J. Math. Biol. (1988) 26: 93-103

Journal of
Mathematical
Biology



# Multiparameter bifurcation diagrams in predator-prey models with time lag

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**Abstract.** A predator-prey model is considered in which prey is limited by the carrying capacity of the environment, and predator growth rate depends on past quantities of prey. Conditions for stability of an equilibrium, and its bifurcation are established taking into account all the parameters.

**Key words:** Andronov-Hopf bifurcation — Delay — Paradox of enrichment

## 1. Introduction

The system

$$\dot{N}(t) = \varepsilon N(t)(1 - N(t)/K) - \alpha N(t)P(t)$$
$$\dot{P}(t) = -\gamma P(t) + \beta P(t) \int_{-\infty}^{t} N(\tau)G(t-\tau)\, d\tau \tag{1.1}$$

describes the dynamics of interaction between a predator and a prey species. $N(t)$ and $P(t)$ are the quantities of prey and predator, respectively, at time $t$. Dot denotes differentiation with respect to time. The parameter $K > 0$ is the carrying capacity of the environment with respect to the prey, $\varepsilon > 0$ is the intrinsic growth rate of prey, $\alpha > 0$ is the predation rate, $\gamma > 0$ is the mortality of predator in the absence of prey, $\beta > 0$ is the conversion rate. The system has a memory represented by the weight function $G: \mathbb{R}^+ \mapsto \mathbb{R}^+$ which satisfies also $\int_0^\infty G(s)\, ds = 1$. Thus the predator's present growth rate is affected by past values of prey quantity. Several authors, among others Cushing [2], Dai [3], MacDonald [8], Farkas [4], Farkas, A., Farkas, M., Kajtár, L. [5], and Szabó [11] have studied system (1.1) under the assumption that

$$G(s) = G_0(s) = a \exp(-as), \qquad a > 0. \tag{1.2}$$

(Stépán [10] has studied the system assuming different weight functions). The present authors and Kajtár have managed to characterize the bifurcation of the equilibrium of the system in case (1.2) when $\mu = 1/a$ was considered as a bifurcation parameter. One may consider the value of this parameter as the measure of the effect of the past or, simply, as the delay. The first two authors [6] have established an Andronov–Hopf bifurcation and managed to characterize it in the more realistic case when the weight function is

$$G(s) = G_1(s) = a^2 s \exp(-as), \qquad a > 0. \tag{1.3}$$

In this case $\varepsilon$ was assumed for bifurcation parameter.

In this paper based on earlier results of the authors a unified treatment is given to the two cases, see Fig. 1. In both cases, primarily, the measure of the dealy $\mu = 1/a$ and the carrying capacity $K$ will be considered as bifurcation parameters. From a biological point of view the most reasonable thing is, probably, to vary $K$ and to fix the values of the rest of the parameters. For particular species $\varepsilon$, $\gamma$, $\alpha$, $\beta$ and $\mu$ may be considered as parameters determined by the genotype, while the carrying capacity $K$ of the environment may vary. The response of the system to the variation of the carrying capacity depending on the values of the other parameters is an important and interesting phenomenon. The dependence of the phenomenon on the delay $\mu$ can be interpreted especially clearly. The system exhibits the *paradox of enrichment* (see Rosenzweig [9]) in both cases. This means that the increase of the carrying capacity beyond a certain value destabilizes the formerly stable equilibrium of the system, the system undergoes an Andronov–Hopf bifurcation and begins to oscillate. However the character of the bifurcation and the value of $K$ at which it takes place depends on the delay. *The larger the delay is the earlier the bifurcation occurs.*

In case the weight function is given by (1.2), i.e. the effect of the past is fading away exponentially as we go backwards in time, there is a certain delay under which the bifurcation is supercritical and above which it is subcritical. This means that in this case if the delay is small then after the destabilization of the equilibrium the system begins to oscillate with small amplitude stably. If the delay is large then approaching the critical value of the carrying capacity from below the region of attractivity of the equilibrium is decreasing, and the system is becoming unpredictable.

