

A Size-Structured Model for Cannibalism

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A size-structured model for the dynamics of a cannibalistic population is derived under the assumption that cannibals (successfully) attack only smaller bodied victims, as is generally the case in the biological world. In addition to the resulting size-dependent death rate, the model incorporates the positive feedback mechanism resulting from the added resource energy obtained by the cannibal from the consumption of the victim. From the nonlinear partial integro-differential equation model, it is shown how to obtain a complete analysis of the global dynamics of the total population biomass. This analysis yields many dynamical features that have been attributed to cannibalism in the literature, including density self-regulation, a "life-boat strategy" phenomenon by which a population avoids extinction by practicing cannibalism under circumstances when it would otherwise go extinct, and multiple stable positive equilibrium states and hysteresis. © 1992 Academic Press, Inc.

1. INTRODUCTION

Intraspecific predation, or cannibalism, occurs in a wide variety of organisms, including many species of protozoa, rotifers, gastropods, copepods, insects, fish, and some species of amphibians, birds, and mammals (Fox, 1975, Polis 1981). Although field and laboratory studies have attributed several interesting features of the population dynamics of cannibalistic populations specifically to the occurrence of cannibalism, only a handful of mathematical models for the dynamics of cannibalistic populations have been studied (see Landahl and Hansen, 1975; Botsford, 1981; van den Bosch *et al.*, 1988; Cushing, 1991). Phenomena that have been attributed to the practice of cannibalism include (but are not limited to) the self-regulation of population density (Fox, 1975; Polis, 1981); "life-boat" effects which allow survival in circumstances when the population, in the absence of cannibalism, would be in danger of extinction (Giese, 1973;

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Polis, 1981); multiple stable equilibrium states and resulting hysteresis effects (Botsford, 1981); and in some circumstances, population oscillations and losses of entire age or size classes (Polis, 1981).

In order to build adequate models that incorporate cannibalism, or indeed any form of intraspecific competition, some detail concerning individual behavior and its effects on vital rates of growth, reproduction, and death must be included. Such effects often can be strongly correlated with some measurable scalar attribute of an individual, such as age or body size (Werner and Gilliam, 1984; Calder, 1984). The methodology for modeling populations "structured" by such scalar attributes now is readily available, both for continuous models (Metz and Diekmann, 1986) and discrete models (Caswell, 1989; Cushing, 1988). The models of cannibalism that have appeared in the literature have, with few exceptions (e.g., see Botsford, 1981), been based upon age classes and include discrete matrix models (Landahl and Hansen, 1975; Cushing, 1991) and continuous partial differential equation models (van den Bosch *et al.*, 1988). Cannibalism correlates in general with relative body size, where larger individuals are usually more voracious cannibals and victims almost always are smaller (Polis, 1981, 1988). If an individual's growth rate is dependent upon resource uptake, then a cannibal's growth rate is dependent (at least in part) upon the population density of smaller individuals. This implies that the dynamics of cannibalistic populations is more appropriately described by size-structured models rather than age-structured models.

The details of interactions between conspecifics which can effect vital growth, reproductive, and growth rates are extraordinarily diverse throughout the biological world (see, e.g., Werner and Gilliam, 1984). The same is true of cannibalistic interactions (Fox, 1975; Polis, 1981, 1984). To focus on to specific a form of cannibalistic behavior would not only detract from the generality of the model and its implications, but given the complexities of relating size-specific vital rates to specific physiological, behavioral, and environmental characteristics would very likely result in an analytically intractable system of model equations. Our first goal here is to derive a tractable model which captures (without getting involved with such details) the essential properties of cannibalism, including the assumption that cannibals are in general larger than their victims and that cannibalism not only affects the size-specific death rates, but also affects the growth and reproductive rates by providing an alternative energy source for the cannibals. In order to do this and to focus on the effects of cannibalism alone we will need, of course, to make many simplifying assumptions. In particular no other regulatory interactions, such as, for example, the many forms of intraspecific competition, will be taken into account. Consequently, the model will exhibit linear exponential dynamics in the absence of cannibalism. Second, we will show how such a "simple"

model can account for most (all but the last) of the dynamical phenomena attributed to cannibalism described above. If such phenomena are present in even the simplest of cannibalism models, then presumably they would be present in more complex models as well (depending, of course, on the nature of the size-specific competitive interaction).

