

A DOMINANT PREDATOR, A PREDATOR, AND A PREY

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ABSTRACT. A two-predator, one-prey model in which one predator interferes significantly with the other predator is analyzed. The dominant predator is harvested and the other predator has an alternative food source. The response functions used are Holling type II and they are predator-dependent and include the effects of interference. The analysis centers on bifurcation diagrams for various levels of interference in which the harvesting is the primary bifurcation parameter. There are different attractors for the high-interference and no-interference cases and these are discussed within an ecological context.

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1. Introduction. In this paper, a two-predator, one-prey model in which one predator interferes with the other predator is analyzed. The model includes harvesting of the dominant predator and an alternative food source for the second predator. The analysis of the dynamics centers on bifurcation diagrams in which harvesting is varied for different levels of interference.

Holling type II-like response functions are developed using time-budget arguments which incorporate the interference of the dominant predator on the second predator and a factor for the self-interference of the second predator; i.e., a predator-dependent response function. Kuang and collaborators incorporated interference competition and showed how it could account for the stable coexistence of the predators [13]. Beddington and DeAngelis ([3], [8]) introduced predator dependence into the response functions, and many studies have since indicated that adjusting the typical Holling response types to include predator dependence is more reflective of actual predator-prey systems ([1] [2] [5] [17] [18] [20]).

The problem studied here bears some significant resemblance to the work of Courchamp and Kuang (and their respective collaborators) in that there are two predators and a shared prey ([6] [7] [12]). However, in their work, one of the predators (the superpredator) preys on the other predator (the mesopredator) rather than merely interfering with it. They were concerned with how the introduction or elimination of a mesopredator or superpredator would affect the population size of a desirable prey.

A motivation for studying this problem is to be another voice in helping to understand the reasons for the depletion of cod in the North Atlantic. Cod is a highly effective predator and, when stocks are healthy, effectively interferes with its

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competitors (skates, rays) for its food [14]. Wikan and Eide considered the effects of cannibalism and recruitment on the cod stock dynamics, whereas the approach in this paper is to study the ecosystem dynamics using a predator prey framework [21].

The paper begins with a derivation of model equations using time-budget arguments which incorporate harvesting of the dominant predator, an interference factor for the dominant predator on the second predator, self-interference in the second predator, and an alternative food source for the second predator. An analysis of the steady states and their stability follows, with particular attention given to the levels of harvesting and interference on the coexistence of the three species. Since the parameter relationships are rather entangled, the bifurcation analysis is primarily illustrated with the use of AUTO ([9], [10]).

2. Derivation of the model. The model for the prey growth will be logistic, its response to the predators will be Holling type II, and both predators will have a corresponding response function. The denominators of the response functions will be larger due to the interference factors, thus properly reflecting the mitigation of biomass transfer with increased interference.

The form of the functional responses follow from classical arguments for the time budgets in Holling-type responses ([11], [3]). The adaptations of the Holling type II functional response term to include multiple prey types follow from time-budget analyses and are shown in [4] [15] [16] [19]. The derivation here closely resembles that shown in [12].

We first denote the prey, dominant predator, and second predator by $X(t)$, $Y(t)$, and $Z(t)$, respectively. Let T denote the total time that Z needs to gather food from X and an alternative food source S (which is assumed to be constant in time). This total time has five components:

- T_Z : The time spent by Z searching for X and S
- T_{ZhX} : The time spent by Z handling X
- T_{ZhS} : The time spent by Z handling S
- T_{YZ} : The time wasted by Z due to interference with Y
- T_{ZZ} : The time wasted by Z due to self-interference.

