Destabilizing effect of cannibalism on a structured predator–prey system

Kjartan G. Magnússon *

Division of Applied Mathematics and Computer Science, Science Institute, University of Iceland, Dunhaga 3, IS-107 Reykjavík, Iceland

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Abstract

The dynamics of a predator–prey system, where the predator has two stages, a juvenile stage and a mature stage, are modelled by a system of three ordinary differential equations. The mature predators prey on the juvenile predators in addition to the prey. If the mortality rate of juveniles is low and/or the recruitment rate to the mature population is high, then there is a stable equilibrium with all three population sizes positive. On the other hand, if the mortality rate of juveniles is high and/or the recruitment rate to the mature population is low, then the equilibrium will be stable for low levels of cannibalism, but a loss of stability by a Hopf bifurcation will take place as the level of cannibalism increases. Numerical studies indicate that a stable limit cycle appears. Cannibalism can therefore be a destabilizing force in a predator–prey system. © 1999 Elsevier Science Inc. All rights reserved.

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1. Introduction

Cannibalism has been observed in a great variety of species, including a number of fish species. It is common among piscivores and can make a significant contribution to the diet [1,2]. Rates of losses due to cannibalism can sometimes be ‘impressively high’ [1], e.g. 60% annual mortality of the 0+ group.
has been observed in walleye pollock in the Eastern Bering Sea [3]. It has been demonstrated that adult Atlantic cod eat large numbers of their young, especially those of ages 0 to 2 years [2], and that the frequency of occurrence of cannibalism in the Barents Sea increases with the abundance of juvenile cod. Including cannibalism gives a better fit between abundance indices from surveys and the VPA (Virtual Population Analysis) for cod age groups 1–3 in the Barents Sea [4]. It is therefore believed that cannibalism is sufficiently important to be taken into consideration in the assessment and management of the Barents Sea cod stock [5] and it is suggested that cannibalism is a factor contributing to the observed fluctuations in recruitment of three year old cod [6,7].

It is also well known from theoretical studies that cannibalism can have an important effect on population structure and dynamics. This effect can be positive: for example, Kohlmeier and Ebenhöh [8] have shown that cannibalism by the predator can in some cases lead to a higher long term predator stock size and Bobisud [9] has shown that sufficiently restricted cannibalism in the prey can lead to increased equilibrium population sizes. Furthermore, cannibalism can enable a population to survive when food for the adults is scarce – the so-called life boat effect [10]. On the other hand, van den Bosch and Gabriel [11], using an age-structured model, have shown that “increasing the cannibalistic pressure decreases the adult and large juvenile population density irrespective of parameter values”.

Cannibalism can have either a stabilizing or a destabilizing effect on the population depending on the model used. Gurtin and Levine [12] studied an age-structured population model where the adults feed on the newborns. They used a McKendric–von Foerster model for the population density \( \rho(a,t) \) – of individuals of age \( a \) at time \( t \) – where the number of live newborns that survive cannibalism, per unit time – \( \rho(0,t) \) – is related to the birth rate \( B(t) \) by \( \rho(0,t) = g(P(t),B(t))B(t) \), where \( P(t) \) is the total population at time \( t \). Thus \( g(P,B) \) is the proportion of newborns that survive cannibalism. If there is no cannibalism, i.e. \( g = 1 \), which is a special case of their model A, then \( P(t) \) will tend to 0, to a positive equilibrium \( P_0 \), or to infinity. Periodic solutions are therefore not possible in the absence of cannibalism. However, with a non-constant \( g \), a periodic solution can exist.

Cannibalism did not have a qualitative effect on the dynamic behaviour of the damselfly model of Crowley et al. [13]. On the other hand, Cushing [14], using a discrete model for the juvenile and adult populations, found that cannibalism can have either a stabilizing effect or a destabilizing effect depending on parameter values. Diekmann et al. [15] found that egg cannibalism can have a destabilizing effect leading to oscillations, Hastings [16] found that cannibalism can give rise to oscillations, but Desharnais and Liu [17], using a discrete matrix model, found that egg and pupal cannibalism by adults is stabilizing, whereas egg cannibalism by larvae leads to oscillations. Thus
whether cannibalism is stabilizing is very much model dependent and it is not easy to draw general conclusions.

