0$, it follows that the bifurcation will be subcritical if cannibalism is practiced (i.e., $c > 0$) and if the environmental resource supply rate ρ is sufficiently small. In this event, since there exist positive equilibria for all $r > r_m$, the bifurcating branch must "turn around," and hence at least two positive equilibria must exist for r values less than 1. See Figure 1 for a schematic representation of this theorem (also Figure 4).

It can also happen that multiple positive equilibria exist for some $r > 1$ as well. One result in this direction, for strong nonlinearities in the adult intraspecific competition term f, is contained in the following theorem (a proof of which appears in the Appendix).

THEOREM 3

Assume $c > 0$ (i.e., cannibalism is practiced) and, in addition to (2.4), that $f'(A)A \to 0$ as $A \to +\infty$. Given any constant $J > 0$ sufficiently small, then $r'(J) < 0$ and $r'(0) > 0$ provided $-f'(0) > 0$ is sufficiently large.

Since $r(0) = 1$, $r'(0) > 0$, and $r(+\infty) = +\infty$, the inequality $r'(J) < 0$ implies that Equations (2.6) have several *positive* equilibria for $r = r(J)$ with juvenile component J and that the supercritically bifurcating branch C has an S-shaped bend or hysteresis loop in it. (See Figure 10.)

3.2. *SYNCHRONOUS 2-CYCLES*

There is another bifurcation from the trivial solution that occurs at $r = 1$. A straightforward investigation of the first composite of (2.6) shows that a bifurcating branch of "synchronous" 2-cycles exists for each $r > 1$ as is described in the following theorem. By "synchronous" is meant a cycle in which juveniles appear only at every other time interval (as do the adults, but at alternating time intervals).

THEOREM 4

For each $r > 1$, Equations (2.6) possess a synchronous 2-cycle given by the formulas

$$J(t) = \begin{cases} 0 & \text{for } t = 1, 3, 5, \ldots \\ J_0(r) & \text{for } t = 2, 4, 6, \ldots, \end{cases}$$

$$A(t) = \begin{cases} J_0(r) & \text{for } t = 1, 3, 5, \ldots \\ 0 & \text{for } t = 2, 4, 6, \ldots, \end{cases}$$

where $J_0(r) = f^{-1}(1/r) > 0$.

Theorems 1–4 show that Equations (2.6) can possess, in addition to the trivial equilibrium, one or more positive equilibria and also, at least in the case when $r > 1$, a synchronous 2-cycle. We now consider the stability of these various solutions.

3.3. *STABILITY OF EQUILIBRIA AND SYNCHRONOUS 2-CYCLES*

The Jacobian of (2.6) evaluated at $J = A = 0$ is the matrix

$$\begin{bmatrix} 0 & r \\ 1 & 0 \end{bmatrix}$$

whose eigenvalues are $\pm r^{1/2}$. Thus the trivial equilibrium loses stability at the critical value $r = 1$; that is, it is stable for $r < 1$ and unstable for $r > 1$. Note that at $r = 1$ the eigenvalues are ± 1, which accounts for the simultaneous bifurcation of the positive equilibria of Theorem 1 and the 2-cycles of Theorem 4.

In order to determine the stability of the positive bifurcating equilibria, at least for r close to 1, we consider the two eigenvalues λ^+ and λ^- (near $+1$ and -1, respectively) of the Jacobian of the right-hand sides of Equations (2.6) evaluated at such an equilibrium. The equilibria are stable if both eigenvalues have absolute value less than 1. In the Appendix it is shown that

$$\lambda^+ = 1 - \frac{1}{2}(r - 1) + O(r - 1)^2, \tag{3.3a}$$

$$\lambda^- = -1 - (\Delta^-/2\Delta^+)(r - 1) + O(r - 1)^2. \tag{3.3b}$$

These expressions together with Theorem 2 yield the following result.