In case the weight function is given by (1.3), i.e. the most important moment in the past is $\mu = 1/a$ units before the present time $t$ (the weight function has a hump at $\tau = t - 1/a$, and going further backwards in time the effect of the past is fading away), the phenomenon is richer. In this case we have to take into account the value of the intrinsic growth rate of prey, $\varepsilon$ too. If $\varepsilon$ is small then the bifurcation is supercritical for arbitrary large delay, i.e. after the loss of stability of the equilibrium the system exhibits small amplitude stable oscillations. If $\varepsilon$ is large then the bifurcation is supercritical for small and for very large

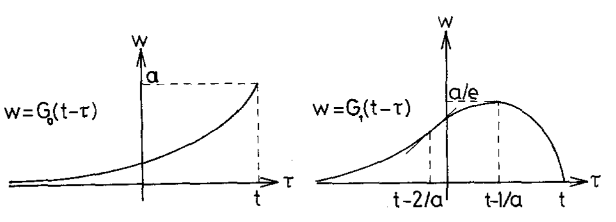


**Fig. 1.** Weight functions (1.2) and (1.3), respectively

delays, however, there is an interval of possible delays such that if the delay falls into this interval the bifurcation is subcritical.

Our results, actually, yield three parameter bifurcation diagrams. In the three dimensional parameter space $\varepsilon/\gamma$, $\kappa/\gamma = K\beta/\gamma$, $\gamma\mu = \gamma/a$ we determine a two dimensional bifurcation surface, and characterize the phenomenon at crossing the latter.

Case (1.2) is treated in Sect. 2, case (1.3) in Sect. 3. The bifurcation diagrams, Figs. 2, 3, and 4, 5 respectively, hopefully, show the results clearly.

In case the bifurcation is subcritical we have some computer simulation evidence of how the system behaves.

## 2. Exponentially fading memory

System (1.1) is considered in this section with weight function given by (1.2):

$$\dot{N}(t) = \varepsilon N(t)(1 - N(t)/K) - \alpha N(t)P(t)$$

$$\dot{P}(t) = -\gamma P(t) + \beta P(t) \int_{-\infty}^{t} N(\tau) a \exp(-a(t-\tau))\, d\tau, \qquad t \in [0, \infty). \tag{2.1}$$

Introducing the notation

$$Q(t) = \int_{-\infty}^{t} N(\tau) a \exp(-a(t-\tau))\, d\tau$$

system (2.1) becomes essentially equivalent to the three dimensional system of ordinary differential equations

$$\begin{aligned} \dot{N} &= \varepsilon N(1 - N/K - \alpha P/\varepsilon) \\ \dot{P} &= P(-\gamma + \beta Q) \\ \dot{Q} &= a(N - Q) \end{aligned} \tag{2.2}$$

on $t \in [0, \infty)$ in the following sense. If $(N, P): [0, \infty) \mapsto \mathbb{R}^2$ is the solution of (2.1) corresponding to the continuous and bounded initial function $\tilde{N}: (-\infty, 0] \mapsto \mathbb{R}$ and the initial value $P_0 = P(0)$ then $(N, P, Q): [0, \infty) \mapsto \mathbb{R}^3$ is the solution of (2.2) corresponding to the initial values $N(0) = \tilde{N}(0)$, $P(0) = P_0$ and

$$Q(0) = Q_0 = \int_{-\infty}^{0} \tilde{N}(\tau) a \exp(a\tau)\, d\tau,$$

and vice versa. (Clearly, if the initial values $N(0)$, $P_0$ and $Q_0$ related to system (2.2) are prescribed then the function $\tilde{N}$ is not uniquely determined).