It has also been shown that cannibalism can have a stabilizing effect on a predator–prey system. Kohlmeier and Ebenhöhh [8] studied a two-dimensional predator–prey system of a Lotka–Volterra type with predator satiation, where cannibalism is incorporated by letting the total food supply for the predator be a weighted sum of the prey biomass and the predator biomass. They show that cannibalism can stabilize a predator–prey system by eliminating cycles that can otherwise occur in the absence of cannibalism. These cycles are caused by the interaction between prey carrying capacity and predator satiation. Recently, van den Bosch and Gabriel [11] showed that cannibalism can stabilize a predator–prey system where the oscillations are due to age structure. Their model is essentially a system of two differential equations for the adult predator population and the prey population, with delays in the equation for the former. This system can oscillate due to the delays, but the stability region (in a two-dimensional parameter space) is enlarged by increasing the ‘cannibalism pressure’. The results of those two papers lead van den Bosch and Gabriel [11] to conclude that “In predator–prey systems, cannibalism by predators can stabilize both externally generated (consumer-resource) as well as internally generated (age-structure) fluctuations”.

There are, however, exceptions to this rule and in this paper we give an example of a simple predator–prey system where cannibalism can lead to oscillations in a system which is otherwise stable. We will show by analytical and numerical methods that a predator–prey system without cannibalism has a stable equilibrium point, but the introduction of cannibalism lowers the stability and can give rise to a supercritical Hopf bifurcation leading to a stable limit cycle.

2. Description of the model

Most papers on cannibalism use a McKendrick–von Foerster age-structured model [10,12,15] but the model is usually rewritten as a system of ordinary differential equations or in some cases as non-linear Volterra integral equations [15,16]. Kohlmeier and Ebenhöhh [8] used a two-dimensional ODE model without any structure, but van den Bosch and Gabriel [11] used a structured model where the life history of the predator is divided into four stages: small juveniles, vulnerable juveniles, large juveniles and adults. Without cannibalism and a juvenile period the model reduces to a Lotka–Volterra model with logistic prey growth.

The predator–prey system studied in this paper is in some ways a simplification of the system studied by van den Bosch and Gabriel [11]. Two simplifications are made: Firstly, it is assumed that all juveniles are vulnerable to...
predation by the adults and, secondly, that instantaneous maturation into the adult class is proportional to the present juvenile biomass – i.e. a constant per capita rate of maturation – whereas van den Bosch and Gabriel [11] take it to be proportional to the fraction of the juvenile biomass \( \tau \) time units ago which survives to the present, where \( \tau \) is the duration of the juvenile stage. The latter assumption is, of course, the more realistic one, since a constant maturation rate implies that some juveniles can mature instantly. However, making this simplifying assumption means that any oscillations that may occur are not caused by a delay inherent in the system, as in the model of van den Bosch and Gabriel [11].

The present model is a system of three coupled ordinary differential equations, for the three state variables; adult predators, juvenile predator and prey. We will make the following assumptions:

(i) The only population structure in the model lies in the separation into mature and juvenile predators.

(ii) There is only inter-class cannibalism, and no intra-class cannibalism; i.e. adults prey on juveniles, but juveniles do not prey on juveniles, nor adults on adults.

(iii) The per capita rate of maturation is constant, see discussion above.

(iv) The interaction terms are linear, i.e. of the Lotka–Volterra type. One reason for studying a system with such simple interaction terms is that it will be extremely difficult to obtain data to estimate the parameters in a more complicated predation relationship. Data for ecosystems, especially marine ecosystems, are notoriously variable and the best one can hope for is to obtain parameters in linear relationships. This assumption also makes the model more manageable. In any case a Lotka–Volterra type model may be regarded as a local approximation to a more complexly non-linear system.

(v) There is no prey density dependence in the stability analysis of the main equilibrium. This simplification is made in order to make the analysis feasible, since otherwise the algebraic difficulties become too great. However, we will show later that including a density dependence term has no effect on the qualitative behaviour of the system.