The model is derived in Section 2 using the methodology of Metz and Diekmann (1986). The result is a complicated nonlinear partial integro-differential equation for the size-specific population density function, subject to a nonlinear integral boundary condition. Despite the complexity of this model, it is shown in Section 3 how a complete analysis of the global dynamics of the total biomass of the population can be carried out. The implications of the analysis are discussed in Section 4.

2. MODEL DERIVATION

Let t denote time and s denote body volume. If we assume that the density of an organism does not change significantly during its lifetime, then s can be equivalently used to denote body biomass. If the population is described by means of a density function $\rho(t, s)$, then the dynamics of ρ are governed by the equations (Metz and Diekmann, 1986)

$$\partial_t \rho + \partial_s (g\rho) = -d\rho, \quad t > 0, s > s_b$$

$$g\rho|_{s=s_b} = \int_{s_b}^{s_m} b\rho \, ds, \quad t > 0.$$

Here we have assumed that newborns all have the same size $s_b > 0$ and that s_m denotes maximal body size (biomass), i.e., the body size at which growth stops. Specifically, we assume that the rate of growth of the total biomass of individuals of size s_m is zero:

$$g\rho(t, s)|_{s=s_m} = 0 \quad \text{for } t \geq 0. \tag{2.1}$$

For simplicity we assume that size scale is chosen so that $s_b = 1$. The birth and death rates (per unit biomass) are denoted by b and d , respectively. The growth rate of individuals (biomass per unit time) is denoted by g . Sub-models for these vital rates must be built so that they reflect the biological features of interest. In general they will depend on time t and body size s and, for density-dependent population dynamics, in some manner on population density ρ .

Many physiological and behavior attributes of organisms scale to a power of body length. In particular, resource consumption often scales to body length raised to a power between two and three (Calder, 1984). In

our simple model we assume that growth and fertility are jointly proportional to body volume or biomass s (length cubed) and (following van den Bosch *et al.*, 1988) to the energy uptake rate E per unit biomass. We distinguish between energy obtained from cannibalism and that obtained from other (non-cannibalistic) resources. We denote these by E_c and E_o , respectively, so that $E = E_c + E_o$. Accordingly, we write

$$g = \gamma(E_c + E_o) s, \quad b = \beta(E_c + E_o) s,$$

where $\gamma > 0$ and $\beta > 0$ are conversion and allocation factors from energy allocated to growth and reproduction, respectively. Thus, in this simplified model, growth occurs during an individual's entire life span and there is no slowing or cessation of the growth rate at larger sizes (Werner and Gilliam, 1984). Consequently we take $s_m = +\infty$. The death rate

$$d = d_c + d_o$$

is broken into two components, the death rate d_c of individuals of size s due to cannibalism and the death rate d_o due to non-cannibalistic causes.

Consider first the non-cannibalistic rates E_o and d_o . We assume that E_o is an increasing function of the amount R of (non-cannibalistic) food resources available per unit time (which is assumed to be constant). For example, $E_o = E_o(R)$ could be chosen to have the form of any of the many commonly used expressions for resource harvesting or predation functional responses, such as the well-known Holling types. For simplicity we will assume that E_o is simply proportional to R , i.e.,

$$E_o = uR, \quad u > 0,$$

and thus ignore saturation effects (as in van de Bosch *et al.*, 1988). Our results are not qualitatively different for more general monotonic dependencies of E_o on R (as a careful study of the mathematical arguments will show). The non-cannibalistic death rate d_o is assumed to be a decreasing function of the energy uptake rate E , decreasing from a "starvation" death rate d_s to a minimal, "natural" death rate d_m due to causes other than cannibalism and starvation. Thus,

$$d_o = d_o(E), \quad d'_o(E) < 0, \quad d_o(0) = d_s > d_m = d_o(+\infty) > 0. \quad (2.2)$$