Each of the last four time components can be expressed in terms of T_Z . To do so, we introduce the following intermediate parameters:

- N_{ZX} : The total number of X caught per Z , which can be expressed as $N_{ZX} = \alpha_{ZX}T_ZX$ where α_{ZX} is the search efficiency of Z for X
- N_{ZS} : The total number of S caught per Z , which can be expressed as $N_{ZS} = \alpha_{ZS}T_ZS$ where α_{ZS} is the search efficiency of Z for S
- N_{YZ} : The number of encounters with Y per Z , which can be expressed as $N_{YZ} = \alpha_{YZ}T_ZY$ where α_{YZ} is the encounter rate of Y and Z
- N_{ZZ} : The number of encounters with Z per Z , which can be expressed as $N_{ZZ} = \alpha_{ZZ}T_Z(Z - 1)$ where α_{ZZ} is the encounter rate of Z with itself.

With these intermediate parameters, the time components are given by

$$T_{ZhX} = t_{ZhX}N_{ZX}, \quad T_{ZhS} = t_{ZhS}N_{ZS}, \quad T_{YZ} = t_{YZ}N_{YZ}, \quad T_{ZZ} = t_{ZZ}N_{ZZ}$$

where the small t parameters denote average handling times in the first two cases and average encounter rates in the latter two cases. With all these definitions, the

total time T is given by

$$T = T_Z + T_{ZhX} + T_{ZhS} + T_{YZ} + T_{ZZ},$$

so that

$$T = T_Z(1 + t_{zhX}\alpha_{ZX}X + t_{zhS}\alpha_{ZS}S + t_{YZ}\alpha_{YZ}Y + t_{ZZ}\alpha_{ZZ}(Z - 1)).$$

With this, the functional response of X to Z , meaning the number of X caught per Z per time, is given by

$$N_{ZX}/T = \alpha_{ZX}X/F(X, Y, S, Z)$$

in which

$$F(X, Y, Z, S) = (1 + t_{zhX}\alpha_{ZX}X + t_{zhS}\alpha_{ZS}S + t_{YZ}\alpha_{YZ}Y + t_{ZZ}\alpha_{ZZ}(Z - 1)).$$

Similar parameter definitions and analyses give us the functional response of S to Z :

$$N_{ZS}/T = e_{ZS}\alpha_{ZS}S/F(X, Y, S, Z)$$

in which e_{ZS} is the efficiency of conversion rate of the biomass of S to Z .

The response of X to Y is given by:

$$\alpha_{YX}X/G(X, Y) \text{ in which } G(X, Y) = (1 + t_{YhX}\alpha_{YX}X + t_{YY}\alpha_{YY}(Y - 1))$$

with the obvious counterpart definitions. It is assumed here that the interference factor of Y on Z does not cause a reciprocating time delay when Y searches for its prey X . This would be the case of a lion (Y) essentially not being bothered by the presence of jackals (Z), whereas jackals would be significantly inhibited by the presence of lions (but are also generally not the prey of lions).

2.1. The unscaled equations. For the prey equation, we assume that the prey would grow logistically in the absence of predators with growth rate r and carrying capacity K . Also, the predators would die out in the absence of prey with death rates D_Y and D_Z . Incorporating the response functions, the equations for $X(t)$, $Y(t)$, and $Z(t)$ are:

$$\begin{aligned} \frac{dX}{dt} &= rX\left(1 - \frac{X}{K}\right) - \frac{\alpha_{YX}XY}{G(X, Y)} - \frac{\alpha_{ZX}XZ}{F(X, Y, Z, S)}, \\ \frac{dY}{dt} &= -D_Y Y + \frac{E_{YX}\alpha_{YX}XY}{G(X, Y)} - HY, \\ \frac{dZ}{dt} &= -D_Z Z + \frac{E_{ZX}\alpha_{ZX}XZ}{F(X, Y, Z, S)} + \frac{E_{ZS}\alpha_{ZS}XS}{F(X, Y, Z, S)}. \end{aligned} \tag{1}$$

In these equations, the terms E_{YX} , E_{ZX} , and E_{ZS} are the efficiency of biomass conversion rates. It is assumed that there is proportional harvesting of the dominant predator. The HY term could of course have been absorbed into the death-rate term, but it is kept separate, since the impact of harvesting of the dominant predator is being studied.