A biological rationale for the equations of the model can be given as follows. Let \( X, Y, \) and \( Z \) be the biomasses of adult predators, juvenile predators, and prey, respectively. Consider the adult predator biomass, and consider only the changes due to deaths and individual growth. Since \( X = NW \), where \( N \) is the number of adults and \( w \) is the average individual weight, we have

\[
\frac{dX}{dt} = \frac{dN}{dt}w + \frac{dw}{dt}N = \left( \frac{1}{N} \frac{dN}{dt} + \frac{1}{w} \frac{dw}{dt} \right)X.
\]

If we assume that the mature predators die at a constant per capita rate, \( M_1 \), and that the specific individual growth rate is linearly related to the biomass of the prey and the biomass of the juvenile predators, i.e.
\[ \frac{1}{w} \frac{dw}{dt} = -b_0 + BY + CZ, \]  

where \( b_0, B, \) and \( C \) are constants, then

\[ \frac{dX}{dt} = -M_1 X + (-b_0 + BY + CZ)X = -M_{\text{mat}}X + BXY + CXZ, \]

where \( M_{\text{mat}} = M_1 + b_0. \) Since it is assumed that juveniles are recruited to the adults class at a constant specific rate – which we will denote by \( A \) – the equation governing the adult biomass becomes

\[ \frac{dX}{dt} = -M_{\text{mat}}X + AY + BXY + CXZ. \]

Note that we can also let the adult death rate depend on the juvenile and the prey biomass, i.e.

\[ M_1 = M_{10} - b_1 Y - c_1 Z, \]

for example, and add \( b_1 \) and \( c_1 \) to the parameters \( B \) and \( C \) in Eq. (2). All the parameters in Eqs. (1) and (3) could be estimated by regressing specific individual growth rate and adult mortality rate against the biomasses of juveniles and prey.

The equation for juvenile biomass can be derived in a similar way. Assuming that the specific individual growth rate is a constant, the per capita death rate is \( m_0 + SX \), where \( m_0 \) and \( S \) are constants, and the birth rate is proportional to the adult biomass, the equation for the juvenile biomass becomes

\[ \frac{dY}{dt} = RX - AY - M_{\text{juv}} Y - SXY, \]

where \( M_{\text{juv}} = m_0 - h \), where \( h \) is the growth rate of individuals. Again, all parameters can be estimated from growth, mortality and biomass data. Note that it is possible that \( M_{\text{juv}} < 0 \). However, since the juvenile population must disappear if there are no births \( (X = 0) \), necessarily \( A + M_{\text{juv}} > 0 \), which we will take for granted throughout.

Finally, assuming that the birth rate of prey is \( tZ \), the specific growth rate \( s_0 - s_1 Z \), and the per capita death rate \( v_0 + v_1 Z + VX \), we get the equation for the prey

\[ \frac{dZ}{dt} = TZ - UZ^2 - VXZ, \]

where \( T = t + s_0 - v_0 \) and \( U = s_1 + v_1. \) Note that \( T \) must be greater than zero.

Collecting the three equations together, we have the full model

\[ \begin{align*}
\frac{dX}{dt} &= -M_{\text{mat}}X + AY + BXY + CXZ, \\
\frac{dY}{dt} &= RX - AY - M_{\text{juv}} Y - SXY, \\
\frac{dZ}{dt} &= TZ - UZ^2 - VXZ.
\end{align*} \]
If the components are harvested, the rates $M_{\text{mat}}$, $M_{\text{juv}}$, and $T$ will include a harvesting mortality term, $F_{\text{mat}}$, $F_{\text{juv}}$, and $F_{\text{prey}}$, respectively (with a negative sign in the case of the prey). We can introduce density dependence in the predator birth rate by letting the birth rate decrease with increasing juvenile biomass, i.e. $(R - S_{1}Y)X$. Thus a high juvenile density will inhibit reproduction (for example due to egg-eating by juveniles). The term $S_{1}XY$ can be incorporated into the term $SXY$. The interaction term between adult and juvenile predators in the equation governing the juvenile biomass can therefore be regarded as being composed of two terms, i.e. $SXY = S_{1}XY + S_{2}XY$. The first term describes the density dependence in birth rate and the second the effect of cannibalism on the juvenile stock. Thus $S_{2}$ is the cannibalism attack rate and therefore the interaction parameter in the differential equation for $X$ can be written as $B = \gamma S_{2}$, where $\gamma$ is the conversion efficiency of eaten juveniles into adult biomass. The aim of this paper is to investigate how the stability properties change with changing level of cannibalism, as defined by the cannibalism attack rate. In order not to confuse this issue, we will take $S_{1} = 0$, and thus let $S$ denote the cannibalism attack rate, and put $B = \gamma S$.