The following facts have been established earlier (see, e.g. Farkas, M. [4]). System (2.2) has three equilibria: $(0, 0, 0)$ which is unstable; $(K, 0, K)$ representing the absence of predators which is asymptotically stable if $\gamma/K\beta > 1$, and unstable if

$$\gamma/K\beta < 1; \tag{2.3}$$

and $E_0 = (\gamma/\beta; (1 - \gamma/K\beta)\varepsilon/\alpha; \gamma/\beta)$ which lies in the interior of the positive octant of $N, P, Q$ space exactly when (2.3) holds. Introducing the notations

$$\mu = 1/a, \qquad \mu_0(K) = K\beta/(K^2\beta^2 - K\beta\gamma - \gamma\varepsilon), \tag{2.4}$$

$S=\{(K,\mu): K>\gamma/\beta, \mu>0$, and if $\mu_0(K)>0$ then $\mu<\mu_0(K)\}$, we have that $E_0$ is asymptotically stable if $(K,\mu)\in S$ and it is unstable if $0<\mu_0(K)<\mu$. As a consequence, $E_0$ is asymptotically stable for all $\mu>0$ if (2.3) holds, and $\gamma/K\beta+\gamma\varepsilon/(K\beta)^2\geq 1$, i.e. if

$$K_0<K\leq K_1 \quad \text{where } K_0=\gamma/\beta,\ K_1=(\gamma+(\gamma^2+4\gamma\varepsilon)^{1/2})/2\beta.$$

If $K>K_1$, and the parameters $K,\mu$ are varied so that $(K,\mu)$ crosses graph $\mu_0$ from the convex to the concave side then $E_0$ loses its stability. This loss of stability is characterised by the following theorem where

$$K_d=\frac{\gamma(\varepsilon+2\gamma)+(\gamma(\varepsilon+2\gamma)(8\varepsilon^2+9\varepsilon\gamma+2\gamma^2))^{1/2}}{2\beta(\varepsilon+2\gamma)}. \tag{2.5}$$

**Theorem 2.1.** *If the parameter values $K>K_1$, $\mu>0$ are varied through graph $\mu_0$ from the convex to the concave side then at $(K,\mu_0(K))$ the equilibrium $E_0$ undergoes an Andronov-Hopf bifurcation; if the crossing of graph $\mu_0$ takes place in the interval $K\in(K_d,\infty)$ then the bifurcation is supercritical; if it takes place in the interval $K\in(K_1,K_d)$ then the bifurcation is subcritical* (See Fig. 2).

*Proof.* This follows from Theorem 1 in [4] and from the Theorem in [11] if we rewrite the supercriticality (resp. subcriticality) condition of the latter the following way:

$$1-\gamma/K\beta-(1+\varepsilon/(2\gamma+\varepsilon))\gamma\varepsilon/(K\beta)^2>0, \quad (\text{resp. } <0).$$

This condition holds if $K>K_d$ (resp. $K_1<K<K_d$).

As we have already mentioned, the biologically most reasonable standpoint is to consider $K$ as the bifurcation parameter. If we introduce the notation

$$\mu_d=\mu_0(K_d)=\frac{\gamma(\varepsilon+2\gamma)+(\gamma(\varepsilon+2\gamma)(8\varepsilon^2+9\varepsilon\gamma+2\gamma^2))^{1/2}}{2\varepsilon^2\gamma} \tag{2.6}$$

we have

**Corollary 2.2.** *If $\mu>0$ is fixed and $K$ is increased through the value $\mu_0^{-1}(\mu)$ then the equilibrium $E_0$ undergoes an Andronov-Hopf bifurcation; if $\mu<\mu_d$ (resp. $\mu>\mu_d$) then the bifurcation is supercritical (resp. subcritical).*