Before proceeding with the analysis, some scaling needs to take place so as to be better able to discern how the parameters affect the dynamics. To this end, the variables are scaled as,

$$x = \frac{X}{K}, \quad y = \frac{Y}{rKt_{YhX}}, \quad z = \frac{Z}{rKt_{ZhX}}, \quad t_{new} = r t_{old},$$

and the other parameters are made dimensionless, as follows:

$$s = \frac{S}{K}, a_{yx} = Kt_{YhX}\alpha_{YX}, a_{zx} = Kt_{ZhX}\alpha_{ZX}, a_{zs} = Kt_{ZhS}\alpha_{ZS}, a_{yz} = Kt_{YZ}\alpha_{YZ},$$

$$a_{zz} = Krt_{ZZ}t_{ZhX}\alpha_{ZZ}, a_{yy} = Krt_{YY}t_{YhX}\alpha_{YY}, b = t_{YY}\alpha_{YY}, c = t_{ZZ}\alpha_{ZZ}, h = \frac{H}{r}$$

$$\text{and } e_{yx} = \frac{E_{YX}}{t_{YhX}}, e_{zx} = \frac{E_{ZX}}{t_{ZhX}}, e_{zs} = \frac{E_{ZS}}{t_{ZhS}}, d_y = \frac{D_Y}{r}, d_z = \frac{D_Z}{r}.$$

2.2. The working equations. With these changes substituted into (1), we get the following working equations:

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{a_{yx}xy}{g(x,y)} - \frac{a_{zx}xz}{f(x,y,z,s)}, \\ \frac{dy}{dt} &= -d_yy + \frac{e_{yx}a_{yx}xy}{g(x,y)} - hy, \\ \frac{dz}{dt} &= -d_zz + \frac{e_{zx}a_{zx}xz}{f(x,y,z,s)} + \frac{e_{zs}a_{zs}sz}{f(x,y,z,s)}, \end{aligned} \quad (2)$$

in which $f(x,y,z,s)$ and $g(x,y)$ are given by:

$$f(x,y,z,s) = 1 + a_{zx}x + a_{yz}y + a_{zs}s + a_{zz}z - c \quad \text{and} \quad g(x,y) = 1 + a_{yx}x + a_{yy}y - b. \quad (3)$$

A word on the parameters is now in order. The primary purpose of this paper is to see how two effects, the level of interference (a_{yz}) of the dominant predator upon the second predator and the harvesting (h) of the dominant predator, influence the dynamics of the system. To better focus on these (by making the analysis cleaner), it will be assumed that there is no self-interference within the dominant predator, implying that $a_{yy} = b = 0$. It will be assumed that there is some secondary predator self-interference, however, so that $a_{zz} \neq 0$. It can be assumed that $c = 0$, since a further rescaling of all parameters of the form a_{**} by a factor of $(1-c)$ would effectively eliminate c . Importantly, it will further be assumed that a_{yx} is significantly larger than a_{zx} reflecting the better capability of the dominant predator to capture the shared prey.

3. Steady states and stability. The first step in the bifurcation analysis is to find the steady states. The equations (2) admit solutions that are naturally conjectured. There is an all-trivial steady state, a steady state in which z subsists alone on its alternative food source s , and a steady state with the prey population at its carrying capacity ($x = 1$) and no predators. There are two two-species steady states with the prey and only one nonzero predator, and finally there is a steady state with all three populations coexisting. For any given steady state, the local stability and conditions for bifurcations can be determined by finding the corresponding eigenvalues of the system (2) linearized about the steady state. Please note that the algebraic details are often quite messy and, when they are, they are not shown.

3.1. The trivial steady state and single-species steady states. The trivial steady state, $(x, y, z) = (0, 0, 0)$, can easily be shown to be unstable since one of the eigenvalues is always 1, independent of the other parameters.