In order to reduce the number of parameters, we will non-dimensionalize the variables by putting

$$x = X/L, \quad y = Y/N, \quad z = Z/P, \quad \tau = M_{\text{mat}}t,$$

where $L = M_{\text{mat}}/S$, $N = M_{\text{mat}}^{2}/(SA)$, and $P = M_{\text{mat}}/C$. The new dimensionless system becomes

$$\frac{dx}{d\tau} = -x + y + axy + xz,$$

$$\frac{dy}{d\tau} = bx - gy - xy,$$

$$\frac{dz}{d\tau} = sz - rz^{2} - vxz,$$

where $a = BM_{\text{mat}}/(SA) = \gamma M_{\text{mat}}/A$, $b = RA/M_{\text{mat}}^{2}$, $g = (A + M_{\text{juv}})/M_{\text{mat}}$, $s = T/M_{\text{mat}}$, $r = U/C$, and $v = V/S$.

The objective is to investigate the changes in the qualitative dynamical behaviour of this predator–prey system when the level of cannibalism is varied, and in particular the possibility of oscillations arising. We will therefore consider the changes which take place as the cannibalism attack rate, $S$, varies. The only parameter in system (7) which depends on $S$ is $v$, which is inversely related to $S$.

The state space for (7) is the positive octant, $\{(x,y,z): x \geq 0, y \geq 0, z \geq 0\}$, which is clearly an invariant set for the system of differential equations since $dx/d\tau > 0$ in the $yz$-plane, and similarly $dy/dt > 0$ and $dz/dt \geq 0$ in the $yz$- and
xy-planes respectively. For later reference this system of equations (7) will be written in vector notation as

$$\frac{dX}{dt} = F(X)$$

where $X = (x, y, z)'$.

3. Equilibrium and stability analysis

The system of ordinary differential equations, (7), can have four equilibria. There is one, $(x_1, y_1, z_1)$, in the interior of the positive octant and three on the boundary, i.e. $(0, 0, 0)$, $(0, 0, K)$, where $K = slr$ is the carrying capacity of the prey species, and $(x_0, y_0, 0)$. It is easy to see that the equilibrium with no prey, $(x_0, y_0, 0)$, is positive and stable under perturbations in the predator plane if and only if $g < b < 1/a$, and unstable with respect to perturbations with a positive z-component if and only if $b < g + s(1 - ag)/(v + as)$. Furthermore, using the Bendixson–Dulac criterion, it follows easily that there are no periodic solutions in the predator plane. Thus, the presence of non-zero prey is necessary for sustained oscillations. Finally, $(0, 0, 0)$ is unstable under perturbations into the positive octant, and $(0, 0, K)$ also, provided $K > 1$.

It is a common feature of predator–prey models that the prey can exist in a stable state in the absence of the predator, but in this model, the predator can persist in the absence of the prey, which means that it is only partially coupled to the prey [18]. This implies of course that the predator has an alternative food source (which is not modelled explicitly), although the prey species in the model may be the preferred food.

The equilibria on the boundary are of limited interest here, and we will concentrate on the interior equilibrium $(x_1, y_1, z_1)$.