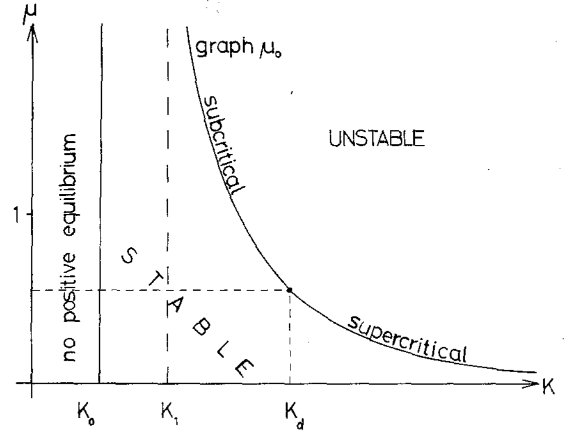


**Fig. 2.** Bifurcation diagram for system (2.2) in the $K,\mu$ plane

We may put these results into a generalized context refraining from specifying the bifurcation parameter. In system (2.2) the parameter $\alpha$ can be transformed out by introducing $\alpha P$ as the second coordinate. The bifurcation of the system depends upon three independent parameters, namely:

$$u = \varepsilon/\gamma, \qquad v = \kappa/\gamma = K\beta/\gamma, \qquad w = \gamma\mu = \gamma/a.$$

In the long run, $N$ cannot stay above $K$, and so the specific growth rate of predator cannot stay above $\kappa - \gamma$. In the positive orthant of the parameter space $u$, $v$, $w$ condition (2.3) restricts consideration to $1 < v$, i.e. we have an equilibrium $E_0$ in the positive octant of $N$, $P$, $Q$ space if and only if this condition holds. Rewriting the conditions based on formulae (2.4) and (2.5) we get

**Corollary 2.3.** *The equation of the bifurcation surface in the three dimensional parameter space is given by*

$$w(v^2 - v - u) - v = 0 \tag{2.7}$$

*if this surface is crossed an Andronov-Hopf bifurcation takes place*; *the bifurcation is supercritical, resp. subcritical according as*

$$2v - 1 - ((8u^2 + 9u + 2)/(u + 2))^{1/2} > 0, \tag{2.8}$$

*resp.* $< 0$ *at the crossing.*

In Fig. 3 the situation is shown in the three dimensional space of $u$, $v$, $w$. The surface $F$ is defined by (2.7); this is the bifurcation surface. Behind this, and in front of the vertical plane $L\colon v = 1$ the equilibrium $E_0$ is asymptotically stable, in front of $F$ it is unstable. The curve $g$ divides $F$ into two according as (2.8) is positive or negative. The bifurcation is supercritical, resp. subcritical according as the crossing takes place below or above this curve. Figure 2 may be obtained taking an $u = \varepsilon/\gamma = \text{constant}$ section of $F$.

*Remark.* If surface $F$ is crossed at a point of the curve $g$ we get a degenerate Andronov-Hopf bifurcation. Generically this bifurcation is of codimension 1 and should be of type (3) according to the Golubitsky-Langford classification

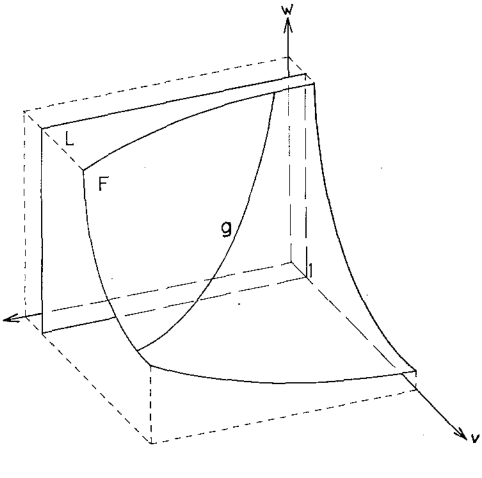


**Fig. 3.** Bifurcation diagram for system (2.2) in the three dimensional parameter space $u$, $v$, $w$

([7] Proposition 3.47, see also Chow–White [1]). Actually, we have obtained computer simulation evidence that at parameter configurations where the bifurcation is subcritical (and near to $g$) large amplitude stable periodic solutions exist close to the critical parameter values. Thus, out of the three independent parameters (any) one can be considered as the bifurcation parameter, another one as an unfolding parameter, and the third one is superfluous. However, we cannot rule out the possibility that there is a point on $g$ where the bifurcation is of codimension two (of type (5) according to the classification quoted). If this was the case this point would be the organizing centre of the bifurcation diagram and all three parameters would be needed.