THEOREM 5

The trivial equilibrium $J = A = 0$ of (2.6) is stable for $r < 1$ and unstable for $r > 1$. If $\Delta^+ < 0$, then the bifurcation of positive equilibria at $r = 1$ is subcritical and unstable; that is, the positive equilibria near the trivial equilibrium exist and are unstable for r less than but close to 1. On the other hand, if $\Delta^+ > 0$, then the positive equilibiria that bifurcate supercritically are stable when $\Delta^- < 0$ and unstable when $\Delta^- > 0$, at least for r greater than but close to 1.

In the case $\Delta^+ < 0$, when locally near the bifurcation point $(r, J) = (1, 0)$ the subcritically bifurcating positive equilibria are unstable, we know that the branch C must "turn around" and that there must be multiple positive equilibria for $r < 1$. Although we have no proof, we anticipate that the positive equilibrium with the larger juvenile component J, on the "upper part of the branch," is in general stable. Evidence from computer-gener-

ated orbit diagrams seem to indicate that this is in general true; see Figure 5 for an example.

The bifurcating positive equilibria are also unstable when the bifurcation is supercritical ($\Delta^+ > 0$) but $\Delta^- > 0$. In this case, as we will now see, the bifurcating 2-cycles are stable.

The point $J = J_0(r)$, $A = 0$ associated with the 2-cycle in Theorem 4 is a fixed point of the first composite of Equations (2.6). In order to investigate the stability of the bifurcating 2-cycles we need to calculate the eigenvalues of the Jacobian matrix of this first composite at this point. The 2-cycles are stable if both of these eigenvalues have absolute value less than 1. This matrix is an upper triangular matrix whose eigenvalues are

$$\lambda_1 = 1 + rf'(J_0(r))J_0(r),$$

$$\lambda_2 = r\left[1 - c\Psi(J_0(r))\right]\left[f(J_0(r)) + \frac{\rho}{c}\Phi(J_0(r))\psi(0)\right],$$

which, near $r = 1$, can be written

$$\lambda_1 = 1 - (r - 1) + O(r - 1)^2,$$

$$\lambda_2 = 1 + \frac{\Delta^-}{f'(0)}(r - 1) + O(r - 1)^2.$$

Note that $\lambda_2 \to +\infty$ as $r \to +\infty$. We can now state the following theorem.

THEOREM 6

For r close to 1, *the synchronous 2-cycles in Theorem* 4 *are unstable if* $\Delta^- < 0$ *and stable if* $\Delta^- > 0$. *In any case they are unstable for r sufficiently large.*

In summary, we have found that there are three possible bifurcation scenarios near the critical value $r = 1$: *stable super*critically bifurcating equilibria accompanied by *unstable super*critically bifurcating synchronous 2-cycles; *unstable super*critically bifurcating equilibria accompanied by *stable super*critically bifurcating synchronous 2-cycles; or *unstable sub*critically bifurcating equilibria and *unstable super*critically bifurcating synchronous 2-cycles. These different cases, which are determined by the signs of the quantities $\Delta^\pm$, are schematically illustrated in Figure 2. Treating these quantities as functions of c and ρ, one can easily sketch the regions in the $c\rho$ plane where each of these bifurcation cases occurs. This is done in Figure 3, where the importance of the magnitude of the resource supply rate ρ can be seen. If $\rho < 1$, then the bifurcating synchronous 2-cycles are never stable, whereas if $\rho > 1$, they will bifurcate stably if the cannibalism coefficient c is sufficiently large. The inequality $\rho > 1$ ($\rho < 1$) means that

(a) $\Delta^- < \Delta^+ < 0$

(b) $\Delta^- < 0 < \Delta^+$

(c) $0 < \Delta^- < \Delta^+$
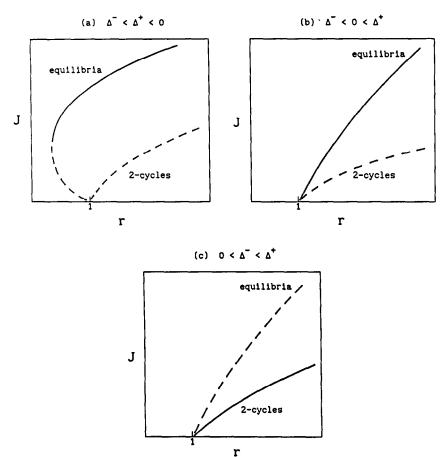
Fig. 2. The three possible local bifurcation and stability scenarios near $r = 1$ illustrated schematically by plotting both the juvenile components J of the bifurcating positive equilibria and the maximum component of the bifurcating synchronous 2-cycles against the inherent net reproductive number r. The dashed lines indicate instability. The graphs are drawn only schematically and are not meant to imply any general geometric details (such as relative magnitudes, slopes, etc.). Also see Figure 3.

the amount of energy supplied to each adult per unit time is more (less) than that derived from the cannibalism of one juvenile individual.