3.1. Equilibrium

We consider the existence of an equilibrium in the interior, i.e. $(x_1, y_1, z_1)$, where all components are non-zero. We then have to solve the set of equations:

$$-x + y + axy + xz = 0, \quad bx - gy - xy = 0, \quad sz - rz^2 - vxz = 0. \quad (8)$$

In order to study the stability properties of $(x_1, y_1, z_1)$, we will make the simplifying assumption that there is no density dependence on the prey, i.e. $r = 0$. This is done purely in order to make the algebra manageable. We will see later that the existence and stability properties of $(x_1, y_1, z_1)$ remain unchanged for small $r$. 
When \( r = 0 \), the equilibrium is given by
\[
\begin{align*}
    x_1 &= \frac{s}{v}, \\
    y_1 &= \frac{bs}{gv+s}, \\
    z_1 &= \frac{v(g-b) + s(1-ab)}{gv+s}.
\end{align*}
\]
(9)

Note that \( z_1 > 0 \), if \( g > b \) and \( 1 > ab \); alternatively, \( z_1 > 0 \) is equivalent to \( b < g + s(1-ag)/(v+as) \).

3.2. Stability analysis when \( r = 0 \)

The Jacobian matrix of \( F \) about \((x_1,y_1,z_1)\), is
\[
F'(x_1,y_1,z_1) = \begin{pmatrix}
-1 + ay_1 + z_1 & 1 + ax_1 & x_1 \\
     b - y_1 & -(g + x_1) & 0 \\
    -vz_1 & 0 & 0
\end{pmatrix}.
\]
(10)

The characteristic equation is
\[
\lambda^3 + A\lambda^2 + B\lambda + C = 0,
\]
where
\[
A = g + x_1 + 1 - ay_1 - z_1 = g + x_1 + \frac{y_1}{x_1}, \quad B = sz_1 + \frac{bs(1-ag)}{gv+s},
\]
\[
C = v(g + x_1)x_1z_1 = (gv + s)x_1z_1,
\]

It follows from the Routh–Hurwitz stability criteria that all the eigenvalues have negative real part if
\[
A > 0, \quad C > 0, \quad AB - C > 0.
\]
(12)

It is obvious that the first two conditions are always satisfied. Furthermore
\[
AB - C = b(sz_1 + \left(\frac{gv+s}{v} + \frac{bv}{gv+s}\right) \frac{bs}{gv+s} (1-ag))
\]
(13)

The third condition in (12) is therefore satisfied if \( ag < 1 \). Thus \((x_1,y_1,z_1)\) is asymptotically stable if \( ag < 1 \). Therefore, if the equilibrium point is to lose stability as cannibalism increases, necessarily, \( ag > 1 \).

We will now consider how the stability of \((x_1,y_1,z_1)\) changes with the level of cannibalism, as defined by the attack rate \( S \). Recall that \( v \) is the only parameter which depends on \( S \) and that \( v = V/S \). We assume that \( ag > 1 \).

Consider the first case when there is no cannibalism, i.e. \( S = 0 \) and hence \( v \to \infty \). Then \( z_1 \to 1 - bg \), as \( v \to \infty \), and for a positive equilibrium we require \( b < g \). Now, if \( v \to \infty \), it follows that \( AB - C \to bs(1-b/g)/g > 0 \) and \((x_1,y_1,z_1)\) is therefore asymptotically stable when there is no cannibalism.

On the other hand, as \( S \) increases and hence \( v \to 0 \), we get \( z_1 \to 1 - ab \), and for a positive equilibrium we require \( ab < 1 \). As \( v \to 0 \), \( AB - C \sim bs/v(1-ag) < 0 \), provided \( ag > 1 \) which we have assumed.
We have therefore shown that \( AB - C \) is positive for \( S = 0 \) (no cannibalism) and negative for sufficiently large \( S \). Denote the value of \( S \) for which \( AB - C = 0 \), by \( S^* \). For the equilibrium to be positive and lose stability as \( S \) increases, we require

\[
b < g, \quad ab < 1, \quad \text{and} \quad ag > 1.
\]

The first inequality is superfluous and in terms of the original parameters the remaining two become

\[
0 < \frac{R}{M_{\text{mat}}} < \frac{1}{\gamma} < 1 + \frac{M_{\text{juv}}}{A}.
\]

In order to investigate the nature of the equilibrium point \((x_1, y_1, z_1)\), we note that

\[
\det F'(x_1, y_1, z_1) = -w_1z_1(g + x_1).
\]

This determinant is always negative as long as the equilibrium is positive. This means that zero is never an eigenvalue of \( F'(x_1, y_1, z_1) \) and therefore the only way whereby \((x_1, y_1, z_1)\) can become unstable (as \( S \) passes through \( S^* \)) is for a pair of complex eigenvalues to cross the imaginary axis from the left half plane into the right half plane. The real eigenvalue is always negative. Thus we can conclude that for \( S < S^* \), \((x_1, y_1, z_1)\) is a stable spiral point, but as \( S \) passes through \( S^* \), a Hopf bifurcation occurs. Hence \( S^* \) will be called the bifurcation value.