The eigenvalues of the linearized system about the prey-only $(x, y, z) = (1, 0, 0)$ steady state are,

$$-1, \frac{e_{yx}a_{yx}}{1+a_{yx}} - (d_y + h), \text{ and } \frac{e_{zx}a_{zx} + e_{zs}a_{zs}s}{1+a_{zx}+a_{zs}s} - d_z.$$

To be stable, all the eigenvalues must be negative, and this will occur when there is a sufficiently large death rate d_z of the predator z and relatively large death and harvest rate $d_y + h$ of the predator y . This makes sense ecologically since the high death rates mean that the two predators wouldn't be able to survive.

There is a steady state in which the subdominant predator z persists by itself with zero populations for both the prey x and dominant predator y . This steady state is given by

$$z = \frac{(e_{zs} - d_z)a_{zs}s - d_z}{a_{zz}d_z}, \quad x = 0, \quad y = 0.$$

This steady z value will be positive when $(a_{zs}s > d_z/(e_{zs} - d_z))$, a condition which means that z 's alternative food supply, s , is large enough.

3.2. Two-species steady states. There are two steady states in which the prey coexists with only one of the predators.

3.2.1. The xy steady state. The dominant predator/prey steady state is given by:

$$x = \frac{d_y + h}{a_{yx}(e_{yx} - d_y - h)}, \quad y = \frac{(1-x)(1+a_{yx}x)}{a_{yx}}, \quad z = 0. \quad (4)$$

A few simple observations are in order. For x to be positive, the combined death and harvest rate, $d_y + h$, cannot exceed e_{yx} , the efficiency at which y converts x into y biomass. Furthermore, y being positive requires that x must be less than 1 and both of the conditions imply that

$$d_y + h < \frac{a_{yx}}{1+a_{yx}}e_{yx}.$$

The stability of the steady state (4) is determined by linearizing equations (2) about the steady state. The resulting characteristic equation for the eigenvalues λ is of the form,

$$(\lambda - D)(\lambda^2 - A\lambda - BC) = 0, \quad (5)$$

in which

$$A = \frac{(d_y + h)[(a_{yx} - 1)e_{yx} - (d_y + h)(a_{yx} + 1)]}{e_{yx}a_{yx}(e_{yx} - (d_y + h))}.$$

The stability, of course, depends on the sign of D and the roots of the quadratic term. The algebra is messy, but it can be seen that $BC < 0$ (when $x, y > 0$) and A can be either positive or negative. A Hopf bifurcation occurs when $A = 0$, and this readily translates into

$$d_y + h = \frac{(a_{yx} - 1)e_{yx}}{a_{yx} + 1}. \quad (6)$$

Noting the sign of A , the steady state will be unstable if $d_y + h > \frac{(a_{yx} - 1)e_{yx}}{1 + a_{yx}}$, which makes sense, since the death and harvest rate of the predator y would simply be too large to sustain the y population. The steady state may be stable if

$d_y + h < \frac{(a_{yx}-1)e_{yx}}{1+a_{yx}}$. However, determining the conditions for stability in general is more difficult, since D is a complicated expression of the parameters. Nonetheless, it is evident from considering D that this steady state will be stable when, by and large, one of the following conditions prevail (all of which make ecological sense):

- the death rate d_z of predator z is large enough,
- the interference rate, a_{yz} , of the dominant predator y on the second predator z is large enough, or
- the rate, a_{zx} , at which z effectively searches for x is not too high.

3.2.2. *The xz steady state.* The steady state in which there is no dominant predator is given by

$$y = 0, \quad x = \frac{d_z(1 + a_{zz}z) - (e_{zs} - d_z)a_{zs}s}{a_{zx}(e_{zx} - d_z)}, \quad z = \frac{(1 - x)(1 + a_{zs}s + a_{zx}x)}{a_{zx} + a_{zz}(x - 1)}. \quad (7)$$

There are no clean conditions for the overall stability of this steady state since the characteristic equation of the linearized system is algebraically complicated. A detailed numerical investigation in parameter space would need to be done to thoroughly analyze the stability, but that would not lead to any readily useful ecological insights. However, as it turns out, one eigenvalue is

$$\frac{e_{yx}a_{yx}x}{1 + a_{yx}x} - (d_y + h),$$

which implies that this steady state will be stable (as long as then other two eigenvalues have negative real parts) when the death and harvest rate $d_y + h$ of the predator y is sufficiently large. This could have been conjectured on ecological grounds, but the more interesting case occurs when the dominant predator is nonzero, which can occur when $d_y + h$ is not too big. This is the subject of the next section.