Consider now the cannibalistic rates E_c and d_c . In keeping with our goal of deriving a simple and tractable model we will not attempt to account for any detailed behavioral mechanisms involved in interactions between cannibals and their victims, which in general can be quite varied and complex. Besides the behavioral factors that are often dealt with when modeling predator-prey interactions (such as searching methods, handling times,

etc.) a general model would have to deal with complications due to body size. For example, consideration should be given to the possibilities that the attack probability and success of cannibals, as well as the successful defense and escape of potential victims from cannibalistic attacks, could depend on their relative sizes; that the energy obtained by a cannibal might significantly depend upon the victim's size; that safe refuges might be available to smaller potential victims; and so on. Our goal here is to capture in an analytically tractable model only the fundamental fact that cannibalism is almost always practiced by larger individuals upon smaller victims. Therefore, we will make the assumption that the (per unit biomass) energy uptake rate E_c of a cannibal of size s and the death rate d_c of an individual of size s due to cannibalism depend only on the biomasses of the classes of individuals of size smaller and larger than s , respectively. The biomasses of these size classes are given by the formulas

$$S(t, s) = \int_1^s \rho(t, s) s \, ds, \quad L(t, s) = \int_s^\infty \rho(t, s) s \, ds.$$

More specifically, we assume that E_c and d_c are proportional to these biomasses:

$$E_c = cS(t, s), \quad c \geq 0, \quad \text{and} \quad d_c = \delta L(t, s), \quad \delta \geq 0.$$

In summary, the dynamics of the density function $\rho(t, s)$ for our model cannibalistic population are governed by the integro-partial differential equations

$$\begin{aligned} \text{(a)} \quad & \partial_t \rho(t, s) + \partial_s (\gamma E(t, s) \rho(t, s) s) = - (d_o(E(t, s)) + \delta L(t, s)) \rho(t, s) \\ \text{(b)} \quad & \gamma E(t, s) \rho(t, s) s|_{s=1} = \int_1^\infty \beta E(t, s) \rho(t, s) s \, ds, \end{aligned} \quad (2.3)$$

where $E(t, s) = uR + cS(t, s)$. The total biomass of the population is given by

$$B(t) = \int_1^\infty \rho(t, s) s \, ds.$$

The dynamics of $B(t)$ is analyzed in the next section. Amongst other things it will be shown that $B(t)$ is either monotonically unbounded or monotonically equilibrates.

3. MODEL ANALYSIS

In order to determine the asymptotic dynamics of the total population biomass, we derive an equation for $B(t)$ from the model equations (2.3). This is done by multiplying Eq. (2.3a) by s and integrating the result from $s = 1$ to $s = +\infty$. The first term in Eq. (2.3a) immediately yields $B'(t)$. The second term can be integrated by parts to obtain

$$\int_1^{\infty} \partial_s (\gamma E(t, s) \rho(t, s) s) s ds = \gamma E(t, s) \rho(t, s) s^2 \Big|_1^{\infty} - \int_1^{\infty} \gamma E(t, s) \rho(t, s) s ds$$

By assumption (2.1) and Eq. (2.3b), the boundary term on the right-hand side of this equation is

$$\gamma E(t, s) \rho(t, s) s^2 \Big|_1^{\infty} = - \int_1^{\infty} \beta E(t, s) \rho(t, s) s ds$$

and as a result

$$\int_1^{\infty} \partial_s (\gamma E(t, s) \rho(t, s) s) s ds = -(\beta + \gamma) \int_1^{\infty} E(t, s) \rho(t, s) s ds.$$

The term on the right-hand side of Eq. (2.3a) yields

$$- \int_1^{\infty} (d_o(uR + cS(t, s)) + \delta L(t, s)) \rho(t, s) s ds.$$

Gathering all of these results together we obtain

$$B'(t) = \int_1^{\infty} \left\{ \frac{n}{r} (uR + cS(t, s)) - d_o(uR + cS(t, s)) - \delta L(t, s) \right\} \rho(t, s) s ds.$$

In this equation we have introduced the parameter $n = (s_b \beta + \gamma) r = (\beta + \gamma) r$ where $r = uR/d_o(uR)$. This equation can be further simplified by means of the Lemma proved in the Appendix, part (i), (with $h(x, y) = n(uR + cx)/r - d_o(uR + cx) - \delta y$) to obtain the equation

$$B' = f(B), \quad f(B) = \frac{uR}{r} \left(n + \frac{c}{2uR} \left(n - r \frac{\delta}{c} \right) B \right) B - \int_0^B d_o(uR + cz) dz, \quad (3.1)$$

for the total population biomass $B(t)$.