From Figure 3 we see that in the absence of cannibalism ($c = 0$) the positive equilibria bifurcate stably, but that the introduction of cannibalism (i.e., an increase in c) can change the stability properties of the bifurcating branches near $r = 1$. It is also interesting to note that the introduction of cannibalism can change the equilibrium levels of J and A. The following theorem is proved in the Appendix.
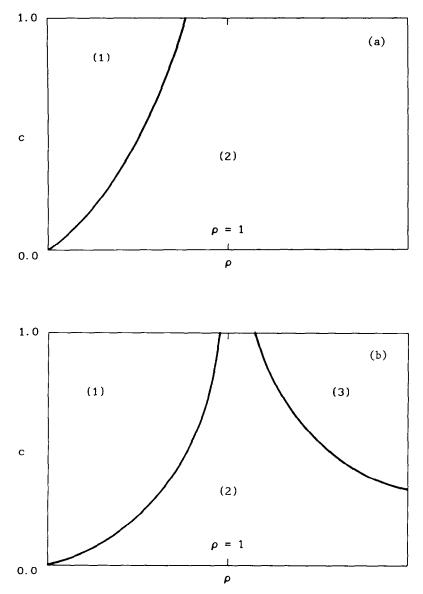
FIG. 3. Regions in the ρc parameter plane that correspond to the three different local bifurcation diagrams in Figure 2 are shown schematically. These regions appear as in (a) when $-f'(0)/\psi(0) \geqslant 1$ and as in (b) when $-f'(0)/\psi(0) < 1$. Thus, (a) occurs when intraspecific adult competition for the environmental resource is strong, whereas (b) occurs when this competition is weak. In the regions labeled (1) a subcritical bifurcation of unstable equilibria occurs as shown in Figure 2a. In regions labeled (2) a supercritical bifurcation of stable equilibria occurs as in Figure 2b, whereas in the region labeled (3) stable 2-cycles bifurcate as in Figure 2c.

THEOREM 7

For $c = 0$ *and for* $r > 1$ *but close to* 1,

$$(1 - \rho)\frac{dJ}{dc} > 0, \qquad (1 - \rho)\frac{dA}{dc} > 0.$$

Consequently, for fixed $r > 1$ near 1, equilibrium levels for both J and A increase or decrease with the introduction of cannibalism ($c > 0$, but small) provided $\rho < 1$ or $\rho > 1$, respectively.

4. DISCUSSION

That self-regulation, stability, and increased resilience can be benefits derived from the practice of cannibalism is a major point in the survey article of Polis [18]. On the other hand, cannibalism cannot be expected to be stabilizing under all environmental and demographic conditions. Oscillations in some populations have been attributed to cannibalism—for example, in *Tribolium* species. In extreme cases, cannibalism can result, in fact, in oscillations in which an entire age class is lost [18].

The possibility of these various dynamical consequences of cannibalism is predicted by our model equations (2.6). If we restrict our attention for the moment to the possible bifurcation scenarios that can occur at the critical value $r = 1$, as are summarized in Figures 2 and 3, we can see that the effect that cannibalism has on our simple two-age class model population depends on the amount ρ of environmental resource made available to an adult per unit time and on the degree of cannibalism practiced, as measured by the magnitude of c. We first consider the case when the environmental resource supply rate is low, specifically when $\rho < 1$ and the amount supplied to each adult in one unit of time has less energetic value than does one cannibalized juvenile.