3.3. **The three-species steady state.** The coexistence of the three species is the most interesting situation and the most difficult to examine. However, keeping in mind the goals of determining how the dynamics of the system depend on the harvest rate h and the level of interference a_{yz} of the dominant predator on the secondary predator, some very useful insights can be obtained with AUTO ([9], [10]).

The steady-state value for the prey x is given by

$$x = \frac{d_y + h}{a_{yx}(e_{yx} - d_y - h)}. \quad (8)$$

It naturally increases as the predator harvesting rate increases, but decreases as the search efficiency, a_{yx} , of y for x increases. The steady state values of y and z are quite parametrically entangled. They are given implicitly as solutions to the equations,

$$1 - x - \frac{a_{yx}y}{g(x, y)} - \frac{a_{zx}z}{f(x, y, z, s)} = 0, \quad -d_z + \frac{e_{zx}a_{zx}x}{f(x, y, z, s)} + \frac{e_{zs}a_{zs}s}{f(x, y, z, s)} = 0, \quad (9)$$

which come from (2) and (3) with x as above.

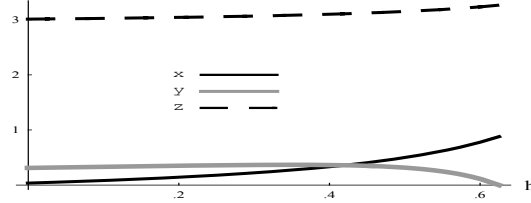


FIGURE 1. The steady state of the three-species steady state with prey x , dominant predator y , and subdominant predator z is shown versus the harvesting rate h for the no interference case ($a_{yz} = 0$). The other parameters are $a_{yx} = 3, a_{zx} = .2, d_y = .1, d_z = .2, e_{yx} = 1, e_{zx} = .5, a_{zz} = 1, s = 1, a_{zs} = 1, e_{zs} = 1$.

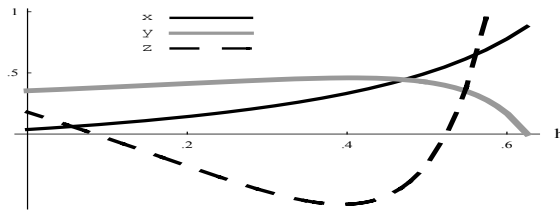


FIGURE 2. The steady state of the three-species steady state with prey x , dominant predator y , and subdominant predator z is shown versus the harvesting rate h for the high interference case ($a_{yz} = 8$). The other parameters are the same as in Figure 1.

4. Bifurcation analysis. In this section bifurcation diagrams will illustrate the changes in dynamics as the harvest rate h of the dominant predator y increases and as the predator interference rate a_{yz} is varied. The other parameters will generally be fixed, and it will be assumed that the search efficiency a_{yx} of the dominant predator y for the prey x will be significantly larger than the search efficiency a_{zx} of predator z for the prey x .

Figures 1 and 2 illustrate the basic dependence of the three-species steady states on the harvest rate h for two different values of the interference parameter a_{yz} . In Figure 1, there is no interference ($a_{yz} = 0$), whereas there is a high level of interference ($a_{yz} = 8$) in Figure 2. The primary difference to note is that the population of the second predator z is significantly suppressed when the interference rate is high - as would be expected. What is not shown is the stability and how the three-species steady state interacts with the other steady states; this will be shown using AUTO.

