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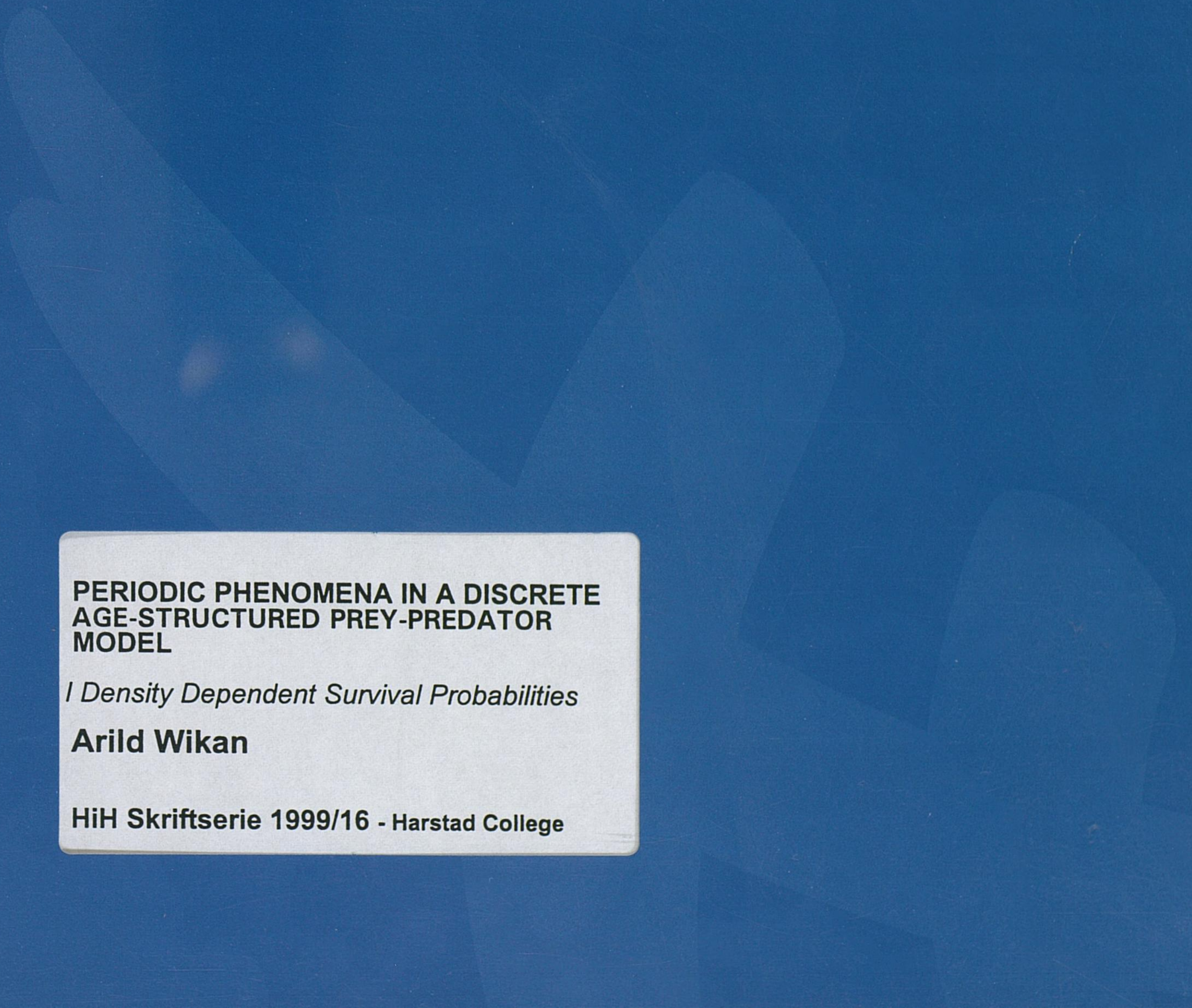

PERIODIC PHENOMENA IN A DISCRETE AGE-STRUCTURED PREY-PREDATOR MODEL

I Density Dependent Survival Probabilities

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The possible qualitative dynamical changes of a discrete age-structured prey population exposed to predation from an age-structured predator population are analyzed. It is shown that increased interaction between the two populations may act both as a stabilizing and destabilizing effect, depending on whether the survival probabilities are overcompensatory or compensatory. Moreover, we have found that possible periodic dynamics of low period, either exact or approximate, may not be generated by the predator, but it may indeed be generated by the prey. Finally, what is most interesting from the biological point of view, is that increased predation is not capable of altering the periodicity of an initial low periodic dynamics of the prey in any substantial way, provided the populations are in unstable parameter regions.

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Periodic Phenomena in a Discrete Age-Structured Prey-Predator Model

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1 Introduction

The use of nonlinear matrix models as a strong and powerful tool in the description of various properties of a population with non-overlapping generations (or stages) is well documented in Caswell's book [1]. Indeed, in consideration of problem within population dynamics, Guckenheimer et al. [2] used a 2×2 Leslie matrix model in order to study the chaotic behaviour of a two-stage class species. Levin and Goodyear [3] and later Levin [4] formulated and analyzed their striped bass fishery model in terms of a nonlinear matrix. DeAngelis et al. [5] and Bergh and Getz [6] focused on return paths and return times to the stable equilibrium after small perturbations. A logistic matrix model was developed and presented by Liu and Cohen [7] and applied with good results by Desharnais and Liu [8] on the flour beetle Tribolium castaneum.

Other authors have from a more theoretical point of view paid attention to the qualitative behaviour of an age-structured population in unstable parameter regions, see f.ex. Silva and Hallam [9], Wikan and Mjølhus [10] in case of density dependent fecundity terms, and Wikan and Mjølhus [11], Wikan [12] in case of density dependent survival probabilities. Information of general ergodic properties of nonlinear one-population matrix models may be obtained in Cushing's papers [13, 14] and in Crowe [15], and most interesting, it has recently been demonstrated by Cushing and collaborators (see Cushing's book [16]) that 3×3 matrix models indeed may be used in order to predict nonstationary and even chaotic behaviour of laboratory populations (flour beetles).

The purpose of this work is to extend results from the previously quoted "one-population papers" by considering a discrete nonlinear age-structured prey–predator model formulated within the framework of Leslie matrices. The main question which we consider is to reveal what kind of qualitative dynamical changes a discrete age-structured prey population may undergo by including a certain number of predators from an age-structured predator population. More specific:

(1) What kind of qualitative behaviour will the prey and predator exhibit outside the stable parameter region?

(2) Given that the prey, in absence of the predator, exhibits almost periodic chaotic oscillations, what effects (stabilizing or destabilizing) will the inclusion of a certain number of predators have, and what about the periodicity?

Is it possible to stabilize a "chaotic prey population" by adding a sufficiently large number of predators?

In this paper, the questions above shall be answered by considering density dependent (year-to-year) survival probabilities and constant fecundity terms. In a forthcoming paper density-dependent fecundities shall be considered.

2 The Model

Let $\mathbf{x} = (x_1, ..., x_n)^T$ consist of n nonoverlapping age classes of the prey population and let $\mathbf{y} = (y_1, ..., y_m)^T$ be m nonoverlapping age classes of the predator. Define the prey–predator vector $\mathbf{z} = (\mathbf{x}, \mathbf{y})^T$. Then we express the relation between $\mathbf{z}$ at two consequtive time steps (years) t and $t+1$ as

$$\mathbf{z}_{t+1} = A\mathbf{z}_t \tag{1}$$

where the transition matrix A is of a block diagonal form

$$A = \begin{pmatrix} A_1 & 0 \\ 0 & A_2 \end{pmatrix} \tag{2}$$

where the two blocks A_1 and A_2 are of dimension $n \times n$ and $m \times m$, respectively. Further we let each of these blocks have the structure of a Leslie matrix. We define the prey block

$$A_1 = \begin{pmatrix} f_1 & \dots & & & f_n \\ p_1 & 0 & \dots & & 0 \\ 0 & \ddots & & & \vdots \\ \vdots & & & & \\ 0 & \dots & 0 & p_{n-1} & 0 \end{pmatrix} \tag{3}$$

and the predator block

$$A_2 = \begin{pmatrix} g_1 & \cdots & & & g_m \\ q_1 & 0 & \cdots & & 0 \\ 0 & \ddots & & & \vdots \\ \vdots & & & & \\ 0 & \cdots & 0 & q_{m-1} & 0 \end{pmatrix} \tag{4}$$

where f_i and g_i are the fecundity elements for the prey and predator, respectively, and p_i and q_i denote the corresponding year-to-year survival probabilities.