In the absence of cannibalism $1/d_o(uR)$ is the expected life span of a unit of biomass when the resource is a level R . Since uR is the amount of resource consumed by a unit of biomass per unit time, we see that r is

the expected amount of resource consumed by a unit of biomass during its life if cannibalism is absent. Thus, during its life, a unit of biomass is expected to contribute to the population an amount βr of biomass by reproduction and an amount γr of biomass by growth. This means that n is the total biomass contributed by a unit of biomass to the population, by both reproduction and growth, during its life provided cannibalism is absent. Therefore we call n the “inherent net reproductive number.”

Since Eq. (3.1) is a scalar ordinary differential equation it follows that $B(t)$ cannot oscillate in time and *the total population biomass must monotonically equilibrate or tend to $+\infty$ as $t \rightarrow +\infty$.*

The non-negative zeros of $f(B)$ are the equilibrium states whose stability is determined by the sign of the derivative $f'(B)$ at that point (assuming it is not zero). In the “generic” case when $f'(B)$ does not vanish at any of the zeros, the equilibria of Eq. (3.1) (including $B=0$), when ordered by increasing magnitude, will then alternate between stable and unstable. Positive equilibria are the roots of the equation

$$L(B) = D(B), \tag{3.2}$$

where

$$L(B) = n + \frac{c}{2uR} \left(n - r \frac{\delta}{c} \right) B \quad \text{and} \quad D(B) = \frac{1}{B} \int_0^B \frac{d_0(uR + cz)}{d_0(uR)} dz. \tag{3.3}$$

Thus, positive equilibria are the intersection points of the straight-line graph of $L(B)$ and the graph of the average $D(B)$.

Consider first the case when cannibalism is absent, i.e., $c = \delta = 0$. Then (3.1) reduces to the linear equation

$$B' = d_0(uR)(n - 1) B. \tag{3.4}$$

We have assumed no mechanism is present, other than possibly cannibalism, that could regulate population growth and hence in the absence of cannibalism it comes as no surprise that the population either goes extinct, when $n < 1$, or explodes exponentially, when $n > 1$.

If cannibalism is present, then (3.4) is also the linearization of (3.1) at the equilibrium $B=0$. Thus $B=0$ is stable if $n < 1$ and unstable if $n > 1$. This means that for $n < 1$ populations that initially are small will go extinct as $t \rightarrow +\infty$. We will see below, however, that $B=0$ may not be a global attractor and that populations initially “large” may not go extinct when cannibalism is practiced. Also, for $n > 1$ populations in which cannibalism occurs may not explode.

To find positive equilibria Eq. (3.2) must be solved. This depends crucially on the properties of the natural death rate $d_0(E)$ as a function of the

energy uptake rate E . Besides the monotonicity assumption (2.2) we will consider two cases: when $d_o(E)$ is everywhere concave up and when $d_o(E)$ is concave down near $E=0$. For fixed $d'_o(0)$, the latter case can be thought of as that of a population whose death rate, when resources are scarce and population density is low, is "quick" to decrease from the starvation rate d_s with increased energy uptake, while in the former case this death rate drops more slowly.

Clearly $D(B) > 0$ and $D(0) = 1$. It is shown in the Appendix, part (ii), that $D'(B) < 0$ and $D(+\infty) = d_m/d_o(uR) > 0$.