Figure 3 shows the bifurcation diagrams for $x, y,$ and z versus the harvesting for the no interference case, $a_{yz} = 0$. It is important to observe that the three-species steady state (8, 9) is unstable as the harvest rate h of the dominant predator

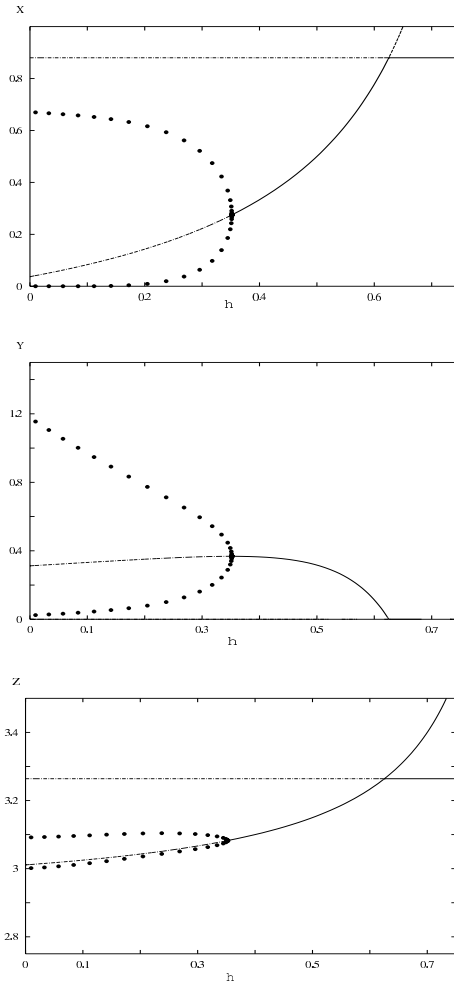
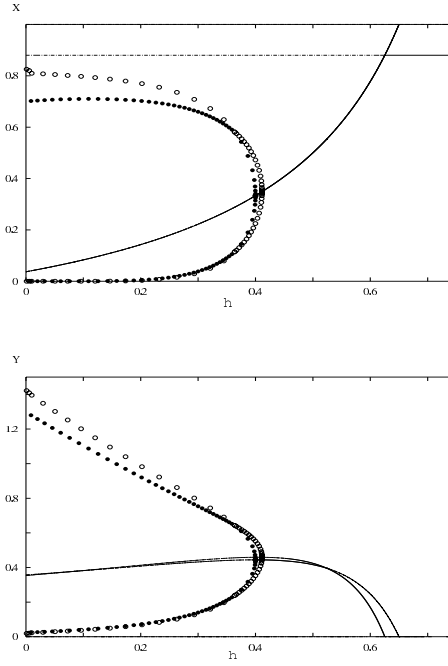


FIGURE 3. The bifurcation diagrams of the three-species x , y , z are shown for the no interference case ($a_{yz} = 0$). The other parameters are the same as in Figure 1. The light curves are the unstable steady states and the darker curves are the stable steady states. All the periodic solutions are stable and are denoted by solid circles.

increases up to the value of h^* that corresponds to a value of y just beyond its peak value where there is a Hopf bifurcation. The lack of stability of this branch partially explains the seemingly odd behavior in which the predator population (y) increases when it is harvested more. This is further understood to be ecologically sensible by observing that there is a stable periodic solution branch for these harvesting values and the amplitude of y becomes larger when there is less harvesting.

As h increases beyond the Hopf bifurcation point $h = h^*$, the three species steady state becomes stable and features a decreasing y population (eventually to zero) and increasing x and z populations. When y becomes zero, there is a bifurcation with the xz steady state (7) at the harvesting value labelled h_{y0} and the stability is transferred to that branch. As a side note, the xy steady state (4) with $z = 0$ is



unstable so it was not shown in the bifurcation diagram. This lack of stability is explicable in light of the fact that z is not interfered with by y .

To summarize this case, the three species are stable, oscillating populations for small enough harvesting rates; become stable steady-state populations as the harvesting increases further (with y declining); and finally only the prey x and second predator z persist as the harvesting rate becomes too large for the dominant predator y to survive.