## 3. Memory with a hump

In this section system (1.1) is considered with weight function given by (1.3):

$$\begin{aligned}&\dot N(t)=\varepsilon N(t)(1-N(t)/K)-\alpha N(t)P(t)\\&\dot P(t)=-\gamma P(t)+\beta P(t)\int_{-\infty}^{t} N(\tau)a^2(t-\tau)\exp(a-(t-\tau))\,d\tau,\qquad t\in[0,\infty).\end{aligned}\tag{3.1}$$

Introducing the notations

$$Q(t)=\int_{-\infty}^{t} N(\tau)a^2(t-\tau)\exp(-a(t-\tau))\,d\tau$$

$$R(t)=\int_{-\infty}^{t} N(\tau)a\exp(-a(t-\tau))\,d\tau$$

system (3.1) becomes equivalent to the four dimensional system of ordinary differential equations

$$\begin{aligned}\dot N&=\varepsilon N(1-N/K)-\alpha NP\\ \dot P&=P(-\gamma+\beta Q)\\ \dot Q&=a(R-Q)\\ \dot R&=a(N-R)\end{aligned}\tag{3.2}$$

on $t\in[0,\infty)$ in the sense analogous to that specified after (2.2).

We rewrite the results established in [6] for the present purpose.

System (3.2) has three equilibria: $(0,0,0,0)$ which is unstable; $(K,0,K,K)$ representing the absence of predators which is asymptotically stable if $\gamma/K\beta>1$ and unstable if (2.3) holds; and $E_1=(\gamma/\beta;(1-\gamma/K\beta)\varepsilon/\alpha;\ \gamma/\beta;\ \gamma/\beta)$ which lies in the interior of the positive orthant of $N, P, Q, R$ space exactly when (2.3) holds. Considering the stability of $E_1$, and assuming (2.3) throughout, the part of the positive orthant of the $u=\varepsilon/\gamma$, $v=\kappa/\gamma$, $w=\gamma\mu$ parameter space characterized by $1<v$ can be divided into three regions.

(i) If $w(v-1)>2$ then $E_1$ is unstable (for all $\varepsilon>0$).

(ii) If $w(v-1)<1/2$ then $E_1$ is asymptotically stable (for all $\varepsilon>0$).

(iii) If

$$1/2<w(v-1)<2,\tag{3.3}$$

and

$$\frac{uw(\sqrt{2}-\sqrt{w(v-1)})}{\sqrt{2}v(\sqrt{2w(v-1)}-1)}>1 \tag{3.4}$$

then $E_1$ is asymptotically stable; if (3.3) holds and the inequality in (3.4) is reversed then $E_1$ is unstable. (Note that in view of (3.3) both the numerator and the denominator is positive on the left-hand side of (3.4)).

**Theorem 3.1.** *If* $1<v$, (3.3) *holds, and the surface given by*

$$\frac{uw(\sqrt{2}-\sqrt{w(v-1)})}{\sqrt{2}v(\sqrt{2w(v-1)}-1)}=1 \tag{3.5}$$

*is crossed transversally the equilibrium* $E_1$ *undergoes an Andronov–Hopf bifurcation.*

*Proof.* This is an immediate consequence of Theorem 1.1 in [6]. There $\varepsilon$ is decreased through the value determined by (3.5) for the destabilization of $E_1$. It is easy to see that this direction of crossing corresponds to the decrease of $\gamma$, resp. the increase of $\mu$, resp. the increase of $\kappa=K\beta$ (keeping the rest of the parameters constant in all these cases).