The matrix elements may be density dependent or not. In consideration of one-population models of the form

$$x_{t+1} = A_1 x_t \tag{5}$$

the usual approach has been to include density effects in the fecundity terms f and not in the year-to-year survival probabilities, cf. [3], [4], [9], [10], and [17]. Especially in fishery models, this has often been motivated by the fundamental assumption that most density effects occur within the first year of life. Another strategy is to consider density dependent survival terms, cf. [11] and [12], and as mentioned, this is the strategy which we shall adopt in the prey–predator model (1).

2.1 Density-dependent survival probabilities

In this section we apply the following specifications for the prey:

$$f_i = \begin{cases} 0 & i = 1 \\ F_i \text{ (constant)} & i = 2, \ldots, n \end{cases} \tag{6a}$$

$$p_i = p_i(x, y) = P_i(1 - \gamma x)^{1/\gamma}(1 - \gamma\beta y)^{1/\gamma} \qquad i = 1, \ldots, n-1 \tag{6b}$$

and in the predator block we define

$$g_j = \begin{cases} 0 & j = 1 \\ G_j \text{ (constant)} & j = 2, \ldots, m \end{cases} \tag{7a}$$

$$q_j = q_j(x, y) = Q_j(1 - \gamma y)^{1/\gamma}\left(1 - (1 - \gamma\beta x)^{1/\gamma}\right) \qquad j = 2, \ldots, m-1 \tag{7b}$$

where F_i and G_j are the density independent fecundities for the prey and predator, respectively, and P_i and Q_j the density independent part of the year-to-year survival probabilities. $x = \sum x_i$, $y = \sum y_i$, $\gamma \leq 0$. The parameter $\beta \geq 0$ which shall be our bifurcation parameter describes the coupling between the prey and predator. When $\beta \to 0$ it is clear from (7b) that the predator will die and consequently that (1) is nothing but the one-population model

$$\begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix} \to \begin{pmatrix} 0 & F_2 & \dots & & F_n \\ p_1 & 0 & & & 0 \\ 0 & \ddots & & & \vdots \\ \vdots & & & & \\ 0 & 0 & \dots & p_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix} \tag{8}$$

where $p_i = P_i(1 - \gamma x)^{1/\gamma}$.

The model (8) has been studied in [11] and later by Wikan [18] and one important conclusion from these studies is that the nonstationary dynamics has a strong resemblance of 4-cycles, wither exact or approximate. An interesting question is how this dynamics will change as we start is how to increase β in (1) under the specifications (6) and (7).

However, let us first show that the general model (1) (under the assumptions above) possesses a nontrivial equilibrium. To this end, assume

$$\sum_{i=2}^{n} F_i \prod_{j=1}^{n-1} > 1 \qquad \sum_{i=2}^{m} G_i \prod_{j=1}^{m-1} Q_j > 1 \tag{9}$$

From the prey block in (1) we have

$$\left(\prod_{i=1}^{n-1} P_i\right) F_n w^{n-1} + \left(\prod_{i=1}^{n-2} P_i\right) F_{n-1} w^{n-2} + \cdots + P_1 F_{2w} - 1 = 0 \tag{10}$$

where $w = [(1 - \gamma x)(1 - \gamma\beta y)]^{1/\gamma}$.

Since there is only one change of sign in (10), we may by applying Descartes' rule of sign, cf. [19], directly conclude that there is only one positive real root w of (10), hence there must be a unique correspondence between x and y.

Now, consider (cf. the predator block in (1))

$$\left(\prod_{i=1}^{m-1} Q_i\right) G_m u^{m-1} + \cdots + Q_1 G_2 u = 1 \tag{11}$$

where

$$u = (1-\gamma a(x))^{1/\gamma}[1-(1-\gamma\beta x)^{1/\gamma}]$$

and

$$a(x) = \frac{1}{\gamma\beta}\left(1 - \frac{r\gamma}{1-\gamma x}\right)$$

where r is the positive real solution of (10).

Here we may notice that $x \to 0$ implies that the left-hand side of (11) $\to 0$ and if x becomes large it follows from (9) that the left-hand side of (11) is greater than 1. Finally, if we regard the left-hand side as a function of x, say $v(x)$, it is immediately clear that $v'(x) > 0$ which proves that $x = x^*$ is uniquely determined from (11).

The relations between the total population and the various age classes at equilibrium are

$$x_i^* = \frac{l_i^*}{\sum_{i=1}^{n} l_i^*} x^* \qquad y_j^* = \frac{k_j^*}{\sum_{j=1}^{m} k_j^*} y^* \tag{12}$$

where $l_i^* = p_1^* \dots p_{i-1}^*$ and $k_j = q_1^* \dots q_{j-1}^*$.

—o—

Our next goal is to study stability properties and the qualitative behaviour of the populations in unstable and chaotic parameter regions. In order to do so we restrict the analysis to two age classes for both the prey and the predator (that is $n = m = 2$) and we let $\gamma \to 0$ in (6) and (7). Then we are left with the map

$$f : \mathbb{R}^4 \to \mathbb{R}^4 \quad (x_1, x_2, y_1, y_2) \to [F_2 x_2,\ P e^{-(x+\beta y)} x_1;\ G_2 y_2,\ Q e^{-y}(1-e^{-\beta x}) y_1] \tag{13}$$

The equilibrium is

$$x_1^* = \frac{F_2}{1+F_2} x^* \qquad x_2^* = \frac{1}{1+F_2} x^* \qquad y_1^* = \frac{G_2}{1+G_2} y^* \qquad y_2* = \frac{1}{1+G_2} y^* \tag{14}$$

$$y^* = \frac{1}{\beta}[\ln(PF_2) - x^*]$$

and x^* must be obtained by means of numerical methods from the equation

$$QG_2(PF_2)^{-1/\beta}\, e^{(1/\beta)x^*}(1-e^{-\beta x^*}) = 1$$

By use of standard linearization techniques, see [1], the eigenvalue equation may, after some algebra, be cast in the form

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0 \tag{15}$$

where

$$\begin{aligned}
a_1 &= \frac{x_1^*}{F_2} + \frac{y_1^*}{G_2} \\
a_2 &= x_1^* + y_1^* - 2 + \frac{x_1^* y_1^*}{F_2 G_2}(1-\beta^2) + \frac{\beta^2 Q x_1^* y_1^*}{F_2}\epsilon^{-y^*} \\
a_3 &= -\frac{x_1^*}{F_2} - \frac{y_1^*}{G_2} + \frac{x_1^* y_1^*}{F_2}(1-\beta^2) + \frac{x_1^* y_1^*}{G_2}(1-\beta^2) + \beta^2 Q x_1^* y_1^* \epsilon^{-y^*}\left(1 + \frac{G_2}{F_2}\right) \\
a_4 &= 1 - (x_1^* + y_1^*) + x_1^* y_1^*(1-\beta^2) + \beta^2 Q G_2 x_1^* y_1^* \epsilon^{-y^*}
\end{aligned}$$

The fixed point (12) is locally stable as long as the spectral radius of (15) is less than unity.