For the bifurcation diagrams in Figure 4, the interference rate is large ($a_{yz} = 8$) and the behavior is more complicated than in the no-interference case. The three-species steady state is unstable for harvesting values all the way to the value of h_3 at which the branch hits the xy steady state (4), in which $z = 0$. After that harvesting value, the three-species steady state becomes stable until the harvesting value h_{y0} , at which y becomes zero and x and z persist; i.e., a bifurcation with (7). There is a Hopf bifurcation on the three-species branch before that and the periodic solution emanating from it is unstable at first. As h decreases, however, there is a secondary bifurcation at $h = h^*$ with the heretofore stable periodic solution branch featuring periodic x and y and a zero population of z . Figure 5 shows a blow-up of this region. The stability is transferred at this bifurcation point, so that all three species are given by stable periodic solutions when $h < h^*$.

For h increasing from $h = 0$, the stable attractors can be characterized as follows: For $0 \leq h < h^*$ the three species coexist and are periodic. As h approaches h^* from the left, the amplitude of z diminishes to zero, but x and y remain as stable periodic solutions until the Hopf bifurcation value of h_2 on the xy steady state (4) (see Figure 5). As h goes beyond h_2 , z remains zero and x and y are stable but no longer periodic. As h increases further, there is a bifurcation point of this steady branch (4) with the three-species steady state (8, 9) at h_3 , so that z becomes nonzero again. As h continues to increase, the stable populations of x

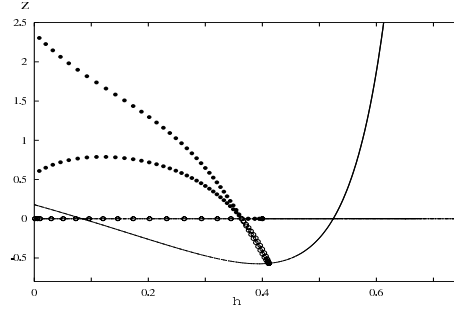
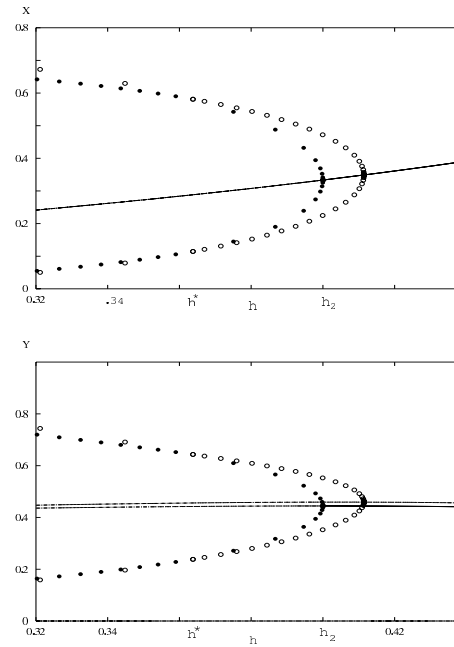


FIGURE 4. The bifurcation diagrams of the three species x , y , z are shown for the high-interference case ($a_{yz} = 8$). The other parameters are the same as in Figure 1. The light curves are the unstable steady states, and the darker curves are the stable steady states. The open circles denote unstable periodic solutions, and the solid circles are the stable periodic solutions.



and z increase, but the stable y decreases further until it becomes zero. Past this harvesting rate (h_{y0}), the populations of x and z are the only ones that persist.

In Figures 1–5, the efficiency which the dominant predator searches for the prey is fairly high ($a_{yx} = 3$), and the three-species steady branch is unstable for harvesting values up to the Hopf bifurcation point. This unstable part of the branch was characterized by an increasing y population as the harvesting of it increased. This is seemingly counterintuitive, but the fact that this part of the steady state was unstable made this ecologically palatable, especially when it was seen that a robust *periodic* predator population existed in its place. In contradistinction with this case, different behavior is seen when the search efficiency is lower. Figure 6 shows the case in which $a_{yx} = 1$ with moderate interference ($a_{yz} = 2$). In this situation,