Case 1. Suppose that $d''_o(E) > 0$ for $E > 0$. It is shown in the Appendix, part (iii), that $D''(B) > 0$. For a fixed resource availability level R the equilibrium equation (3.2) can be graphically solved for B by finding the intersection of the monotonically decreasing, concave upward graph of $D(B)$ with the straight-line graph of $L(B)$. The line $L(B)$, and hence the equilibrium B , depends upon n . A study of this geometric procedure shows four different situations arise,

$$\begin{aligned} \text{(a)} \quad & n_1 < d_m/d_o(uR) \\ \text{(b)} \quad & d_m/d_o(uR) < n_1 < 1 \\ \text{(c)} \quad & 1 < n_1 \quad \text{and} \quad D'(0) < L'(0) \\ \text{(d)} \quad & 1 < n_1 \quad \text{and} \quad D'(0) > L'(0), \end{aligned} \tag{3.5}$$

where

$$n_1 = \frac{uR\delta}{d_o(uR)c}, \quad D'(0) = \frac{cd'_o(uR)}{2d_o(uR)}, \quad L'(0) = \frac{c}{2uR} \left(n - r \frac{\delta}{c} \right). \tag{3.6}$$

As an illustration case (b) is shown in Fig. 1. The results of this solution procedure can be graphically plotted in the form of bifurcation diagrams in which the equilibria B are plotted against n . The four cases in (3.5) are drawn in Fig. 2. The illustration in Fig. 1 appears in case (b) in Fig. 2.

The four cases (3.5)–(3.6) can be re-interpreted in terms of the resource availability R . It is shown in the Appendix, part (iv), that there exist three positive numbers $R_1 < R_2 < R_3$ such that these four cases, and those appearing in Fig. 2, correspond respectively to the following four inequalities:

$$\begin{aligned} \text{(a)} \quad & 0 < R < R_1 = d_m c / u\delta \\ \text{(b)} \quad & R_1 < R < R_2 \\ \text{(c)} \quad & R_2 < R < R_3 \\ \text{(d)} \quad & R_3 < R. \end{aligned} \tag{3.7}$$

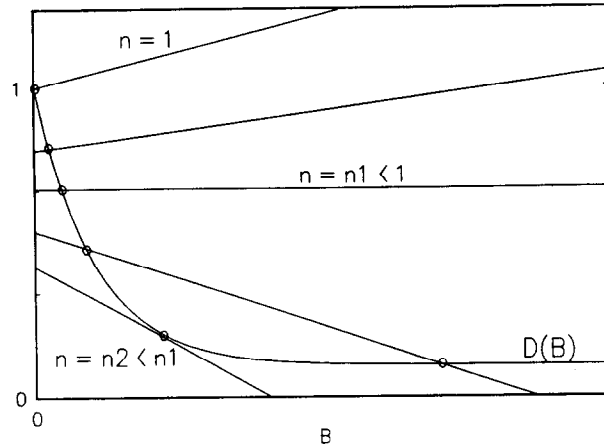


FIG. 1. The graphs of selected lines $L(B)$ for several different values of the inherent net reproductive number n are shown superimposed on the graph of $D(B)$ in the case (3.5b) when the non-cannibalistic death rate $d_o(E)$ is a decreasing, but concave upward function of consumed energy E (which implies that $D(B)$ is concave upward as a function of B). For a given line (value of n) the intersection point(s) determine positive equilibrium levels for total population biomass B . The results of this case are graphically illustrated in the bifurcation diagram appearing in Fig. 2b. Other cases, depending upon the location of the horizontal line ($n = n_1$) and the relative slopes of $D(B)$ and $L(B)$ at the point $(n, B) = (0, 1)$, are drawn similarly and result in the other bifurcation diagrams shown in Fig. 2.