When $\beta = 0$ map (13) becomes

$$(x_1, x_2) \rightarrow (F_2 x_2,\ P\epsilon^{-x} x_1) \tag{16}$$

and it was proved in [11] that the corresponding fixed point $(\overline{x}_1, \overline{x}_2)$ is stable whenever

$$P < \frac{1}{F_2}\epsilon^{2(1+F_2)/F_2} \tag{17}$$

and undergoes a supercritical Hopf bifurcation as (17) is violated. Moreover, at bifurcation, the dominant eigenvalues cross the unit circle close to the imaginary axis, which again implies that the dynamics in unstable and chaotic parameter regions has a strong resemblance of 4-cycles, either exact or approximate.

Next, consider the fixed parameter se $P = 0.6$, $F_2 = 25$. Then the prey will exhibit chaotic oscillations, cf. [11]. Now, introduce the predator parameters $Q = 0.6$, $G_2 = 12$. Starting with $\beta = 0$, our goal is to reveal what kind of qualitative changes the prey (and the predator) will undergo as we increase the number of predators in the model (13) by increasing the coupling parameter β.

When $\beta = 0.10$ the prey (and also the predator) is still in the chaotic regime. This is exemplified in Figure 1. Note that each of the four disjoint subsets of the chaotic attractor

is visited only once every fourth iteration so clearly the attractor has a 4-period structure which is qualitatively similar to the case $\beta = 0.0$, cf. [11].

As we continue to increase the coupling parameter the chaotic attractor disappears and we enter a part of the unstable parameter region where the attractor is a stable exact periodic orbit of period $4 \cdot 2^k$, $k = 0, 1, 2, ...$, where k becomes smaller as β becomes larger. Thus an increase of β leads to the period doubling route to chaos in the opposite direction. In Figures 2a and 2b we show an exact 4-period orbit ($k = 0$) for both the prey and the predator. Through further enlargement of β the dynamics is restricted on an invariant curve but on this curve the original map (13) is topologically equivalent to a circle map with rotation number close to $1/4$, hence the dynamics now is an almost four period orbit.

When $\beta = 0.28$ the dominant complex eigenvalues λ become less than unity so consequently, the fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$ of map (13) becomes stable. At this point in parameter space, $y^* \approx 0.53x^*$. It is a well-known fact from the literature that an increase of the number of predators in a prey–predator model may act as a stabilizing effect, cf. [20], [21], and [22]. Thus, what we have demonstrated in our model is that increased predation may indeed be a strong stabilizing effect, it is capable of bringing a system from chaos to stability.

Now, in order to explain the 4-periodic behaviour of the prey–predator system, assume for a moment that $\beta > 0.28$. Then by decreasing β to the value 0.28 the Jury expression, see [19]

$$S5 = |(1 - a_4^2)^2 - (a_3 - a_4 a_1)| - |(1 - a_4)^2 (a_2 - a_4 a_2) - (a_3 - a_4 a_1)(a_1 - a_4 a_3)| \tag{18}$$

fails to be positive, thus $(x_a^*, x_2^*, y_1^*, y_2^*)$ undergoes a (supercritical) Hopf bifurcation at instability threshold. Consequently, for $\beta < 0.28$, $|\beta - 0.28|$ small, the dynamics is restricted on an invariant curve and (13) is nothing but a circle map on the form

$$\theta \to \theta + c - \frac{bd}{a} u \tag{19}$$

where b and $c = \arg \lambda$ give asymptotic information on rotation numbers, $u =$ bifurcation parameter, $d = (d/du)|\lambda(0)|$, a is the stability coefficient, cf. [23].

At our bifurcation, $\beta = 0.28$, the spectral radius is $\lambda_{1,2} = -0.0216 \pm 0.9998i$, hence $c \approx \pi/2$ which means that the rotation number $\sigma \approx 1/4$ which again implies an almost four period orbit. Then by further decrease of β the exact four period orbit is established due to frequency locking.

As mentioned, if $\beta = 0.0$ the predator will die and with our choice of prey parameters map (16) gives a chaotic attractor with a four periodic structure. Thus another way of implementing our results so far is that although the predator may stabilize the prey, the predator is not capable of altering the periodicity of the prey dynamics in any substantial way, that is as long as $y^* < 1/2x^*$ (roughly!). This suggests that periodic oscillations of low period observed in nature for many species (especially small rodent populations, see [20], [21] and [22]) is not caused by any external force (predators) but that the populations' "own" parameters are the important ones.

—o—

Our next question is concerned with the dynamics when β is further enlarged. In the interval $0.28 < \beta < 1.41$ the fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$ is stable but when β superceedes 1.41 the fixed point undergoes another (supercritical) Hopf bifurcation as the Jury expression

$$S3 = 1 - |a_4| \tag{20}$$

fails to be positive. The values of the quantities $S3$ and $S5$ are shown in Figure 3. The stable parameter region corresponds to the case where both $S3$ and $S5$ are positive. When $S3$ fails to be positive, $y^* \approx 2.25x^*$, the dominant modulus 1 eigenvalues are $\lambda_{3,4} = 0.6753 \pm 0.7356i$ and clearly we have now entered a region in parameter space where an increase of the number of predators acts as a destabilizing effect. Note that the location of $\lambda_{3,4}$ in the right half plane is far away from the axes. This location excludes periodic dynamics of low period, exact or approximate, hence the only outcome in the unstable parameter region $\beta > 1.41$, $|\beta - 1.41|$ small is a quasistationary orbit with a

possible long periodic behaviour. For example, we have verified numerically that there exists a small "β-window" where the dynamics is an exact 14-period orbit.

In case of higher β values the prey–predator system returns through the Curry and Yorke route [24] to chaos. In Figure 4 we show the chaotic attractor in the case $\beta = 2.0$. Note that there is no sign of any periodicity which is in sharp contrast to the situation in Figure 1.

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Although the conclusions above are based upon one parameter set only they illustrate a fairly general principle. Starting with a prey population which exhibits exact or almost periodic oscillations of low period, the inclusion of a predator in the model is capable of stabilizing the prey, but as long as the spectral radius of (15) is located outside the unit circle the predator is not capable of altering the period of the oscillations in any substantial way. This is strongly related to the fact that the dominant eigenvalues enter the unit circle close to the imaginary axis.

In Table 1 we show where the spectral radius enters the unit circle (column 4) for several different choices of G_2.

Table 1 (last column) also show the location of the dominant eigenvalues at the second instability threshold β_2. These computations suggest that in case of $\beta > \beta_2$ the dynamical behaviour must be qualitatively similar to the case already discussed. This result has also been verified through several numerical simulations.

—o—

Finally, let us close this section with a few results obtained by considering F_2 values that satisfy Equality (17), which means that the prey in absence of the predator possesses a stable fixed point. As expected, with this choice of F_2 predation acts as a destabilizing effect only and by increasing the coupling parameter β the fixed point eventually becomes unstable through a (supercritical) Hopf bifurcation as the Jury condition (20) fails to be positive. The locations of the dominant eigenvalues at bifurcation are similar to what

Table 1: Parameter values and location of dominant eigenvalues at the two bifuraction thresholds. Starting with chaotic prey oscillations $\beta = 0$, $F_2 = 25$, $P = 0.6$. β_1 is the β value where $(x_1^*, x_2^*, y_1^*, y_2^*)$ becomes stable. $\lambda_{1,2}$ the corresponding dominant eigenvalues. β_2 is the β value at the second instability threshold where the eigenvalues leave the unit circle. $\lambda_{3,4}$ is the corresponding spectral radius.