The Poincaré constant of the bifurcation has been determined in [6]. Its sign is equal to the sign of

$$\Phi(\theta, \gamma/\kappa)=Y_2(\theta)(1/v)^2+Y_1(\theta)1/v+Y_0(\theta) \tag{3.6}$$

where

$$\theta=(2/(\mu(\kappa-\gamma)))^{1/2}=(2/(w(v-1)))^{1/2}$$

$$Y_2(\theta)=-2\theta^5+23\theta^4-86\theta^3+134\theta^2-90\theta+20$$

$$Y_1(\theta)=2\theta^6-10\theta^5-6\theta^4+102\theta^3-187\theta^2+119\theta-20$$

$$Y_0(\theta)=2\theta(\theta-1)(2-\theta)(\theta^3-3\theta^2-4\theta+10).$$

Thus, we have

**Theorem 3.2.** *If* $1<v$, (3.3) *holds and* $\Phi(\theta, 1/v)$ *is negative (resp. positive) then the bifurcation at* (3.5) *is supercritical (resp. subcritical).*

Condition (3.3) is equivalent to $1<\theta<2$. The third degree polynomial occurring in the expression for $Y_0$ has a single root in the interval $1<\theta<2$, namely

$$\theta_0=1+2(7/3)^{1/2}\cos((4\pi+\cos^{-1}(-2(3/7)^{3/2}))/3)\approx 1.6027,$$

while $Y_2<0$ and $Y_1<0$ in this interval. Thus, we have

**Corollary 3.3.** *If* $1<v$, *and at* (3.5)

$$1/2<w(v-1)\leq 2/\theta_0^2\approx 0.7786$$

*then the bifurcation is supercritical.*

In case $0.7786<w(v-1)<2$ the determination of the sign of $\Phi$ is more tricky. Clearly, in this case if $v$ is large then the bifurcation is subcritical, if $v$ is close

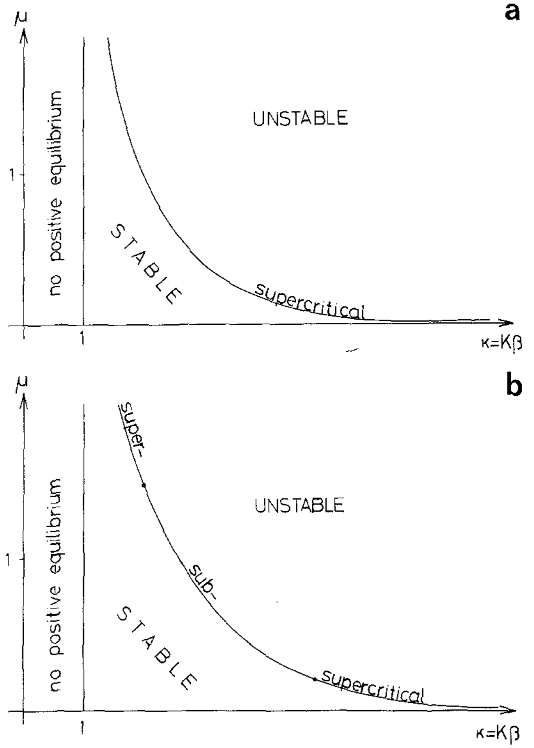


**Fig. 4.** Bifurcation diagrams for system (3.2) in the $\kappa$, $\mu$ plane. **a** $\gamma = 1$, $\varepsilon = 5$; **b** $\gamma = 1$, $\varepsilon = 20$

to one then it is supercritical. It can be seen from (3.5) that if, say, $w(v-1)$ is fixed in the interval (0.7786; 2) then large $v$ corresponds to large $u$ and small $v$ to small $u$, the correspondence depending on the value of $w$, too. Hence, in this case the bifurcation is supercritical (resp. subcritical) according as $u$ is small (resp. large). In Fig. 4 $\gamma$ has been fixed for good, and the bifurcation curves are shown in the parameter plane $\kappa = K\beta$, $\mu$ for two typical values of $\varepsilon$.