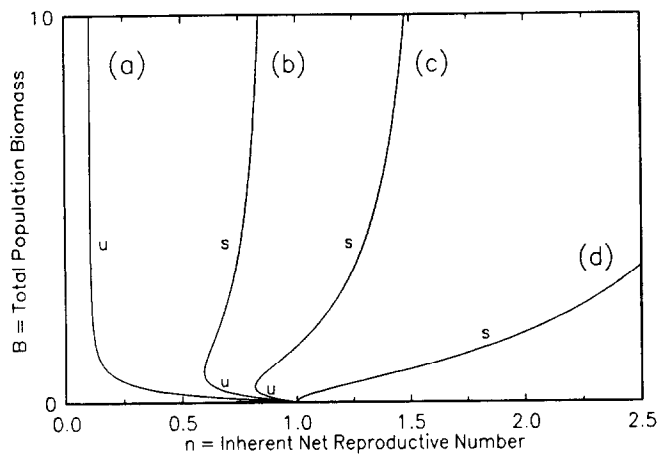


FIG. 2. Four qualitatively different bifurcation diagrams, which plot positive total biomass equilibria against the inherent net reproductive number n , arise when the non-cannibalistic death rate $d_m(E)$ is a decreasing, but concave upward function of total consumed energy E . These four cases correspond to resource availability R given by the inequalities in (3.7). All branches of positive equilibria have a vertical asymptote at $n = n_1$ (not shown). Equilibria on increasing portions of the branch are stable (indicated by s) while equilibrium on decreasing portions are unstable (indicated by u). The zero equilibrium $B = 0$ is stable for $n < 1$ and unstable for $n > 1$ (not shown).

Since (3.1) is a scalar, ordinary differential equation, the stability of an equilibrium is determined by the sign of the derivative of the right-hand side with respect to B evaluated at the equilibrium. Moreover, every solution is monotonic and bounded solutions necessarily equilibrate. From these facts it is easy to determine the global stability properties of the equilibria in each of the possible bifurcation diagrams in Fig. 2. Positive equilibria B lying on increasing portions of the bifurcation curves are stable and those lying on decreasing portions are unstable.

All equilibrium branches have a vertical asymptote at $n = n_1$. Consequently, for fixed R , there is in all cases a finite interval (n_2, n_3) , $0 < n_2 \leq 1 \leq n_3 < +\infty$, of inherent net reproductive numbers n for which there exist positive equilibria. For small $n < n_2$, $B(t) \rightarrow 0$ as $t \rightarrow +\infty$ and the population goes extinct while for large $n > n_3$, $B(t) \rightarrow +\infty$ as $t \rightarrow +\infty$ and the population explodes (i.e., cannibalism fails to regulate the exponentially growing population).

Case 2. If $d_0(E)$ and hence $D(B)$ are not everywhere concave upward, then more complicated intersections between $L(B)$ and $D(B)$ are possible. Suppose for example that $d_0''(E) < 0$ on some interval $0 \leq E < E^*$. Then $D''(0) = c^2 d_0''(uR)/3d_0(uR) < 0$ for R not too large. Consider the simplest case when $D(B)$ has but one inflection point (see Fig. 3). If a geometrical analysis of the equilibrium equation (3.2) is carried out as was done in Case 1, one finds qualitatively similar cases (a) and (b). When $n_1 > 1$,

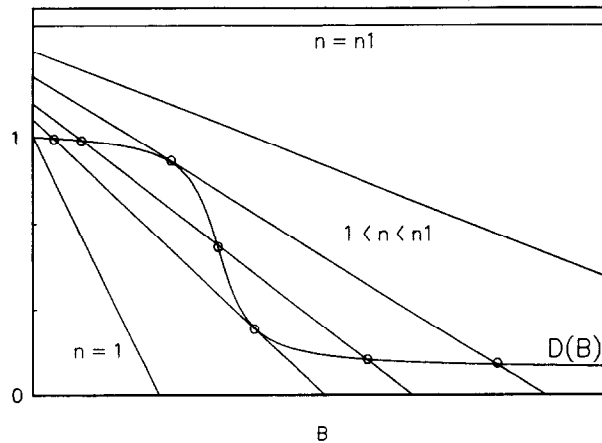


FIG. 3. The graphs of selected lines $L(B)$ for several different values of the inherent net reproductive number n are shown superimposed on the graph of $D(B)$ in a possible configuration that can occur when the non-cannibalistic death rate $d_0(E)$ is concave downward for lower levels of consumed energy E (which implies that $D(B)$ is concave downward for smaller values of B). As in Fig. 1, for a given line (value of n) the intersection point(s) determine positive equilibrium levels for total population biomass B . The resulting bifurcation diagram for this case is shown in Fig. 4b.

function $d_o(E)$ considered in Section 3 our results are summarized in the bifurcation diagrams in Figs. 2 and 4. Because no density effects other than cannibalism are included in the model and as a result, the model population dynamics in the absence of cannibalism are linear (exponentially growing when $n > 1$ and diminishing with $n < 1$), Figs. 2 and 4 show immediately the implications of cannibalism.