F_2	G_2	$P = Q$	β_1	$\lambda_{1,2}$	β_2	$\lambda_{3,4}$
25	2	0.6	3.42	$-0.036 \pm 0.9999i$	18.36	$0.9522 \pm 0.3079i$
25	6	0.6	0.51	$-0.019 \pm 0.9998i$	2.27	$0.7786 \pm 0.6172i$
25	12	0.6	0.28	$-0.0216 \pm 0.9998i$	1.41	$0.6752 \pm 0.7256i$
25	18	0.6	0.21	$-0.0294 \pm 0.9999i$	1.17	$0.6235 \pm 0.7775i$
25	25	0.6	0.77	$-0.5128 \pm 0.8609i$	1.05	$0.5851 \pm 0.8108i$

has been found in the previous case ($F_2 = 25$). A numerical example: $F_2 = 12$, $G_2 = 6$, $P = Q = 0.6$, $\beta = \beta_2 = 2.13 \Rightarrow \lambda_{3,4} = 0.8340 \pm 0.5559i$. Consequently, there is no major change of qualitative behaviour in the case $\beta > \beta_2$.

3 Discussion

Up to this point we have studied the model (13) which is a special case of the four-dimensional map (see (6) and (7))

$$\begin{aligned}(x_1, x_2, y_1, y_2) \to \big(&F_2 x_2,\ P(1-\gamma x)^{1/\gamma}(1-\gamma\beta y)^{1/\gamma} x_1,\ G_2 y_2, \\ &Q(1-\gamma y)^{1/\gamma}[1-(1-\gamma\beta x)^{1/\gamma}] y_1\big)\end{aligned} \tag{21}$$

and when $\beta \to 0$, map (21) degenerates (see (8)) to the one-population model

$$(x_1, x_2) \to (F_2 x_2,\ P(1-\gamma x)^{1/\gamma} x_1) \tag{22}$$

So far, we have covered the case $\gamma \to 0$. In [18] it was proved that whenever

$$\gamma > \gamma_c = -\frac{F_2}{2(1+F_2)} \tag{23}$$

then, in case of sufficiently large F_2 values, the fixed point of (22) will undergo a supercritical Hopf bifurcation at instability threshold and moreover that the nonstationary dynamics has a strong resemblance of 4-cycles.

Our first goal in this section is to reveal the dynamical properties of (21) when we restrict γ to the interval $\gamma_c < \gamma < 0$. The conclusion (mainly based upon simulation results and Jury condition calculations (cf. (18) and (20))) is that the qualitative picture found in the case $\gamma \to 0$ also takes over to the interval $\gamma_c < \gamma < 0$. Thus, starting with P and F_2 values which in the absence of predators imply prey oscillations with period $\simeq 4$, an increase of β eventually results in a stable fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$ but as long as the spectral radius of the linearized map is outside the unit circle the period of the oscillations is not altered in any substantial way. Large values of β also imply nonstationary dynamics, but also in this part of parameter space the dynamics is similar to the case $\gamma \to 0$.

—o—

Our next goal is to study the dynamics when $\gamma < \gamma_c$. To this end, suppose $\gamma = -1$. Then we are left with the map

$$(x_1, x_2, y_1, y_2) \to \left(F_2 x_2, \frac{P}{(1+x)(1+\beta y)} x_1, G_2 y_2, \frac{Q}{1+y}\left(1 - \frac{1}{1+\beta x}\right) y_1\right) \tag{24}$$

which possesses the unique nontrivial equilibrium:

$$x_1^* = \frac{F_2}{1+F_2} x^* \qquad x_2^* = \frac{1}{1+F_2} x^* \qquad y_1^* = \frac{G_2}{1+G_2} y^* \qquad y_2^* = \frac{1}{1+G_2} y^* \tag{25}$$

$$y^* = \frac{1}{\beta}\left(\frac{PF_2}{1+x^*} - 1\right) \qquad x^* = \frac{-b - \sqrt{b^2 - 4ac}}{2a}$$

where $a = \beta^2 - \beta - \beta^2 Q G_2$, $b = \beta^2 - 1 + \beta P F_2 - \beta^2 Q G_2$, and $c = \beta + PF_2 - 1$. Note that when $\beta \to 0$ the corresponding one-population model becomes

$$(x_1, x_2) \to \left(F_2 x_2, \frac{P}{1+x} x_1\right) \tag{26}$$

and it was proved in [18] that the fixed point $(\overline{x}_1, \overline{x}_2)$ of (26) is always locally stable. This implies that in case of small values of β, the fixed point (25) is also locally stable, hence the pronounced 4-periodic dynamics is absent. The question now is if it is possible to obtain any periodic dynamics by increasing β to a level where (25) becomes unstable. The eigenvalue equation of the linearized map becomes

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_2\lambda + a_4 = 0 \tag{27}$$

where

$$
\begin{aligned}
a_1 &= \frac{x_1^*}{F_2(1+x^*)} + \frac{y_1^*}{G_2(1+y^*)} \\
a_2 &= \frac{x_1^* y_1^*}{F_2G_2(1+x^*)(1+y^*)} + \frac{\beta x_1^* y_1^*}{F_2G_2x^*(1+\beta x^*)(1+\beta y^*)} + \frac{x_1^*}{1+x^*} + \frac{y_1^*}{1+y^*} - 2 \\
a_3 &= \frac{\beta x_1^* y_1^*}{F_2x^*(1+\beta x^*)(1+\beta y^*)} + \frac{\beta x_1^* y_1^*}{G_2x^*(1+\beta x^*)(1+\beta y^*)} \\
&\quad + \frac{x_1^* y_1^*}{F_2(1+x^*)(1+y^*)} + \frac{x_1^* y_1^*}{G_2(1+x^*)(1+y^*)} - \frac{x_1^*}{F_2(1+x^*)} - \frac{y_1^*}{G_2(1+y^*)} \\
a_4 &= 1 - \frac{x_1^*}{1+x^*} - \frac{y_1^*}{1+y^*} + \frac{x_1^* y_1^*}{(1+x^*)(1+y^*)} + \frac{\beta x_1^* y_1^*}{x^*(1+\beta x^*)(1+\beta y^*)}
\end{aligned}
$$

and by applying the Jury conditions on (27) we have verified numerically that the spectral radius of (27) is located within the unit circle for all combinations of the parameters, hence provided the relations (9) are satisfied the only dynamics of map (24) is stable fixed point.

Finally, to close the discussion, let us consider a mixed choice of overcompensatory and compensatory survival probabilities, i.e. let us examine the model

$$(x_1, x_2, y_1, y_2) \to \left(F_2G_2,\ Pe^{-(x+\beta y)}x_1,\ G_2y_2,\ \frac{Q}{1+y}\left(1 - \frac{1}{1+\beta x}\right)y_1\right) \tag{28}$$

which possesses a unique nontrivial equilibrium where the values of the total prey and predator populations are

$$x^* = \frac{u + \sqrt{u^2 + 4\beta v}}{2\beta}$$

where

$$
\begin{aligned}
u &= \beta \ln(PF_2) + \beta^2(1 - QG_2) - 1 \\
v &= \ln(PF_2) + \beta
\end{aligned}
\tag{29}
$$

and

$$y^* = \frac{1}{\beta}[\ln(PF_2) - x^*]$$

The analysis of map (28) follows the same pattern as of map (13): we use fixed parameter values F_2 and P which ensures that the prey in absence of the predator is in the chaotic regime and exhibits almost periodic oscillations with period close to four. Then we look for qualitative changes of the prey population by increasing the coupling parameter

β. Stability properties of the fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$ of (28) revealed by use of the Jury criteria on the eigenvalue equation