For a Hopf bifurcation from a stable positive equilibrium to be possible, (15) must hold. This means the birth and recruitment rates \((R \text{ and } A)\) must be low compared to the mortality rates \((M_{\text{mat}} \text{ and } M_{\text{juv}})\). The positive equilibrium is stable when there is no cannibalism. The stability is preserved – the equilibrium point is a stable spiral point – with low levels of cannibalism, but loss of stability occurs if the level is sufficiently high. Thus cannibalism is destabilizing in this particular predator–prey model.

### 3.3. Equilibrium and stability for non-zero \( r \)

We will now consider the existence and stability properties of the equilibrium \((x_1, y_1, z_1)\) when \( r \) is non-zero. This will be done indirectly via the Implicit Function Theorem. Let the parameters \( r \) and \( S \) be variable; then the equilibrium condition is

\[
F(r, S, X) = 0
\]

where \( X = (x, y, z) \) and the vector field \( F \) depends on the parameters \( r \) and \( S \). For \( r = 0 \),

\[
F(0, S, X_1(S)) = 0
\]
where $X_1(S) = (x_1,y_1,z_1)$ is the equilibrium corresponding to $r = 0$, as a function of the cannibalism parameter. We have seen that $X_1(S)$ exists and is positive. The Jacobian matrix of $F$ with respect to $X$, evaluated at $r = 0$, $S$, and $X_1(S)$, $F'(0,S,X_1(S))$, is non-singular since $\lambda = 0$ is not an eigenvalue as was demonstrated above. It then follows from the Implicit Function Theorem that for each $S$, there exists a continuous function of $r$, $X_1(r,S)$ (which is also a continuous function of $S$) in a neighbourhood of $r = 0$, such that $F(r,S,X_1(r,S)) = 0$. Since $X_1(0,S)$ is positive, $X_1(r,S)$ is also positive for $r$ in a neighbourhood of $r = 0$. Thus, for each $S$, there exists an $r(S)$, such that a positive equilibrium $X_1(r,S)$ exists for $r < r(S)$. Choose $S_1$ and $S_2$ on either side of $S^*$ and put

$$r_0 = \inf_{S\in[S_1,S_2]} r(S).$$

Since $r(S)$ depends continuously on $S$, and the infimum is over a closed bounded interval, it follows that $r_0 > 0$.

Since $X_1$ is a continuous function of $r$, and $F$ a continuous function of $X_1$ it follows that the eigenvalues vary continuously with $r$. Now let $r_1$ be sufficiently small such that for $r < r_1$, $F'(r,S_1,X_1(r,S_1))$ has a complex pair of eigenvalues with negative real parts and one real negative eigenvalue (like $F'(0,S_1,X_1(0,S_1))$). Similarly, let $r_2$ be sufficiently small such that for $r < r_2$, $F'(r,S_2,X_1(r,S_2))$ has a complex pair of eigenvalues with positive real parts and one real negative eigenvalue (like $F'(0,S_2,X_1(0,S_2))$). Finally, put $r^* = \min \{r_0, r_1, r_2\}$ and fix $r < r^*$. Then, a positive equilibrium for (7) exists for all $S \in [S_1, S_2]$. For $S = S_1$, the real parts of the eigenvalues of the Jacobian matrix $F'(r,S_1,X_1(r,S_1))$ are negative. For $S = S_2$, the Jacobian matrix $F'(r,S_2,X_1(r,S_2))$ has two eigenvalues with positive real parts and one negative eigenvalue. Since the eigenvalues of $F'(0,S,X_1(0,S))$ are never zero, the same applies to $F'(r,S,X_1(r,S))$ for small $r$. Thus, as $S$ varies from $S_1$ to $S_2$, two complex eigenvalues must cross the imaginary axis from the left half complex plane into the right half plane, i.e. a Hopf bifurcation occurs.