If $\rho < 1$, then an increase in the degree of cannibalism will increase equilibrium levels (Theorem 7), ultimately raising the bifurcating branch of equilibria and (possibly) causing it to "bend over" and result in a subcritical bifurcation (Figure 3). See Figure 4 for an illustration. Although this latter case destabilizes the low-level positive equilibria near the bifurcation point when $r < 1$ (Theorem 5), it in general leads to higher level stable equilibria even in this case, when extinction would have otherwise occurred (i.e., without cannibalism). We have no proof of this assertion, but numerical evidence points to its general validity. See Figure 5 for an example. For these reasons, cannibalism can be viewed as beneficial when $\rho < 1$ (although there is the danger of a catastrophic collapse of the population should r be decreased to far below 1).
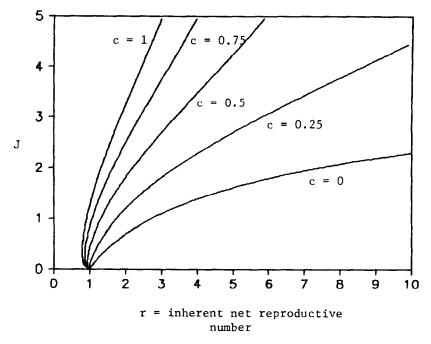
FIG. 4. The effect of increasing the cannibalism coefficient c on the bifurcating branch of equilibria is illustrated by plotting the juvenile components J of the equilibria against the inherent net reproductive number r for several values of c. Note the increase in equilibrium levels with increasing c and the subcritical bifurcation for sufficiently large c. These graphs are from Equations (2.6) with nonlinearities (4.1). Parameter values are $\rho = 1/2$, $d = -f'(0) = 1$, $a = 1/\psi(0) = 1/5$. The increasing values of $c = 0, 1/4, 1/2, 3/4$, and 1 correspond to moving vertically from region (2) into region (1) in Figure 3a. See Figure 5 concerning the stability properties of these equilibria.

The graphs in Figures 4 and 5 were computed for

$$f(A) = \exp(-dA), \qquad \phi(J) = \frac{1}{1+J}, \qquad \psi(A) = \frac{1}{a+A} \qquad (4.1)$$

in Equations (2.6). Here $d > 0$ and $a > 0$ are constants.

The occurrence of stable positive equilibria for $r < 1$ when a subcritical bifurcation occurs under the practice of cannibalism implies the possibility of survival for parameter values that would otherwise lead to extinction. This feature has been used by van den Bosch et al. [20] as theoretical support for what is termed a *lifeboat mechanism or strategy*. Under such a strategy, a species that is threatened with extinction because of periods of resource or prey scarcity survives such a crisis by practicing cannibalism

.375E+01

J

.000E+00
        .250E+00   .200E+01
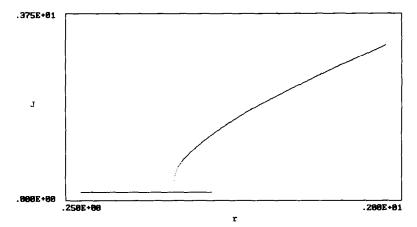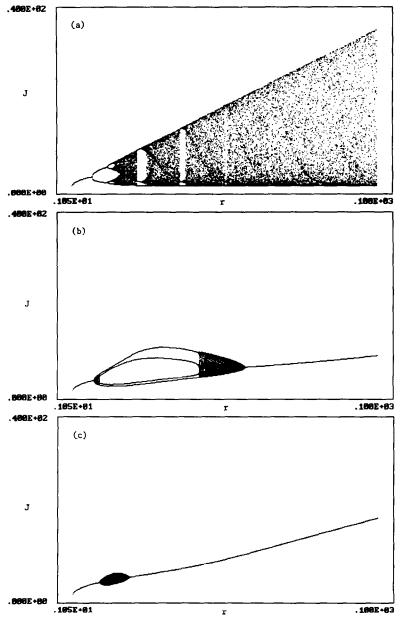
r

FIG. 5. In order to discover their stability properties, the equilibria for (2.6) with (4.1) were dynamically computed for the same parameter values as in Figure 4 but with maximal cannibalism coefficient $c = 1$. Again the juvenile components J of the computed equilibria are plotted against the inherent net reproductive number r. Here the stability of the upper portion of the subcritically bifurcating branch can clearly be seen. Note particularly the stability of the positive equilibria on this branch corresponding to values of r *less than* 1 (for which the stability of the trivial equilibria can also be seen).