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_2\lambda + a_4 = 0 \tag{30}$$

where the coefficients are

$$\begin{aligned} a_1 &= \frac{x_1^*}{F_2} + \frac{y_1^*}{G_2(1+y^*)} \\ a_2 &= \frac{x_1^* y_1^*}{F_2 G_2 (1+y^*)} + \frac{y_1^*}{1+y^*} + \frac{\beta x_1^* y_1^*}{F_2 G_2 x^* (1+\beta x^*)} + x_1^* - 2 \\ a_3 &= \frac{y_1^*}{(1+y^*)} \left(\frac{x_1^*}{G_2} + \frac{x_1^*}{F_2} - \frac{1}{G_2} \right) + \frac{\beta x_1^* y_1^*}{x^*(1+\beta x^*)} \left(\frac{1}{G_2} + \frac{1}{F_2} \right) - \frac{x_1^*}{F_2} \\ a_4 &= 1 - x_1^* + \frac{y_1^*}{1+y^*}(x_1^* - 1) + \frac{\beta x_1^* y_1^*}{x^*(1+\beta x^*)} \end{aligned}$$

The results of the analysis are very similar to what was found from map (13). Starting with $\beta = 0$, an increase of the coupling parameter acts as a stabilizing effect but as long as the population(s) is in the unstable parameter region, the initial four-periodic behaviour is not altered in any substantial way. Stability is achieved at a certain threshold β, and there is clear numerical evidence that (the number of predators/the number of prey) is larger here than in the case where overcompensatory survival probabilities were used for both the prey as the predator.

As we continue to increase β we soon enter a part of parameter space where the increase acts as a destabilizing effect and at the threshold β_2 a secondary Hopf bifurcation occurs. (The interval (β_1, β_2) is smaller than the corresponding interval of map (13).) Beyond β_2 there is no evidence of periodic dynamics of low period, a conclusion which is based upon the location of the dominant eigenvalues at bifurcation threshold. If we use the parameters $P = Q = 0.6$, $F_2 = 25$, $G_2 = 12$, we find that $\beta_1 = 0.26$ with corresponding modulus 1 eigenvalues $\lambda_{1,2} = -0.03058 \pm 0.99934i$ and $\beta_2 = 0.88$ with corresponding modulus 1 eigenvalues $\lambda_{1,2} = 0.77621 \pm 0.63334i$.

—o—

The purpose of this paper has been to reveal possible qualitative dynamical changes of a discrete age-structured prey population as it is exposed to predation from an age-structured predator population. By use of compensatory survival probabilities for both species the only stable attractor found is the fixed point $(x_1^*, x_2^*, y_1^*, y_2^*)$, thus in this case the predator is not capable of altering the prey dynamics.

On the other hand, if we use overcompensatory survival probabilities for both species, or overcompensatory survival for the prey and compensatory survival for the predator, we have found that in case of small values of β, an increase of the coupling parameter acts as a stabilizing effect, and in case of large values of β, a further increase acts as a destabilizing effect. Thus as shown in these cases the dynamics may vary from a stable fixed point to chaotic behaviour. Moreover, we have found that the only β interval where it is possible to obtain periodic dynamics of low period (either exact or approximate) is when $0 < \beta < \beta_1$, and further that the predator is not capable of altering this periodicity. These findings have important biological consequences. There are several examples in nature of species that exhibit almost exact low periodic oscillations. Especially small rodent populations in Fenno-Scandinavia have this property, see [25]. The most famous example is the Norwegian lemming cycle. It has been proposed that predators are responsible for such low period cycles. The results in this paper suggest that such a hypothesis must be false.

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Figure Captions

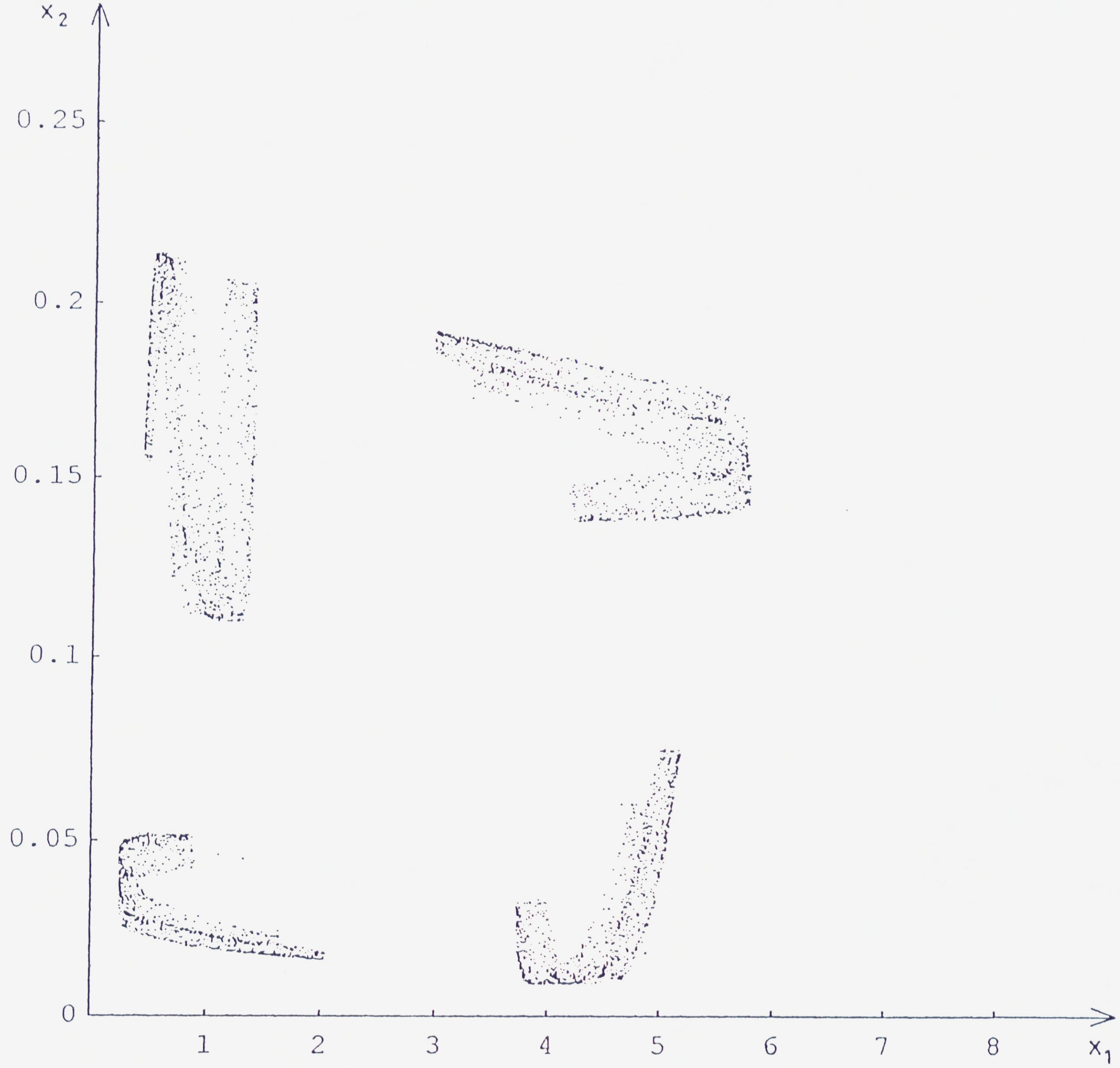
Figure 1a: The prey in the chaotic regime. Each of the four disjoint subsets of the attractor is visited once in each cycle. Parameter values: $F_2 = 25$, $P = Q = 0.6$. $G_2 = 12$. $\beta = 0.10$.

Figure 1b: The predator in the chaotic regime. Same parameter values as in Figure 1a.

Figure 2: An exact four period orbit. (a) prey, (b) predator.. The dynamics goes clockwise. Parameter values as in Figure 1 except $\beta = 0.22$.

Figure 3: The Jury quantities $S3$ (A) and $S5$ (B) (cf. the main text) as function of β. The fixed point is stable as long as both $S3$ and $S5$ are positive.