It comes as no surprise that the practice of cannibalism can be a self-regulating mechanism, i.e., can, under certain circumstances, prevent the unbounded, exponential growth of total biomass in our model population that occurs when the inherent net reproductive number n is greater than 1 and cannibalism is absent. From Figs. 2 and 4 we see that equilibration can occur for values of the inherent net reproductive number n greater than 1 (but not too large) provided the resource availability R is sufficiently large. However, given an intensity level of cannibalism (i.e., coefficients c and δ) n may be too large for cannibalism to regulate the population growth (namely, if $n > n_3$). In other words, self-regulation will occur for $n > 1$ only if the intensity of cannibalism and the resource supply R are sufficiently large. Under these circumstances there is also the possibility of multiple, stable positive equilibrium states (Fig. 4). This occurs in our model when the death rate $d_o(E)$ is concave downward as a function of the energy uptake rate E (per unit biomass), at least at low uptake rates. This can create hysteresis loops with changes in the inherent net reproductive number n , that is to say, population crashes and outbreaks will occur as n is changed and equilibria jump from lower to higher levels or vice versa, at different critical values, as n is increased or decreased. Botsford (1981) seems to have been the first to notice this possible consequence of cannibalism and used it to offer an explanation of the failure of certain over-exploited fish populations to equilibrate at previous equilibrium levels after exploitation ceased.

When $n < 1$ the non-cannibalistic model population goes extinct. From Figs. 2a–2c we see that when the resource supply R is low, cannibalism can prevent extinction when $n < 1$ (at least if the initial biomass is sufficiently large) by either creating a stable positive equilibrium or, in the extreme case of very small R (Fig. 2a), unregulated population growth. For the type of death rate nonlinearity in case (ii) and Fig. 4 we see that population survival for $n < 1$ can also occur for large R as well. In these cases the zero equilibrium state is also stable and consequently population survival is dependent upon initial conditions being sufficiently large. This scenario, in which there is a threshold for the total population biomass below which the population will crash, is similar to that caused by so-called "Allee effects" or that is often referred to as "depensation" (see van den Bosch *et al.*, 1988; Cushing, 1988). Moreover, in this case there is the danger of a sudden catastrophic collapse of the population should n be

decreased below a positive critical point $n_0 < 1$. Nonetheless, the fact that population survival is possible for $n < 1$ under the practice of cannibalism can be interpreted as a version of the "life-boat strategy" (Giese, 1973; Polis, 1988; van den Bosch *et al.*, 1988), by which is meant that a cannibalistic population survives under circumstances when it would go to extinction if it did not practice cannibalism.

These model results are similar in spirit to those of van den Bosch *et al.* (1988) and Cushing (1991). However, the models use by these authors are age- rather than size-structured. Moreover we have succeeded, unlike these authors, in giving a complete global analysis of our model.

Our goal in this paper was to show how even a simple size-structured model of cannibalism can result in a rich diversity of dynamical possibilities and can explain many of the phenomena attributed to the practice of cannibalism that can be found in the literature. It seems reasonable to anticipate that less simplistic and more biologically realistic models would also exhibit these phenomena as well. For example, we have ignored such conceivably important features as juvenile periods, allocation of consumed resources for metabolic demands, growth rate decrease and cessation at larger sizes, maximal body size, saturation effects in both resource uptake and cannibalism, and temporal varying resource availability. As mentioned above, one phenomenon sometimes attributed to cannibalism is oscillations in total population density and/or in size class distribution. Our simple model above cannot account for biomass oscillations. Oscillations could result from a number of those factors omitted in the model. These include a juvenile period (which would place a time delay in the equation for total biomass), a periodic resource availability rate, or a resource supply that dynamically responds to predation by the population. Because cannibalism often is a response to low resource levels (Fox, 1975; Polis, 1988) and is not practiced as severely, if at all, at higher resource availability levels (i.e., c and δ are decreasing functions of R), the latter case is of particular interest. An extension of the above model for dynamically varying R , using methods similar to those used here, would be analytically tractable in that it results in a plane autonomous system of classical type. This will be pursued in another paper.