(see [18] and references cited therein). The occurrence of subcritical bifurcations in our model when the environmental resource supply rate $\rho < 1$ similarly lends theoretical support to this survival mechanism, particularly when it is noted that, all other parameters being held fixed, $r = \rho \zeta e_\rho \rho$ will also be small when ρ is small.

For large values of r, Equations (2.6) in the absence of cannibalism ($c = 0$) readily exhibit equilibrium destabilization, repeated bifurcations,

FIG. 6. These graphs illustrate the effect of introducing the practice of cannibalism into a population when the environmental resource supply rate ρ is low. The juvenile components J of the attractors of (2.6) with (4.1) were dynamically computed and then plotted against the inherent net reproductive number r for three increasing values of the cannibalism coefficient: (a) $c = 0$, (b) $c = 1/20$, and (c) $c = 1/10$. Parameter values are $\rho = 1/2$, $d = -f'(0) = 1$, $a = 1/\psi(0) = 1$. These parameter values lie in region (2) of Figure 3a with $\rho = 1/2 < 1$. Note that in (a), that is, in the absence of cannibalism, stable equilibria bifurcate at $r = 1$ and are followed by the familiar period-doubling cascade to "chaos" and aperiodic oscillations. In (b), where only a moderate level of cannibalism has been introduced, restabilized equilibria occur for large values of r, and oscillations are confined to a finite interval of r values. In (c), where only a slightly larger cannibalism coefficient is used, the range of r values for which there are oscillations has almost totally disappeared, with the result that the branch of equilibria has nearly completed stabilized.
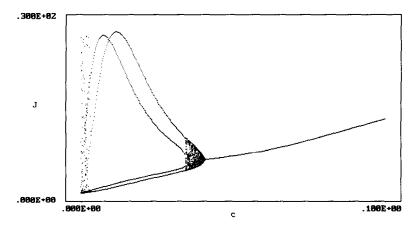
Fig. 6.

.300E+02

J

.000E+00

.000E+00   .100E+00

c

FIG. 7. The stabilizing effect of increased cannibalism is illustrated by plotting the J component of the dynamically computed attractors against the cannibalism coefficient $c \in [0, 1]$. Parameter values in (2.6) with (4.1) are $\rho = 1/2$, $d = -f'(0) = 1$, $a = 1/\psi(0) = 1$, and $r = 75$. This corresponds to moving vertically along a path in region (2) in Figure 3a with $\rho = 1/2 < 1$. Note that the oscillations occurring for c less than a critical value, roughly equal to 0.4, are equilibrated for c larger than this value.

and "chaotic" dynamics (see Figure 6a, for an example). When $\rho < 1$, the introduction of cannibalism will significantly stabilize these dynamics by restricting (if not eliminating) the oscillatory and chaotic parameter range and by stabilizing and increasing equilibrium levels (see Figures 6b, 6c). Figure 7, in which the attractors are plotted against the cannibalism coefficient c, clearly demonstrates this stabilizing property. These results lend further support to the conclusion that cannibalism can be stabilizing when the environmental resource supply rate ρ is small.