Figure 4: (a) The prey, and (b) the predator have reentered the chaotic regime. Parameter values as in Figure 1 except $\beta = 2.0$.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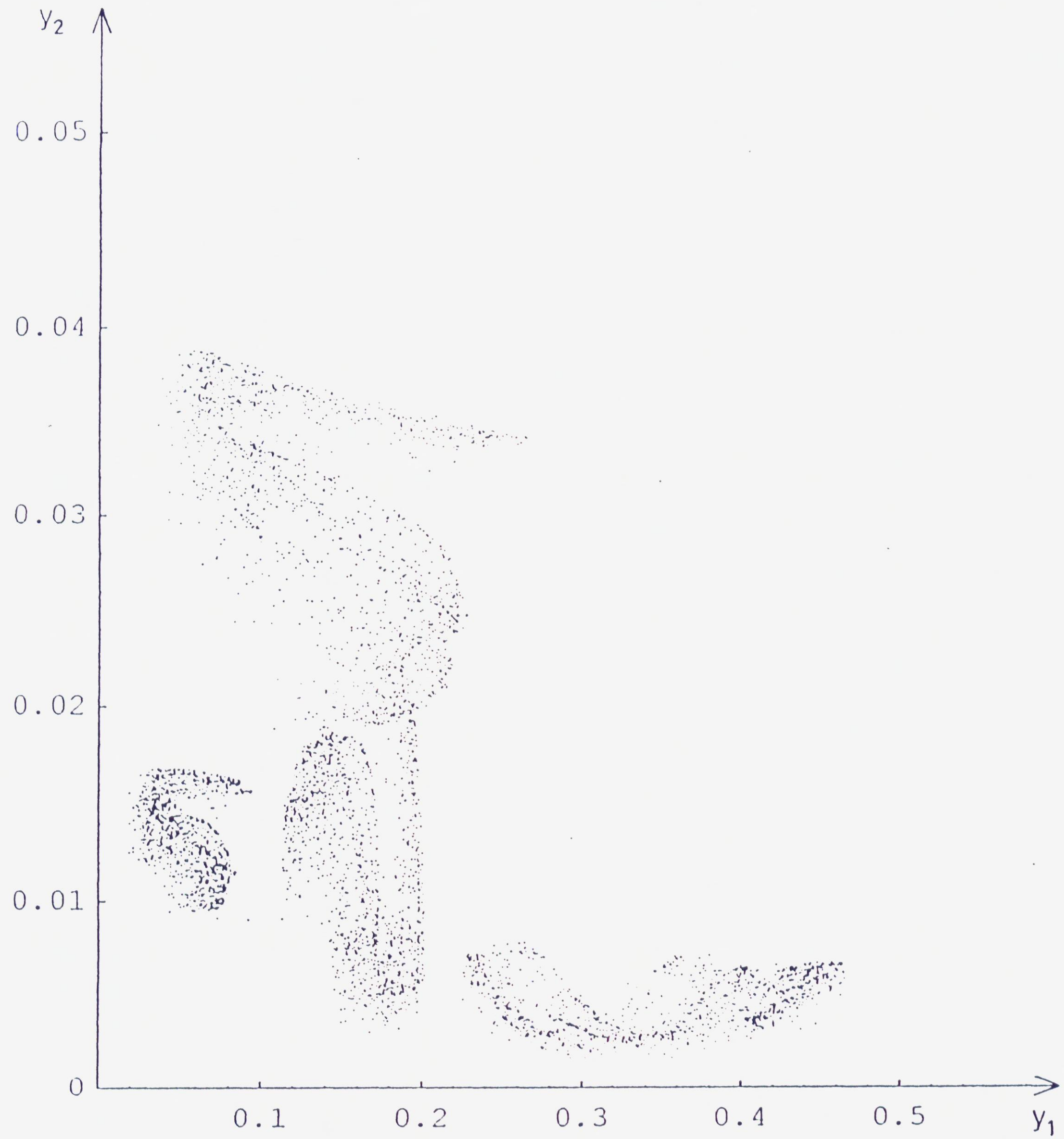