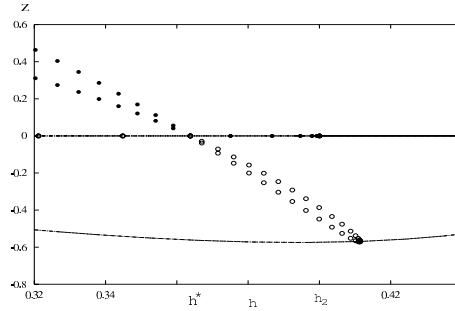


FIGURE 5. A blow-up of the regions in Figure 4 near the Hopf bifurcation points. There is a Hopf bifurcation at $h = h_2$ on the $z = 0, x \neq 0, y \neq 0$ steady branch, and the periodic solution arising therefrom is initially stable. There is a bifurcation of this branch at $h = h^*$ with the all nonzero species periodic branch causing the three-species all nonzero periodic branch to become stable, and it continues to be stable as h decreases from h^* to 0.

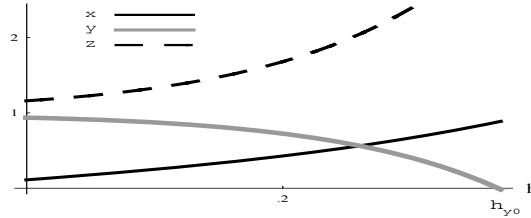


FIGURE 6. The steady state of the three-species steady state with prey x , dominant predator y , and subdominant predator z is shown versus the harvesting rate h for a lower predator search efficiency ($a_{yx} = 1$ compared to $a_{yx} = 3$) than in Figures 1–5. The interference level is moderate ($a_{yz} = 2$), but all of the other parameters are the same as in Figure 1.

the dominant predator population always decreases as the harvesting h increases and there are no Hopf bifurcations. The three-species steady state is stable until the y population becomes zero at $h = h_{y0}$, and the stability is transferred to the non-zero x and z steady state (7).

5. Discussion. The bifurcations and stability of the various branches as the harvesting rate h varies for different levels of interference a_{yz} are complex. In the interest of distilling the major bifurcation phenomena and stability, the following illustrates the stable attractors as h increases:

No interference: $a_{yz} = 0$ (see Figure 3)		
$0 \leq h < h^*$	$h^* < h < h_{y0}$	$h_{y0} < h$
$x, y, z \neq 0$ periodic	$x, y, z \neq 0$ steady	$x, z \neq 0, y = 0$ steady

High interference: $a_{yz} = 8$ (see Figures 4 - 5)		
$0 \leq h < h^*$	$h^* < h < h_2$	$h_2 < h < h_3$
$x, y, z \neq 0$ periodic	$x, y \neq 0, z = 0$ periodic	$x, y \neq 0, z = 0$ steady
$h_3 < h < h_{y0}$	$h_{y0} < h$	
$x, y, z \neq 0$ steady	$x, z \neq 0, y = 0$ steady	

Moderate interference: $a_{yz} = 2$ and lower search efficiency a_{yx} (see Figure 6)	
$0 \leq h < h_{y0}$	$h_{y0} < h$
$x, y, z \neq 0$ steady	$x, z \neq 0, y = 0$ steady

The bifurcations describe features of the predator-prey dynamics that could translate well into real ecological systems. The genuine benefit of predator-prey models for predicting behavior in real ecosystems is generally not in quantitative accuracy, but in capturing important qualitative features. It has been found that in a complex ecosystem such as an ocean, in which a dominant predator such as cod is significantly fished out, alternative, less desirable, subdominant predator species have taken over to a large extent [14]. This suggests that the population of this subecosystem is, at least qualitatively, on the downslope of the stable three-species branch.

As the bifurcation diagrams illustrate and as common sense dictates, it will always be the case that the population of the dominant predator will become zero when the rate at which it is harvested is sufficiently large. What is interesting, though, is the different population behavior found by altering the level of interference, the harvesting rate, and the search efficiency. In real ecological systems, it may be useful to view the potential causes and explanations of certain observed characteristics in this light.

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