APPENDIX

(i) In this section we prove the following lemma which was instrumental in deriving the Eq. (3.1).

LEMMA. *Suppose $h = h(x, y)$ is a continuously differentiable function of $x \geq 0$ and $y \geq 0$. Then*

$$\begin{aligned} \int_1^{sm} h(S(t, s), L(t, s)) \rho(t, s) s ds &= \int_0^{B(t)} h(z, B(t) - z) dz \\ &= \int_0^{B(t)} h(B(t) - z, z) dz. \end{aligned}$$

Proof. Define

$$H(x, y) = \frac{1}{2} \int_0^{x-y} h\left(\frac{x+y+u}{2}, \frac{x+y-u}{2}\right) du.$$

It is straightforward to show that $\partial_x H(x, y) - \partial_y H(x, y) = h(x, y)$ and hence that

$$h(S(t, s), L(t, s)) s \rho(t, s) = \frac{d}{ds} H(S(t, s), L(t, s)).$$

An integration of this equality together with an application of the fundamental theorem of calculus yields the desired result.

(ii) From the definition of $D(B)$ in (3.3) we find from an application of l'Hopital's Rule that $D(+\infty) = d_m/d_o(uR)$. Also from (3.3) follows

$$D'(B) = \left(d_o(uR + cB) - \frac{1}{B} \int_0^B d_o(uR + cz) dz \right) (B d_o(uR))^{-1}. \quad (\text{A.1})$$

Since $d_o(E)$ is a decreasing function of its argument E it follows that the first factor and hence $D'(B)$ are negative.

(iii) A differentiation of (A.1), together with the Mean Value Theorem, yields

$$\begin{aligned} D''(B) &= B^{-3} \left(cB^2 d'_o(uR + cB) - 2 \int_0^B (d_o(uR + cB) - d_o(uR + cz)) dz \right) \\ &= B^{-3} \left(cB^2 d'_o(uR + cB) - 2c \int_0^B d'_o(uR + c\zeta(z))(B - z) dz \right), \end{aligned}$$

where $z \leq \zeta(z) \leq B$. If $d''(E) \geq 0$ then $d'(E)$ is increasing and

$$D''(B) \geq B^{-3} \left(cB^2 d'_o(uR + cB) - 2cd'_o(uR + cB) \int_0^B (B - z) dz \right) = 0.$$

(iv) Consider the four cases in (3.5). That (3.5a) is equivalent to (3.7a) is obvious. Since $d_o(E)$ is assumed decreasing, it follows that $uR/d_o(uR)$ is increasing in R . From this it is easy to see that (3.5b) holds if and only if

(3.7b) holds, where $R_2 > R_1$ is the unique positive root of the equation $uR/d_o(uR) = c/\delta$. Finally, consider (3.5, d) and (3.7c, d). From the formulas in (3.6) we see that $D'(0) < L'(0)$ holds if and only if $f(uR) < 0$, where $f(x) = \delta/c - d_o(x)/x + d'_o(x)$ is a monotonically increasing function that satisfies $f(0) = -\infty$ and $f(+\infty) = \delta/c > 0$. Thus if $R_3 = x_3/u$, where x_3 is the unique positive solution of $f(x) = 0$, then (3.5c, d) are respectively equivalent to (3.7c, d).

Note added in proof. A study of oscillations caused by cannibalism can be found in the following references in which an age-structured model with juvenile period is utilized: Costantino, R. F., and Desharnais, R. A. 1991. "Population Dynamics and the *Tribolium* Model: Genetics and Demography," Springer-Verlag, Berlin; Hastings, A., 1987. Cycles in cannibalistic egg-larval interactions, *J. Math. Biol.* **24**, 651-666; and Hastings, A., and Costantino, R. F. 1987. Cannibalistic egg-larval interactions in *Tribolium*: An explanation for the oscillations in population numbers, *Am. Nat.* **130**, 36-52.

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