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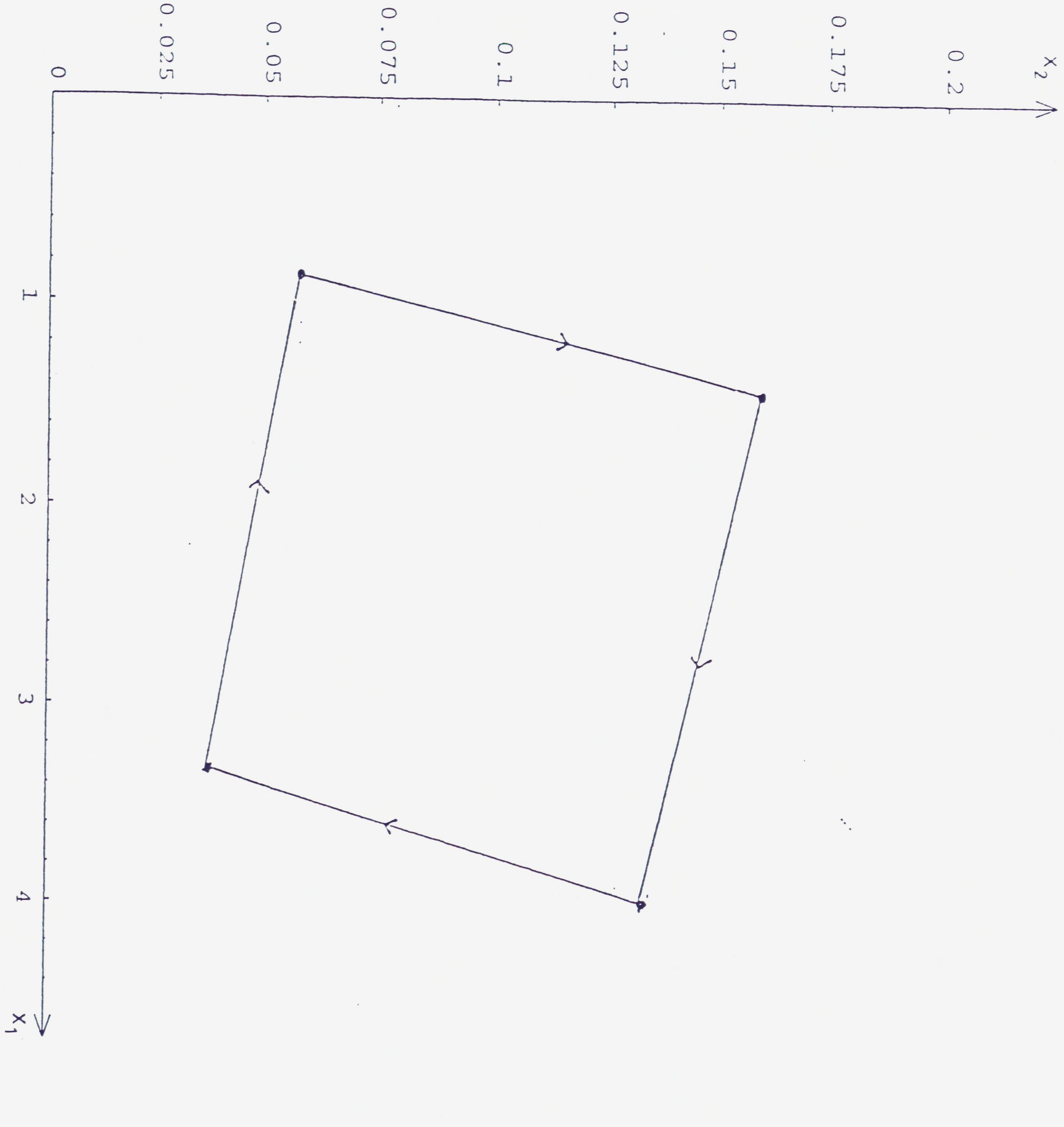
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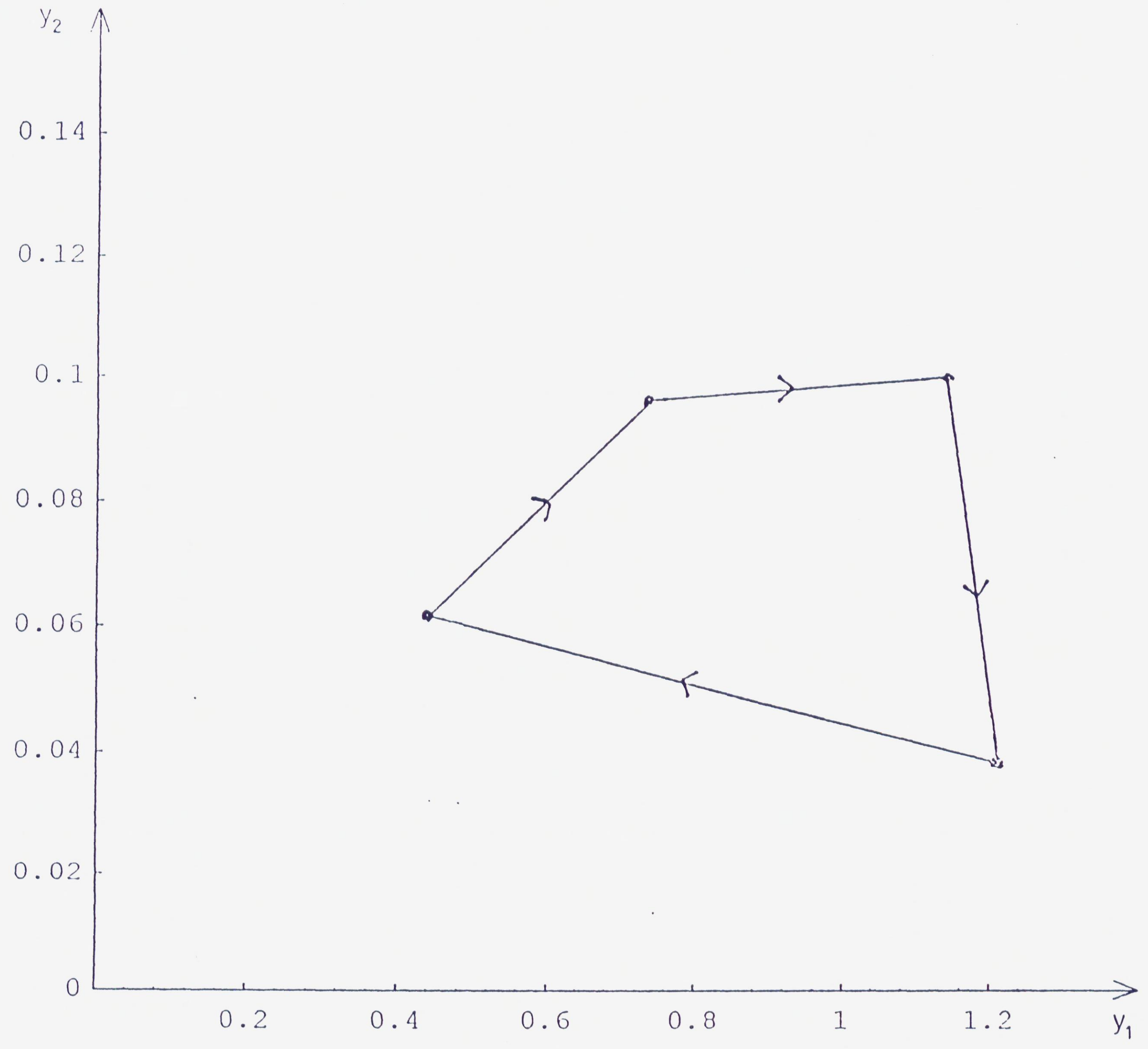
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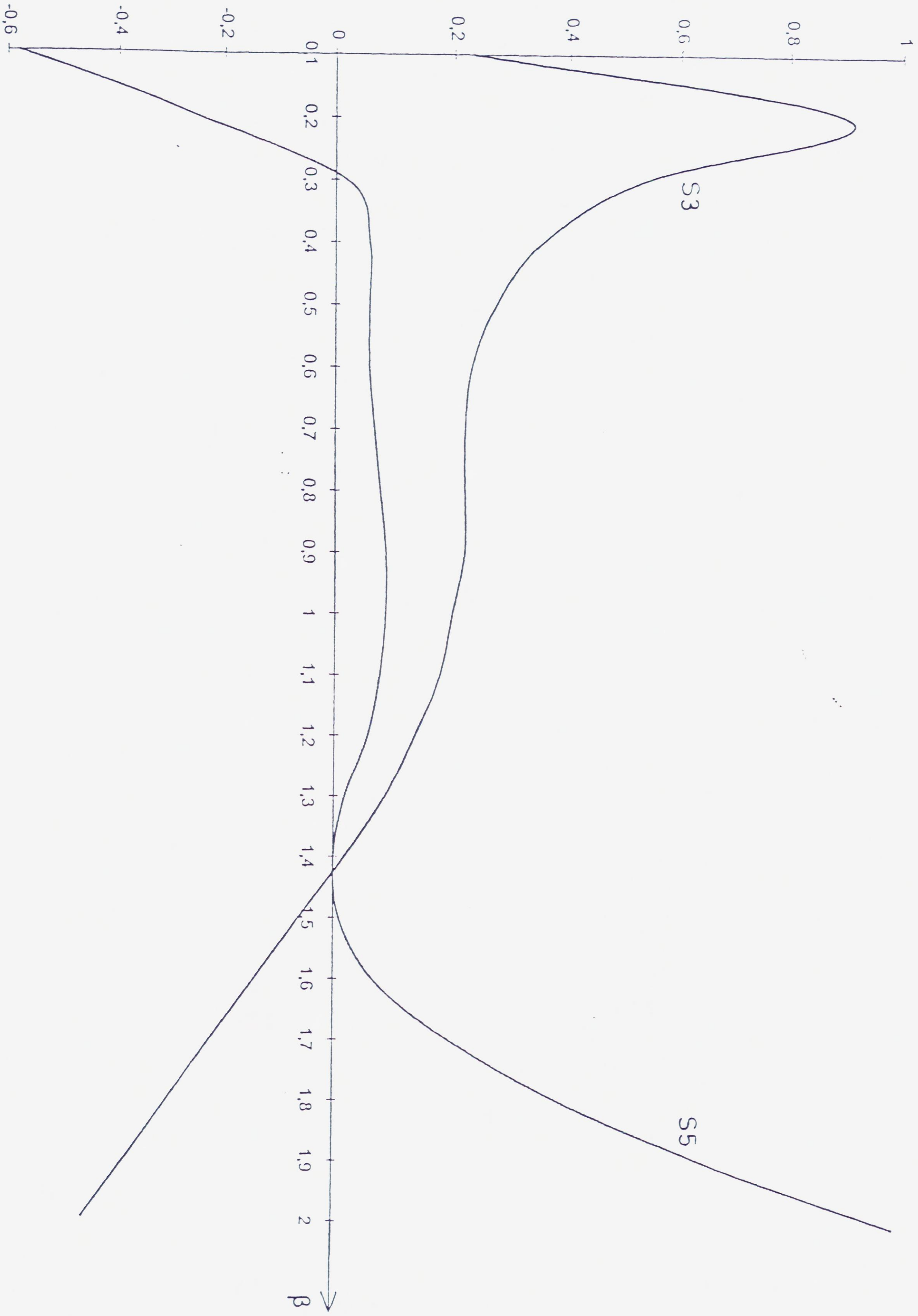