Consider now the case when $\rho > 1$. Referring to Figure 3b, we see that, insofar as small values of the inherent net reproductive number r are concerned, there are two possibilities. Either stable positive equilibria bifurcate at $r = 1$ for all values of the cannibalism coefficient c (Figure 3a) or the stable bifurcating equilibria lose their stability to synchronous 2-cycles for values of c sufficiently greater than 0 (Figure 3b). The latter case, which points to a kind of destabilizing property of cannibalism, occurs if the intraspecific competition between adults for the environmental resource is weak ($|f'(0)|$ is small). This is illustrated by Figure 8, where this exchange of stability from the equilibrium to the 2-cycle as c is increased from 0 to 1 is clearly seen. The stability of the bifurcating 2-cycles does not persist as r is increased, however (Theorem 6). In Figure 9 can be seen an example in which the equilibria, which bifurcate unstably, restabilize as r is increased, whereas the 2-cycles, which bifurcate stably, destabilize. Numeri-
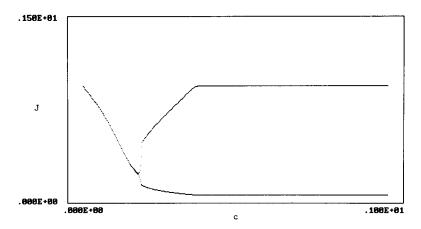
FIG. 8. The juvenile components J of the attractors of (2.6) with (4.1) were dynami-
cally computed and plotted against the cannibalism coefficient c with parameter values
$\rho = 5$, $d = -f'(0) = 1/10$, $a = 1/\psi(0) = 1/10$, and $r = 11/10$. This corresponds to moving
vertically from region (2) to region (3) in Figure 3b and hence moving from the
occurrence of a bifurcating stable equilibrium to the occurrence of a bifurcating syn-
chronous 2-cycle (as in Figures 2b and 2c, respectively). The equilibrium loses stability as
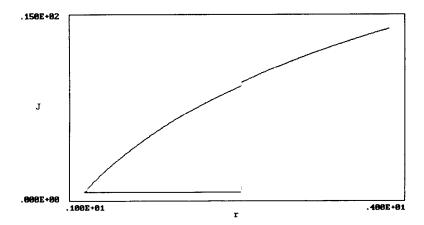c increases from 0 to 1, where a stable synchronous 2-cycle is seen.

FIG. 9. The juvenile components J of the attractors of (2.6) with (4.1) were dynami-
cally computed and plotted against the inherent net reproductive number r. Parameter
values are $\rho = 5$, $d = -f'(0) = 1/10$, $a = 1/\psi(0) = 1/10$, and $c = 3/4$. These parameter
values lie in region (3) of Figure 3b, and hence stable synchronous 2-cycles are observed
bifurcating at $r = 1$. However, these 2-cycles lose stability, and the equilibrium (which
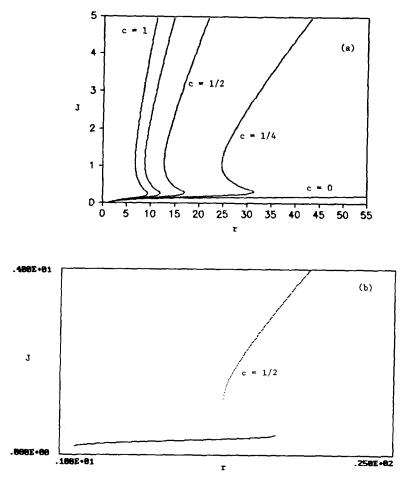bifurcated unstably at $r = 1$) is stabilized for larger values of r.

FIG. 10. In (a) the effect of increasing the cannibalism coefficient c on the bifurcating branch of equilibria is illustrated by plotting the juvenile components J of the equilibria against the inherent net reproductive number r for several values of c. Parameter values in (2.6) with (4.1) are $\rho = 3/2$, $d = -f'(0) = 20$, $a = 1/\psi(0) = 1$ with $c = 0, 1/4, 1/2, 3/4$, and 1. This corresponds to moving vertically through region (2) in Figure 3a with $\rho = 3/2 > 1$. Note the increase in equilibrium levels (for large r) and the development of hysteresis loops with increasing c. In (b) the same graph is shown with $c = 1/2$, but for equilibria that were dynamically computed to demonstrate the stability of the upper and lower portions of the hysteresis loop.

cal simulations suggest in this case (in region 3 of Figure 3b) that the dynamics when r is large is quite complicated, involving many different kinds of attractors and even multiple attractors.