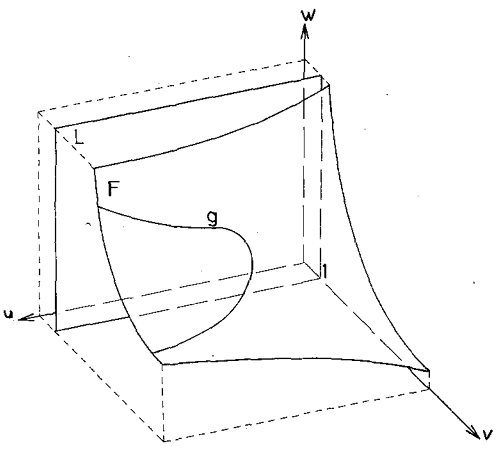


**Fig. 5.** Bifurcation diagram for system (3.2) in the three dimensional parameter space $u$, $v$, $w$

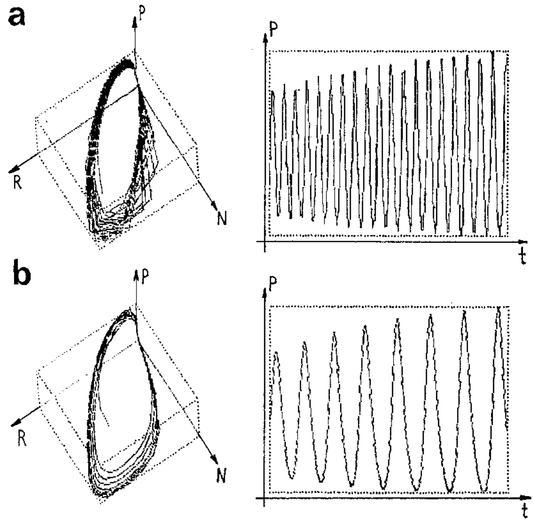


**Fig. 6.** Three dimensional phase space projection of path, and graph of $P$ of a solution of system (3.2) with initial values $(N(0), P(0), Q(0), R(0)) = (2, 13, 2, 2)$. **a** $(u, v, w) = (22, 4, 3/8)$, the amplitudes of $N$ and $P$ are 1.5 and 12.5, respectively. **b** $(u, v, w) = (16.5, 5, 3/8)$, the amplitudes of $N$ and $P$ are 1.7 and 13.5, respectively

In Fig. 5 the situation is shown in the three dimensional space of $u, v, w$. The surface $F$ is defined by (3.5); this is the bifurcation surface. Behind this and in front of the vertical plane $L$: $v = 1$ the equilibrium $E_1$ is asymptotically stable, in front of $F$ it is unstable. The curve $g$ divides $F$ into two according as (3.6) is negative or positive. The bifurcation is supercritical, resp. subcritical according as the crossing takes place "outside or inside the tongue". Figure 4 may be obtained taking an $u = \text{constant}$ section of $F$. If $u$ is small then the section does not cut into the tongue (Fig. 4a); if $u$ is large we get Fig. 4b.

*Remark.* We may repeat here the remark at the end of Sect. 2. Two of our computer generated solutions are presented on Fig. 6 where the parameter values are fixed at $v = 4$, $w = 3/8$. The critical value of the parameter $u$ is then 21.3, i.e. if $u$ is decreased below 21.3 a *subcritical* bifurcation occurs. The initial values are fixed at $(N(0), P(0), Q(0), R(0)) = (2, 13, 2, 2)$. In Fig. 6a $u = 22$, i.e. we are still in the region where the equilibrium is locally asymptotically stable. In Fig. 6b $u = 16.5$. In both cases the solution spirals towards a closed curve whose $N$ and $P$ amplitudes are approximately equal to 1.5 and 12.5, respectively in the first case, and 1.7 and 13.5, respectively in the second case.

## 4. Discussion

We have considered a predator-prey system where prey is limited by the carrying capacity $K$ of the environment, and predator growth rate depends on past values of prey quantity. In the equation governing the growth of predator quantity the average of prey over the past with respect to a weight function occurs. Two cases have been considered; in the first case the influence of past values of prey quantity upon the present growth of predator decreases exponentially as we go back in time; in the second case there is a certain moment in the past at which the quantity of prey influences the present growth of predator the most. In both cases the strength of the delay, the influence of the past can be measured by a positive parameter $\mu$. The behaviour of the system depends upon the intrinsic growth rate of prey $\varepsilon$, the mortality of predator $\gamma$, the delay $\mu$, and the limiting factor of predator $\kappa = K\beta$ where $\beta$ is the conversion rate of prey into predator.