We can therefore conclude, that – at least for small $r$ (i.e. large $K$) – as the cannibalism parameter is increased, the stable positive spiral point of (7) becomes unstable via a Hopf bifurcation.

### 3.4. Numerical examples

We have seen that as $S$ passes through $S^*$, a Hopf bifurcation takes place. In order to determine that the bifurcation gives rise to a stable limit cycle, i.e. is supercritical, rather than subcritical, we present two numerical examples. The parameter values in the examples have no real biological basis, but are chosen simply to illustrate the loss of stability as the level of cannibalism increases.

(a) $a = 1.15$, $b = 0.8$, $g = 1$, $s = 1$, $r = 0.1$, $v = 1.5$. 
In this case \((x_1, y_1, z_1) = (0.66, 0.32, 0.15)\) is a stable spiral point (Fig. 1).

(b) Same parameter values as (a), except \(v = 0.9\). Since \(v = V/S\), this means that the level of cannibalism, as defined by \(S\), is higher than in the previous example.

The equilibrium \((x_1, y_1, z_1) = (1.10, 0.42, 0.14)\) is now an unstable spiral point (Fig. 2). One of the trajectories shown in Fig. 2 is of increasing amplitude and the other of decreasing amplitude, indicating that there is a stable limit cycle for this system. The Hopf bifurcation is therefore super-critical.

The figures also indicate that there is a two-dimensional manifold which is an attracting set and that this manifold is close to being perpendicular to the \(x\)–\(y\) plane. The trajectories tend very rapidly to this set. Furthermore, the oscillations in \(y\) are much smaller than the \(x\) and \(z\) oscillations.

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**Fig. 1.** Phase-space portrait and trajectories of \(x, y,\) and \(z\) as functions of time for low levels of cannibalism. The equilibrium \(P_1 = (x_1, y_1, z_1)\) is a stable spiral point. See main text for parameter values.
4. Summary and discussion

Under certain conditions on the parameters in the predator–prey model (7), the following equilibria and stability configuration exists in the state space \(\{(x,y,z): x \geq 0, y \geq 0, z \geq 0\}\):

(a) A stable equilibrium \(P_1 = (x_1,y_1,z_1)\) exists in the interior of the state space (i.e. all population sizes are non-zero).

(b) The equilibrium \((0,0,0)\) is unstable with respect to all perturbations into the state space.

(c) The equilibrium \((0,0,K)\), where \(K = s/l\), is stable with respect to perturbations along the \(z\)-axis, but unstable with respect to perturbations into the interior of the state space.

(d) An equilibrium \(P_0 = (x_0,y_0,0)\) exists in the predator plane \((x,y)\) plane which is stable under perturbations in the predator plane, but unstable under perturbations into the interior of the state space.

Fig. 2. Phase-space portrait and trajectories of \(x, y,\) and \(z\) as functions of time for high levels of cannibalism. The equilibrium \(P_1 = (x_1,y_1,z_1)\) is unstable. Two trajectories are shown, one with increasing and the other with decreasing amplitude.
This is the natural configuration to expect for a predator–prey system which is only partially coupled, i.e. both predator and prey can exist in the absence of the other, but can also co-exist. It is assumed here that the density dependence parameter, $r$, in the equation for the prey, is ‘small’. The other parameter conditions which guarantee this configuration are the following:

$$g < b < 1/a \quad \text{and} \quad b < g + \frac{s(1-ag)}{v+as}$$

Note that the second condition is necessary and sufficient for a positive $z_1$ as well as for instability of $P_0$ in the $z$-direction. The equilibrium point $P_1$ is positive and asymptotically stable as long as this condition holds and $ag < 1$. The stability of $P_1$ is not affected by changes in the level of cannibalism, as defined by the parameter $S$ in Eq. (6).