On the other hand, strong intraspecific adult competition for the environmental resource (Figure 3a) has a stabilizing influence on the dynamics. In this case, however, multiple stable, positive equilibria can readily occur (Theorem 3). Figure 10a shows an example of the evolution of an S-shaped bend in the equilibrium branch C as the cannibalism coefficient c is increased. Figure 10b shows the stability of the lowermost and uppermost branches of this bend. The importance of this configuration and the implied hysteresis for exploited aquatic (and cannibalistic) populations is discussed at length by Botsford [1]. A population equilibrating at the higher equilibrium state will suddenly "crash" to the lower equilibrium state if some disturbance, such as intense exploitation, reduces r below the critical value defined by the bend at which the upper branch exists. Moreover, if exploitation ceases and r is increased to its former level, the population, now equilibrating on the lower branch, can fail to return to its former higher equilibrium state. Botsford [1] references several instances of such occurrences involving a variety of fish and crab species (which, in fact, practice cannibalism).

5. CONCLUDING REMARKS

We have studied the dynamics of the difference equations (2.6) as a model of an age-structured population whose nonreproducing juveniles are cannibalized by the adults. It was shown how the interplay between the negative and positive feedback mechanisms implied by this cannibalism, even in this simplest of models, can account for several unique features that have been observed in natural and laboratory organisms that practice cannibalism.

First, if the supply rate of environmental resource is low (as measured in units corresponding to the energetic content of one cannibalized juvenile), then the practice of cannibalism has a "stabilizing" influence on the dynamics of our model population (in addition to significantly raising equilibrium levels); otherwise cannibalism can, at least for low inherent net reproductive rates, result in severe sustained oscillations in which both age classes are alternately wiped out.

Second, the practice of cannibalism can allow a population to survive under circumstances when it would otherwise go extinct. In particular, this can occur if the environmental resource supply rate is low and the inherent net reproductive number is below replacement (this is the so-called lifeboat strategy).

Finally, cannibalism can result in a hysteresis effect caused by the occurrence of multiple, stable positive equilibrium states. This in turn can

account for sudden population crashes to lower equilibrium levels as crucial parameters are changed (e.g., if the inherent net reproductive number is decreased) and a failure to return to previous equilibrium levels when parameters are returned to previous values.

The presence of these dynamical features in such a simple model of cannibalism as that considered here suggests that their presence might also be expected in more complicated models of cannibalism. It would be of interest, for example, to consider a model with more than two age classes and adults that reproduce possibly more than once (iteroparity). A more sophisticated model would also include resource dynamics because the intensity of cannibalism is often inversely related to noncannibalism resource availability [18]. Also, as cannibalism usually correlates with body size (rather than age), the study of these dynamical phenomena in a size-structured model of cannibalism would be of interest (see van den Bosch et al. [20]).

APPENDIX

Proof of Theorem 3.   Define $d = -f'(0) > 0$ and $g(A) = f(A/d)$. Then $g(0) = 1$, $g'(0) = -1$, and both $g(A)$ and $Ag'(A) \to 0$ as $A \to +\infty$. With $A = A(J)$ and $f(A) = g(dA)$, we can compute from (3.2a) the derivative $r'(J) = -r^2 \, dn(J, A(J))/dJ$, and from (3.2b) the factor $dn(J, A(J))/dJ$, whose sign determines that of $r'(J)$. The terms in the latter derivative can be placed into two categories: those that depend upon d and those that do not. Note that the adult equilibrium component $A = A(J)$, and hence its derivative $A'(J)$, are independent of f and hence of d (see the discussion preceding Theorem 1). The two stated asymptotic facts about g imply that the terms involving d will tend to 0 as $d \to +\infty$, all other parameters being held fixed, including $J > 0$. The terms independent of d, when evaluated at $J = 0$, turn out to equal $c\Psi'(0)\Phi'(0)/\rho > 0$ and hence are positive for $J > 0$ sufficiently small. Thus $dn(J, A(J))/dJ > 0$, and hence $r'(J) < 0$, for d sufficiently large provided $J > 0$ is sufficiently small. Note that

$$r'(0) = \Delta^+ = \frac{\rho - 1}{\rho} c\Psi'(0) + d > 0$$

for d large.