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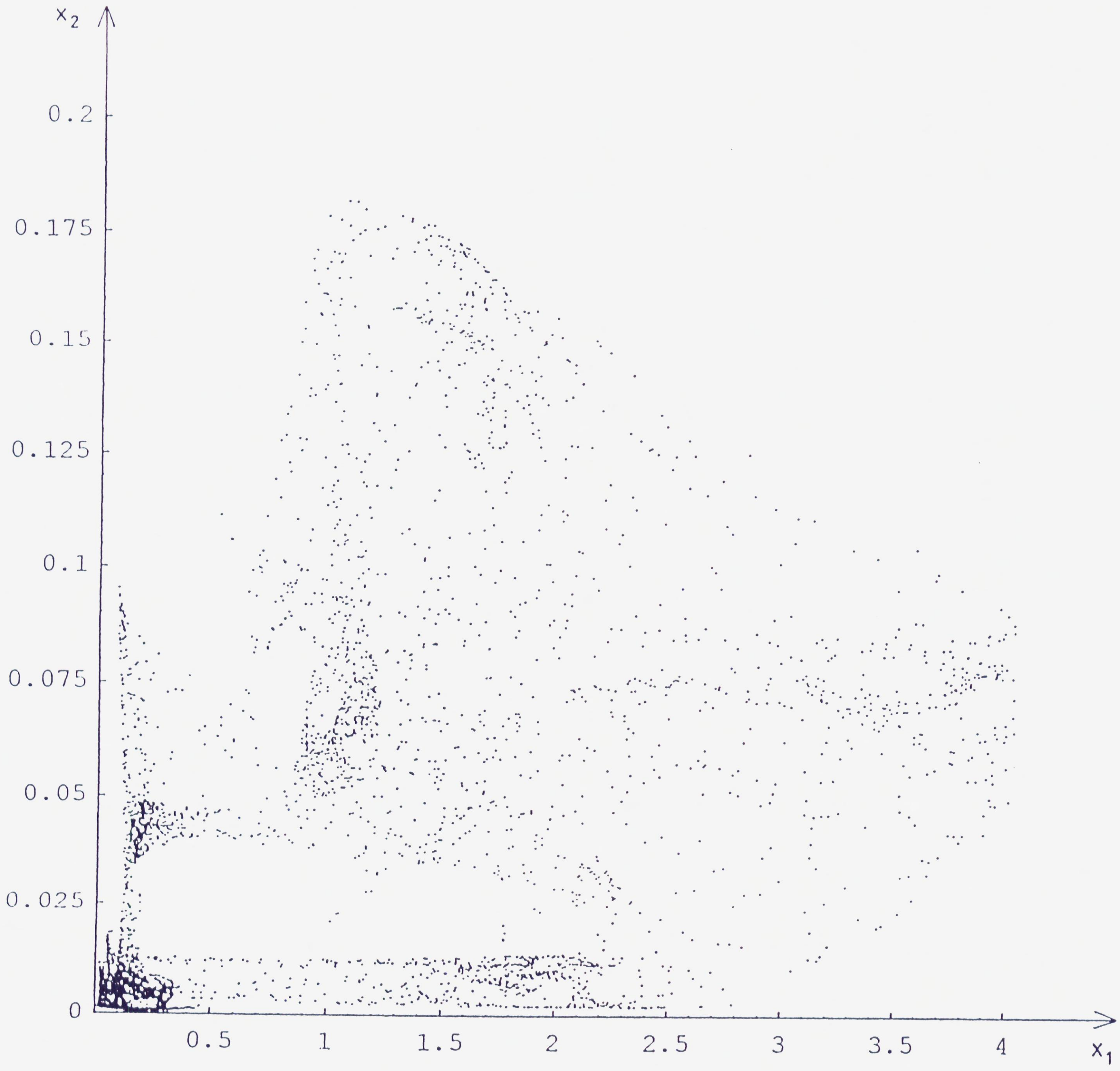
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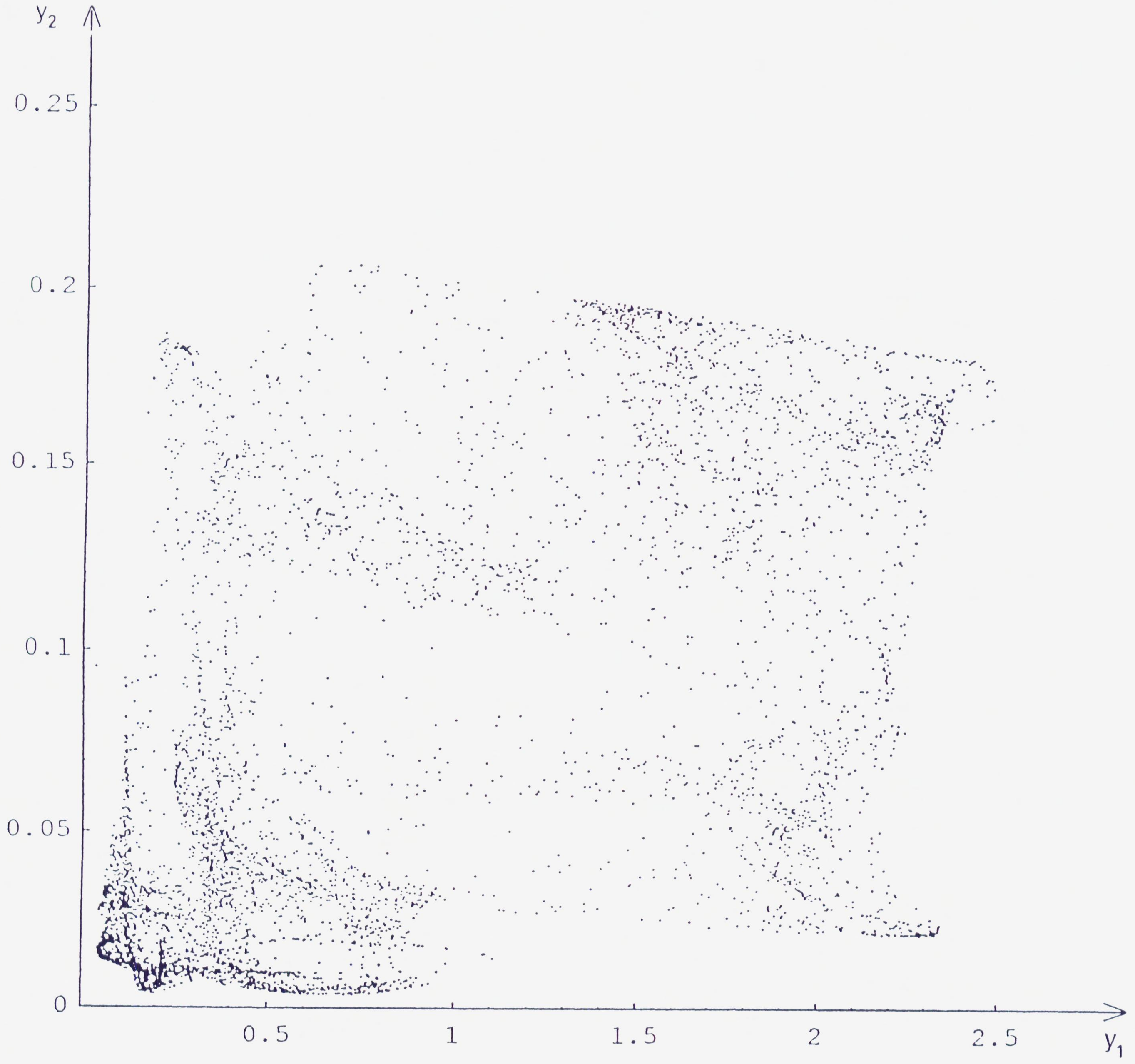
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