On the other hand if $ag > 1$, then a Hopf bifurcation is possible. The point $P_1 = (x_1,y_1,z_1)$ is a stable spiral point for low levels of cannibalism, but as $S$ increases past the bifurcation value $S^*$, $P_1$ loses stability through a Hopf bifurcation. Numerical studies indicate that the bifurcation is supercritical, i.e. a stable limit cycle appears.

In terms of the original parameters the condition $ag > 1$, is $\gamma(1 + M_{juv}/A) > 1$. Thus, high juvenile mortality and/or low recruitment rate, together with high conversion efficiency (but $\gamma < 1$), is necessary for the bifurcation to occur. In addition, $z_1$ must remain positive as $S$ increases. The condition for this (and $ag > 1$) is (15), which implies that the birth and recruitment rates must be low compared to the mortality rates.

Loss of stability is therefore not possible without high juvenile mortality and low recruitment rate. For the Atlantic cod discussed in the Introduction, the mortality rate for juveniles is likely to be high, in particular under harvesting, and the age at maturation of 6–7 years is high. Thus, only a small portion of the total juvenile population will be recruited in any given year and the recruitment rate to the mature population is therefore probably fairly low. The necessary condition for stability (i.e. $ag > 1$) is thus likely to be satisfied for the cannibalistic predator–prey system consisting of Atlantic cod and capelin (Mallotus villosus) which is its main prey species. No estimates exist of the mortality rates due to cannibalism, nor of the other interaction parameters, and it is therefore not possible at this stage to draw any conclusions whether cannibalism might contribute to the fluctuations that characterize the dynamics of the stocks of cod and capelin in the Atlantic. Both stocks are heavily harvested, also at the juvenile stage in the case of cod. It is therefore worth noting that harvesting juvenile fish will make loss of stability more likely, since not only does harvesting increase $M_{juv}$, but it also decreases $A$ since a smaller fraction of the total juvenile population will survive to reach the age of maturity.
The main result in this paper is that sustained oscillations are not possible for low levels of cannibalism, but for sufficiently high levels, oscillations can set in. For this particular predator–prey model it has therefore been demonstrated that cannibalism can be a destabilizing force. This is in contradiction to the results of Kohlmeier and Ebenhöh [8] and van den Bosch and Gabriel [11]. We will therefore briefly consider the differences between those models and the one in this paper.

It is an implicit assumption in this model that the predator has alternative prey and can therefore persist in the absence of the modelled prey. This is not the case for the other models. However, if the parameter values in (7) are such that this persistence is possible, then a loss of stability via a Hopf bifurcation is excluded. Therefore this feature in itself does not cause oscillations. This can also be seen by considering a simple predator–prey system with logistic growth for both species and Lotka–Volterra type interaction terms. Both species can persist in the absence of the other, but oscillations are not possible.

The predator–prey model of Kohlmeier and Ebenhöh [8] has no structure, i.e. the predator is not separated into juveniles and adults. Thus, they are not modelling adults preying on juveniles, but the predator feeding on itself. All individuals are vulnerable to cannibalism, and all indulge in cannibalism. On the other hand, the model of van den Bosch and Gabriel [11] is fully age structured, and cannibalism manifests itself as adults preying on juveniles of a certain age (a vulnerable class). However, the only effect of cannibalism is additional mortality on the vulnerable class of juveniles. The consumption of juveniles does not influence the growth rates of adults, as is the case in the model discussed here. This is equivalent to setting $\gamma = 0$ in the present model, which makes a Hopf bifurcation impossible.

It can therefore be postulated that the following features – all of which characterize this model – are necessary for cannibalism to be destabilizing:

(i) Predator population is separated into adults and juveniles, with adults feeding on juveniles, i.e. only inter-class cannibalism.
(ii) Low recruitment rates to the adult population, for example, due to a high age at maturity, and/or high mortality of juveniles.
(iii) Cannibalism leads to increased growth rates of adults as well as increased mortality rates of juveniles.

Other factors can also play a role and in view of the results of this paper and those of Kohlmeier and Ebenhöh and van den Bosch and Gabriel, it would seem that the effects of cannibalism on the stability properties of predator–prey systems are not straightforward, and that it is not possible to draw general conclusions whether it is a stabilizing or destabilizing force.
References