The system has a unique equilibrium $E_0$ (in the first case), $E_1$ (in the second case) with positive coordinates if and only if $\kappa > \gamma$. This inequality determines the admissible part of the positive orthant of the four dimensional parameter space $\varepsilon, \gamma, \mu, \kappa$. The meaning of the condition $\kappa > \gamma$ is clear: if the mortality of the predator is low, and the carrying capacity and the conversion rate are large then coexistence is possible; if the converse is true then the predator dies out. It is interesting to note that in both cases the increase of the intrinsic growth rate of prey and/or the increase of the carrying capacity for the prey *does not increase the prey* coordinate of the equilibrium but does increase the predator. The increase of the prey coordinate of the equilibrium can be achieved by the increase of predator mortality or by the decrease of conversion rate. In both cases if the parameter values lie in the admissible set, and, loosely speaking, *the intrinsic growth rate of prey $\varepsilon$ and the mortality of predator $\gamma$ are large, and the delay $\mu$ and the limiting factor $\kappa$ are small then the equilibrium is asymptotically stable.* We have determined the equation of the bifurcation surface, (2.7) in the first case, (3.5) in the second. If this surface is crossed by *increasing the delay or the limiting factor, or decreasing the intrinsic birth rate of prey or the mortality of predator* (keeping in all the cases the rest of the parameters constant) *then the equilibrium loses its stability by an Andronov-Hopf bifurcation*, i.e. periodic solutions, closed trajectories occur in the neighbourhood of the equilibrium. The bifurcation surface can be crossed, naturally, by varying two, three or all the four parameters simultaneously leading to the same consequence. We have determined the part of the surface where the bifurcation is supercritical and the part where it is subcritical (Corollary 2.3 and Theorem 3.2). Supercriticality means that we have small amplitude, orbitally asymptotically stable, periodic solutions for parameter values near to the surface on the side where the equilibrium is unstable. Subcriticality means that we have small amplitude, unstable periodic solutions near the equilibrium for parameter values near to the surface on the side where the equilibrium is still stable, and the system behaves unpredictably on the other side. However, we have got computer simulation evidence suggesting that at parameter configurations corresponding to subcritical bifurcation the system has large amplitude stable periodic solutions (see the remarks at the end of Sects. 2 and 3 and Fig. 6).

It is worthwhile to observe the *differences between the two cases.* In doing this we are going to consider "$\gamma$ more fixed than $\varepsilon$ which, in turn, will be more fixed than $\mu$", and $\kappa$ (or $K$ for fixed $\beta$) will be the easiest variable parameter.

In the first case if $\mu\kappa < 1$ then the equilibrium is asymptotically stable for arbitrary (small) $\varepsilon$ and $\gamma$. In the second case the more restrictive $\mu\kappa < 1/2$ must hold for the same effect. On the other hand, in the second case if $\mu(\kappa - \gamma) > 2$ then the equilibrium is unstable for arbitrary (large) $\varepsilon$; in the first case we have no such subset, i.e. the increase of $\varepsilon$ can always stabilize the equilibrium.

In both cases, for fixed values of $\varepsilon, \gamma, \mu$ the increase of $\kappa$ destabilizes the equilibrium at a certain well determined value; the larger the delay $\mu$ is, the sooner this destabilization occurs. This is the phenomenon of the "*paradox of* *enrichment*". However, in the first case there is a *critical delay* (given by (2.6)) under which the bifurcation is supercritical, above which it is subcritical. In the second case, for small fixed $\varepsilon$ the bifurcation is always supercritical, for large fixed $\varepsilon$ the bifurcation is supercritical for small and for very large delay, and it is subcritical if the delay falls into a certain interval in between.

*Acknowledgement.* We would like to thank two reviewers for some valuable suggestions that improved the original manuscript.

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Received March 2/Revised October 13, 1987