Proof of Theorem 5. The formulas in (3.3) can be derived by standard regular perturbation (or Liapunov–Schmidt) techniques in which the bifurcating equilibria, and the Jacobian of the right-hand sides of (2.6) and its eigenvalues $\lambda^{\pm}$, are all expanded in Taylor series in $\epsilon = r - 1$ centered at $\epsilon = 0$. Thus, if the bifurcating equilibria are given by

$$J = J_1\epsilon + 0(\epsilon^2), \qquad A = A_1\epsilon + O(\epsilon^2)$$

for $\epsilon > 0$ small, then we can expand the Jacobian

$$Q = Q_0 + Q_1\epsilon + O(\epsilon^2)$$

and its eigenvalues and associated right (column) and left (row) eigenvectors

$$
\begin{aligned}
\lambda^{\pm} &= \lambda_0^{\pm} + \lambda_1^{\pm}\epsilon + O(\epsilon^2), \\
v^{\pm} &= v_0^{\pm} + v_1^{\pm}\epsilon + O(\epsilon^2), \\
w^{\pm} &= w_0^{\pm} + w_1^{\pm}\epsilon + O(\epsilon^2).
\end{aligned}
\tag{A.1}
$$

Then from $(Q - \lambda I)v = 0$, $w(Q - \lambda I) = 0$, and the Fredholm alternative, it can easily be shown from lower order terms that

$$\lambda_1^{\pm} = w_0^{\pm} Q_1 v_0^{\pm} / w_0^{\pm} v_0^{\pm}.
\tag{A.2}$$

Placing the expansions (A.1) into the equilibrium equations (3.1) and into Equation (3.2a), one easily finds from the resulting terms of lowest order in ϵ that $J_1 = A_1 = 1/\Delta^+$. With these coefficients in hand, one can straightforwardly calculate from the Jacobian

$$
Q =
\begin{pmatrix}
r\dfrac{c}{\rho}\Phi'(J)\psi(A)A & r\left[f(A) + \dfrac{c}{\rho}\Phi(J)\psi(A)\right] \\[2ex]
 & + r\left[f'(A) + \dfrac{c}{\rho}\Phi(J)\psi'(A)\right]A \\[2ex]
1 - c\Phi'(J)\Psi(A) & - c\Phi(J)\Psi'(A)
\end{pmatrix}
$$

the lowest order matrix

$$
Q_0 =
\begin{pmatrix}
0 & 1 \\
1 & 0
\end{pmatrix},
$$

whose eigenvalues $\lambda_0^{\pm} = \pm 1$ and associated eigenvectors

$$
v_0^{\pm} =
\begin{pmatrix}
1 \\
\pm 1
\end{pmatrix},
\qquad
w_0^{\pm} = (1, \pm 1)
$$

are easily calculated. In order to use (A.2) to obtain (3.3) we need only calculate Q_1. This is done by calculating the first-order $O(\epsilon)$ terms in each entry of Q, which results in

$$Q_1 = \frac{1}{\Delta^+} \begin{pmatrix} \dfrac{c}{\rho}\psi(0) & f'(0) + c\psi(0) \\[2mm] -c\psi(0) & -c\psi(0) \end{pmatrix}.$$

(A.2) now easily yields $\lambda_1^+ = -1/2$ and $\lambda_1^- = -\Delta^-/2\Delta^+$, which in turn yield the desired expressions (3.3).

Proof of Theorem 7. The positive equilibria satisfy Equation (3.2a) and are functions of c. A differentiation of (3.2a) with respect to c, together with the facts that $A = J$ and $1 = rf(I)$ when $c = 0$ [cf. (3.1)], yields

$$\frac{dA}{dc} = (1 - r\rho^{-1}) \frac{\Phi(J)\psi(J)}{rf'(J)}.$$

A differentiation of (3.1b) with respect to c, when evaluated at $c = 0$, yields $dJ/dc - dA/dc = \Phi(J)\Psi(J)$, and hence

$$\frac{dJ}{dc} = \left[1 - r\rho^{-1} + rJf'(J)\right] \frac{\Phi(J)\psi(J)}{rf'(J)}.$$

Since $f' < 0$, the signs of these derivatives are the opposite of those of the parenthetical expressions, which at $r = 1$ reduce to $1 - \rho^{-1}$. This proves Theorem 7.

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